

Illustrated Handbook of Succulent Plants

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Urs Eggli · Reto Nyffeler *Editors*

# Monocotyledons

*Second Edition*

 Springer

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# Illustrated Handbook of Succulent Plants

## **Series Editors**

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During evolution, many plant species have adapted to life in seasonally dry and arid environments by developing the ability to store water in their stems, leaves, and/or underground organs – this phenomenon is called “succulence.” Succulent plants can be found in more than 70 plant families. The *Illustrated Handbook of Succulent Plants* (excluding cacti and orchids) was first published in six volumes in 2001–2003. A second revised edition, of which the first volume (treating the family Aizoaceae) was published in 2017, provides a taxonomical treatment of all estimated 11,000 taxa of succulents (excluding orchids). In addition to the volumes on Monocotyledons and Dicotyledons, separate volumes are devoted to those families with an especially great diversity of succulent species, namely, Aizoaceae, Apocynaceae, Cactaceae, and Crassulaceae.

Each volume is organized by alphabet of families, genera, and species, with comprehensive synonymies added at all levels. Detailed descriptions are given for all accepted taxa, together with data on the distribution and typification, and references to the most important literature. Where necessary, information on ecology, ethnobotany, history, etc. is added, and in many places, proposed relationships are critically discussed. Over 2000 superb colour photographs complete this inventory of succulent plants.

More information about this series at <http://www.springer.com/series/4452>

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Editors

# Monocotyledons

Second Edition

With 339 Figures and 12 Tables

 Springer

*Editors*

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## Preface to the Second Edition

Succulents are an attractive group of plants that have for centuries attracted the interest of botanists and gardeners alike, both professionals and hobbyists. During this time, a vast body of specialized books and especially journal papers has accumulated that contains our knowledge of these fascinating plants.

Over time, there were several efforts to collate the existing knowledge and information into lexica devoted to succulent plants and thus allow an ordered presentation of the diversity of succulents. The publication of the first edition of the present series of *Illustrated Handbook of Succulent Plants* in the years 2001–2003 in six volumes marked a milestone in this field, even though coverage remained incomplete since the families *Bromeliaceae* and *Cactaceae* were not included.

The past more than 15 years have seen a continued, and in many fields, revived interest in all aspects of succulent plant biology, and the handbook series soon became a widely accepted taxonomic reference for ordering the biodiversity of succulents. Fifteen years is a long stretch of time for any lexicon, and much new data have been generated by recent research in all fields of botany. During this time, especially molecular studies have led to an improved understanding of the living diversity of plants, and a firm phylogenetic backbone is now in place for most major groups. The past more than 20 years have also seen an important change in the way taxonomical studies are conducted, that is, an increasingly common replacement (or at least support) of intuition-based interpretations with data-derived conclusions. We are now well aware that many of the characters traditionally used to define taxonomical units are homoplasious (i.e., have evolved repeatedly in parallel) and thus are of limited or no value to understand evolutionary pathways.

Such increase in knowledge has led to important changes in the circumscription or affiliation of many groups. Such changes often meet with considerable antipathy from many user groups, but when they are based on firm data derived from adequate sampling depth, they will become the accepted standards in the future. For this handbook series, a phylogenetic approach, based on the most recent available standard phylogenetic framework, has been selected. In cases where the available data is inconclusive, or contradictory, established classifications are usually followed, with the necessary cautious comments (see, e.g., the genus *Aloe*).

For this second edition, the existing entries from the first edition have been thoroughly checked and updated, including revised classifications and new taxa. Especially the discussions of classifications have been expanded considerably within a phylogenetic context but also new data, for example, on ecology or ethnobotany, have been added. For most groups, the original authors have been able to provide these updated treatments, and we are most grateful to our colleagues for their continued support of the project. For some groups, new contributors had to be sought, and we are delighted about the willingness of the respective authors to accept this task. In contrast to the first edition of this volume, the succulent taxa of the pineapple family (*Bromeliaceae*) are now also included, thanks to the energetic help of a group of specialists of that family. With this addition, this volume now covers the monocotyledonous succulents in full with the notable exception of the orchids – the sheer number of possible succulent species makes their inclusion unfeasible.

The overall layout of the volume has changed considerably in comparison with the original edition, while the sequence of information presented for each taxon has largely remained the same. We hope that the new layout, which places the illustrations near the text to which they belong, will prove helpful for the users.

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December 2019

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## From the Preface to the First Edition

Handbooks devoted to succulent plants (including cacti) have a long-standing tradition, and the demand for updated editions is a good indication of the high degree of interest that exists in this fascinating group of plants.

While the first handbooks devoted to the family *Cactaceae* were already published in the nineteenth century, the first handbook dealing with the so-called other succulents was authored by Hermann Jacobsen and published in 1954–1955, then called *Handbuch der sukkulenten Pflanzen*. A revised and enlarged English edition was made available in 1959 and was repeatedly reprinted in the following years.

A major step towards a compact handbook including short descriptions, full synonymy, and hundreds of illustrations was the publication of the first edition of Hermann Jacobsen's celebrated *Sukkulentenlexikon* in 1970, followed by the English edition in 1975, and a revised German edition in 1981, finished by Klaus Hesselbarth following Hermann Jacobsen's death in August 1978.

The demand for updated compact information on succulent plants has not diminished since then, and contrary to Hermann Jacobsen's opinion (preface to the German edition 1970) that the number of papers dealing with succulent plants was on the decline, the interest in succulent plants was growing, both among hobbyists and among botanists. The results are numerous new taxa in many families, and many monographs of previously little-known groups have been published over the years. Accordingly, a need for a "New Lexicon" was beginning to be felt, both for "other" succulents and for cacti.

After some informal initial discussions held among various botanists and interested specialist collectors, and faced with the desire of Gustav Fischer Verlag Jena, the publisher of both Backeberg's *Kakteenlexikon* and Jacobsen's *Sukkulentenlexikon*, to prepare revised editions, a meeting was called for during the 1990 congress of the International Organization for Succulent Plant Study (IOS) in Zürich. There was a general feeling that the situation presented a unique occasion to produce a set of authoritative volumes embracing *all* succulent plants (except orchids), and produced according to a rigid set of common standards adopted to suit all families involved. It was planned that the project, informally termed the "New IOS Succulent Plant Lexicon," should consist of three volumes, one devoted to the *Cactaceae*, one to the *Aizoaceae*, and one to the remaining succulent taxa from various families.

For various reasons, the Lexicon project took much longer to be completed than anticipated. The *Cactaceae* part had not become available in time for



inclusion in the first handbook edition. In the case of the *Aizoaceae*, time permitted a much more complete treatment of the family, which was published in two volumes. Moreover, it soon became apparent that a single volume will not be sufficient to cover the vast array of the “remaining succulents.” Accordingly, they were split into four volumes (Monocotyledons, Dicotyledons, *Asclepiadaceae* (= *Apocynaceae* in the revised edition), and *Crassulaceae*).

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# General Introduction to the Series

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## Setup of the Handbook Series

The present series of handbooks is devoted to a lexicographic treatment of the known diversity of succulent plants (excluding pteridophytes and orchids, see below). The APG III classification (APG 2016) is used as the phylogenetic framework at the rank of order and supraordinal taxa, while the slightly modified APG III classification (APG 2009) as defined by Nyffeler and Egli (2010a) is used at the rank of family.

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## What Is a Succulent?

It is a continuing challenge to define what constitutes a *succulent plant* – at least in view of the several competing definitions (see Egli and Nyffeler 2009 for a review and a modern definition). For the purpose of this handbook, a pragmatic approach has been selected. Apart from the multitude of unambiguous succulents, borderline cases are included as well, especially when they occur sympatrically with undisputed succulents in more or less semiarid regions, and consequently show some degree of xerophytic adaptation, and more so when the species in question are encountered in cultivation together with other succulents. This, then, includes many of the so-called caudex and pachycaul plants popular in cultivation in public and private collections alike.

Other borderline cases included are a number of bulbous and rhizomatous groups, where examples from several genera are covered, as well as some weakly developed leaf succulents from, for example, the *Commelinaceae* and *Gesneriaceae* (e.g., *Columnnea*), and several other families.

Purely halophytic succulents (such as *Salicornia*) are omitted from this series of handbooks since they are as a whole neither adapted to climatically arid or semiarid conditions (see Ogburn and Edwards 2010 for an explanation) nor encountered in collections devoted to succulent plants.

Finally, the family *Orchidaceae* is excluded (apart from a short general overview), despite the uncontested claim to succulence of many taxa. A preliminary count (Nyffeler and Egli 2010a) showed some 2200 succulent species for this family, and a more detailed census (see the family treatment in this volume) arrives at a minimum count of 4500 succulent species – this

makes the *Orchidaceae* the most important family containing succulents in term of species number.

Fortunately, vast specialist literature covering orchids exists, numerous specialist societies are in existence, and the available lexicographic efforts (e.g., Pridgeon & al. 1999, 2001, 2003, 2005, 2009, 2014) do not need to be duplicated here. Also omitted from the series are the pteridophytes, as insufficient knowledge on the – possibly few – marginally succulent taxa is available.

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## Succulence Among Flowering Plants

Succulence, without any doubt, has evolved repeatedly and independently in many clades of the angiosperms. Succulence thus illustrates in an exemplary manner how adaptations to a given set of ecological conditions appear time and again throughout the evolution of the Plant Kingdom (and likely has disappeared again in numerous cases, but as no macrofossils of succulents are known, this will be difficult to prove). Figure 1 illustrates the occurrence of succulence throughout the clades of the angiosperms. Succulent plants are known to occur in 31 out of a total of 64 orders accepted. While some orders only count with a small number of succulent representatives, succulence is a more prevailing character in others. A notable concentration of succulents is to be found in the order Caryophyllales, and its suborder Portulacineae embraces almost exclusively succulent taxa (Nyffeler and Egli 2010b).

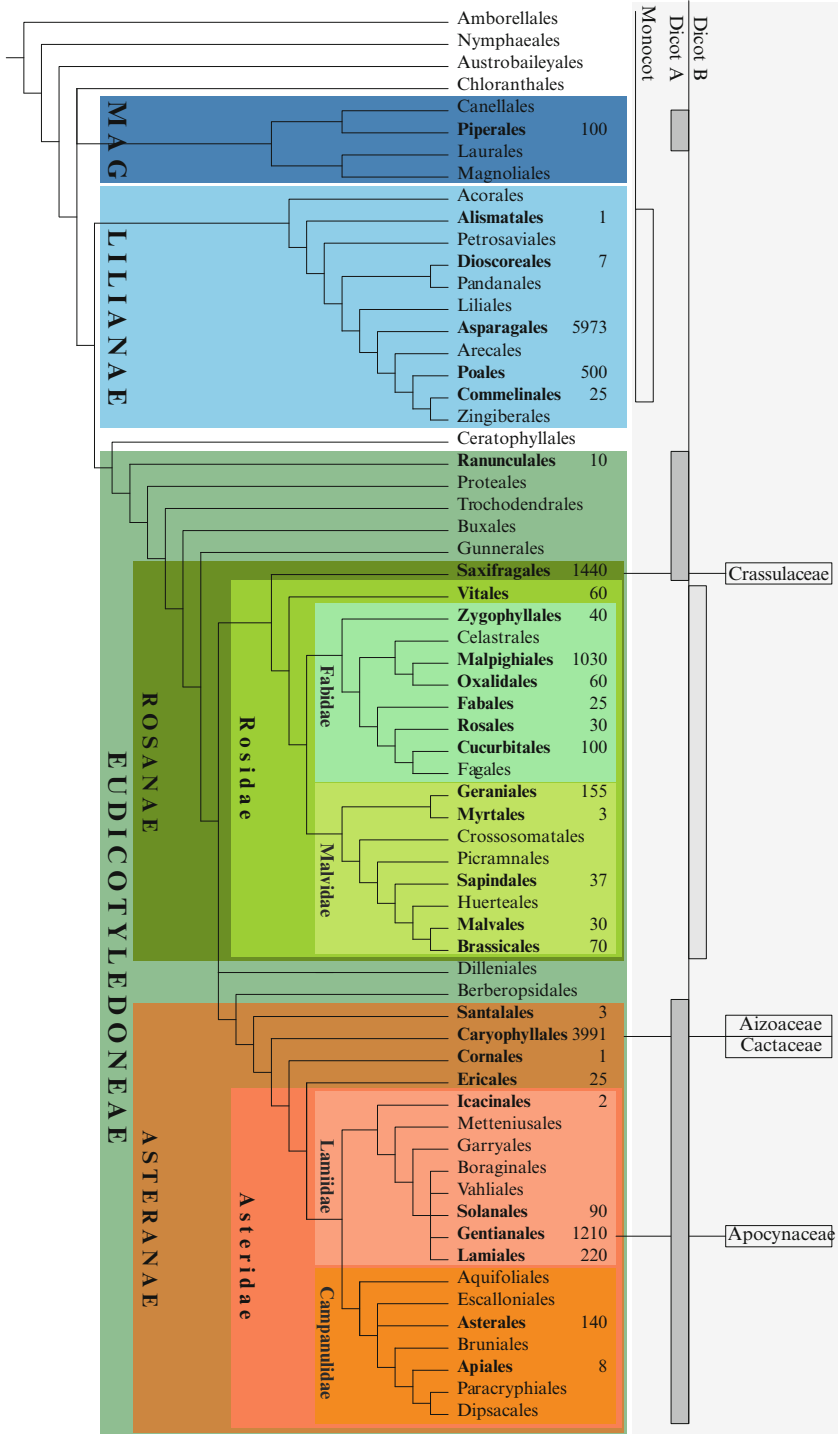
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## Division of the Handbook into Individual Volumes

The handbook is divided into individual volumes that either cover an entire individual family or a coherent group of families. The planned breakdown into volumes is as follows (see also Fig. 1):

- Monocots: Egli, U. & Nyffeler, R. (eds.): Illustrated Handbook of Succulent Plants. Monocotyledons. **This volume.**
- Dicots A: Egli, U. (ed.): Illustrated Handbook of Succulent Plants. Magnoliids and Dicotyledons (excluding Rosids).
- Dicots B: Egli, U. (ed.): Illustrated Handbook of Succulent Plants: Dicotyledons: Rosids.
- *Aizoaceae*: Hartmann, H. E. K. (ed.): Illustrated Handbook of Succulent Plants: *Aizoaceae*. Volumes 1 and 2. **Published 2017.**
- *Apocynaceae*: Meve, U. & Egli, U. (eds.) Illustrated Handbook of Succulent Plants: *Apocynaceae*.
- *Cactaceae*: NN. (ed.): Illustrated Handbook of Succulent Plants: Cactaceae.
- *Crassulaceae*: U. Egli (ed.): Illustrated Handbook of Succulent Plants: *Crassulaceae*.

For ease of reference, an alphabetical list of families, together with the orders to which they belong and the volume of the series which covers them, is also supplied (Table 1).



**Fig. 1** Summary phylogeny of the angiosperms, based on APG IV (2016), Moore & al. (2010), and Soltis & al. (2011). The estimated number of succulent species (modified from Nyffeler and Eggli 2010) is indicated to the right of the order names. Supraordinal names follow Soltis & al. (2011) and Chase and Reveal (2009); their

Lilianae conform to the Monocotyledoneae of Soltis & al., their Rosanae to the Superrosidae, and their Asteranae to the Superasteridae). **MAG** = Magnolianae. The division of the handbook series into individual volumes is shown on the right of the cladogram. (Diagram by Urs Eggli) rats

**Table 1** Alphabetical list of families with their assignments to orders and their assignments to the individual volumes of this handbook series.

Family	Order	Monocot (this volume)	Dicot A	Dicot B (Rosids)	Separate volume
Agavaceae	Asparagales	×			
Aizoaceae	Caryophyllales				×
Amaranthaceae	Caryophyllales		×		
Amaryllidaceae	Asparagales	×			
Anacampserotaceae	Caryophyllales		×		
Anacardiaceae	Sapindales			×	
Anthericaceae	Asparagales	×			
Apiaceae	Apiales		×		
Apocynaceae	Gentianales				×
Araceae	Alismatales	×			
Araliaceae	Apiales		×		
Asparagaceae	Asparagales	×			
Asphodelaceae	Asparagales	×			
Asteraceae	Asterales		×		
Balsaminaceae	Ericales		×		
Basellaceae	Caryophyllales		×		
Begoniaceae	Cucurbitales			×	
Bixaceae	Malvales			×	
Brassicaceae	Brassicales			×	
Bromeliaceae	Poales	×			
Burseraceae	Sapindales			×	
Cactaceae	Caryophyllales				×
Campanulaceae	Asterales		×		
Capparaceae	Brassicales			×	
Caricaceae	Brassicales			×	
Caryophyllaceae	Caryophyllales		×		
Clusiaceae	Malpighiales			×	
Commelinaceae	Commelinales	×			
Convolvulaceae	Solanales		×		
Crassulaceae	Saxifragales				×
Cucurbitaceae	Cucurbitales			×	
Cyperaceae	Poales	×			
Didiereaceae	Caryophyllales		×		
Dioscoreaceae	Dioscoreales	×			
Doryanthaceae	Asparagales	×			
Ericaceae	Ericales		×		
Eriospermaceae	Asparagales	×			
Euphorbiaceae	Malpighiales			×	
Fabaceae	Fabales			×	
Fouquieriaceae	Ericales		×		
Francoaceae	Geraniales			×	
Geraniaceae	Geraniales			×	
Gesneriaceae	Lamiales		×		
Halophytaceae	Caryophyllales		×		
Hyacinthaceae	Asparagales	×			
Icacinaeae	Icacinales		×		

*(continued)*

**Table 1** (continued)

Family	Order	Monocot (this volume)	Dicot A	Dicot B (Rosids)	Separate volume
Lamiaceae	Lamiales		×		
Lentibulariaceae	Lamiales		×		
Limeaceae	Caryophyllales		×		
Loasaceae	Cornales		×		
Loranthaceae	Santalales		×		
Malvaceae	Malvales			×	
Melastomataceae	Myrtales			×	
Meliaceae	Sapindales			×	
Menispermaceae	Ranunculales		×		
Montiaceae	Caryophyllales		×		
Moraceae	Rosales			×	
Nyctaginaceae	Caryophyllales		×		
Orchidaceae	Asparagales	×			
Oxalidaceae	Oxalidales			×	
Passifloraceae	Malpighiales			×	
Pedaliaceae	Lamiales		×		
Phyllanthaceae	Malpighiales			×	
Phytolaccaceae	Caryophyllales		×		
Piperaceae	Piperales		×		
Plantaginaceae	Lamiales		×		
Poaceae	Poales	×			
Portulacaceae	Caryophyllales		×		
Rubiaceae	Gentianales		×		
Ruscaceae	Asparagales	×			
Santalaceae	Santalales		×		
Sapindaceae	Sapindales			×	
Saxifragaceae	Saxifragales		×		
Solanaceae	Solanales		×		
Talinaceae	Caryophyllales		×		
Tropaeolaceae	Brassicales			×	
Urticaceae	Rosales			×	
Vitaceae	Vitales			×	
Zygophyllaceae	Zygophyllales			×	

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## References

- APG [Angiosperm Phylogeny Group] (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161: 105–21. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>.
- APG [Angiosperm Phylogeny Group] (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181(1): 1–20. <https://doi.org/10.1111/boj.12385>.



- Chase, M. W. & Reveal, J. L. (2009) A phylogenetic classification of the land plants to accompany APG III. *Bot. J. Linn. Soc.* 161(2): 122–127. <https://doi.org/10.1111/j.1095-8339.2009.01002.x>.
- Eggl, U. & Nyffeler, R. (2009) Living under temporarily arid conditions – succulence as an adaptive strategy. *Bradleya* 27: 13–36. <https://doi.org/10.5167/uzh-28825>.
- Moore, M. J. [et al. 2010], Soltis, P. S., Bell, C. D., Burleigh, J. G. & Soltis, D. E. (2010) Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. *Proc. Nation. Acad. Sci. USA* 107(10): 4623–4628. <https://doi.org/10.1073/pnas.0907801107>.
- Nyffeler, R. & Eggl, U. (2010a) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>.
- Nyffeler, R. & Eggl, U. (2010b) Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data. *Taxon* 59: 227–240. <https://doi.org/10.1002/tax.591021>.
- Ogburn, R. M. & Edwards, E. J. (2010) The ecological water-use strategies of succulent plants. *Advances Bot. Res.* 55: 179–225. [https://doi.org/10.1016/S0065-2296\(10\)55004-3](https://doi.org/10.1016/S0065-2296(10)55004-3).
- Pridgeon, A. M. [et al. 1999], Cribb, P. J., Chase, M.W.&Rasmussen, F. N. (eds.) (1999) *Genera Orchidacearum*. Volume 1. General introduction, *Apostasioideae*, *Cypripedioideae*. Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [et al. 2001], Cribb, P. J., Chase, M.W.&Rasmussen, F. N. (eds.) (2001) *Genera Orchidacearum*. Volume 2. *Orchidoideae* (part one). Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [et al. 2003], Cribb, P. J., Chase, M.W.&Rasmussen, F. N. (eds.) (2003) *Genera Orchidacearum*. Volume 3. *Orchidoideae* (part two), *Vanilloideae*. Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [et al. 2005], Cribb, P. J., Chase, M.W.&Rasmussen, F. N. (eds.) (2005) *Genera Orchidacearum*. Volume 4. *Epidendroideae* (part one). Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [et al. 2009], Cribb, P. J., Chase, M.W.&Rasmussen, F. N. (eds.) (2009) *Genera Orchidacearum*. Volume 5. *Epidendroideae* (part two). Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [et al. 2014], Cribb, P. J., Chase, M.W.&Rasmussen, F. N. (eds.) (2014) *Genera Orchidacearum*. Volume 6. *Epidendroideae* (part three). Oxford (GB): Oxford University Press.
- Soltis, D. E. [et al. 2011], Smith, S. A., Cellinese, N., Wurdack, K. J., Tank, D. C., Brockington, S. F., Refulio-Rodriguez, N. F., Walker, J. B., Moore, M. J., Carlswald, B. S., Bell, C. D., Latvis, M., Crawley, S., Black, C., Diouf, D., Xi, Z., Rushworth, C. A., Gitzendanner, M. A., Sytsma, K. J., Qiu, Y.-L., Hilu, K. W., Davis, C. C., Sanderson, M. J., Beaman, R. S., Olmstead, R. G., Judd, W. S., Donoghue, M. J. & Soltis, P. S. (2011) Angiosperm phylogeny: 17 genes, 640 taxa. *Amer. J. Bot.* 98(4): 704–730. <https://doi.org/10.3732/ajb.1000404>.

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# How to Use This Handbook

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## Sequence of Information

All information is presented in strictly alphabetical sequence of families, genera, and species within each volume. It is therefore easy to directly find the entry for a given species as long as its family placement is known.

An alternative way is to use the taxonomic cross-reference index supplied at the end of each volume. This index contains all the names covered in the volume and indicates the page where a treatment can be found, or in the case of synonyms gives the page reference where the accepted name is treated.

For each family, the handbook supplies keys to the genera with succulent representatives. Please note that these keys are designed to work for the *succulent* taxa treated and do not account for the total variation encountered in a genus. If the family is not known, the reader is referred to general botanical books that include keys to plant families. Rowley (1980) and Egli (2008) provided keys for flowering and nonflowering succulents, and Geesink & al. (1981) produced a well-known book of keys to all flowering plants worldwide.

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## Scope of Information Presented

### Families

The family names adopted are always conforming to the standard form (ending in *-aceae*); alternative names (such as *Compositae* for *Asteraceae*) are not used. Important synonyms at family rank are indicated, especially when the synonymous names include succulents. The order to which the family belongs is also given.

Within each family, the genera are treated in alphabetical sequence and the same applies to the sequence of species within genera. Some genera of minimal importance or with borderline succulence are only mentioned or at the most described, but no individual species are treated.

The family description characterizes the family as a whole, which often includes much more variation than that observed among its succulent representatives. This is supplemented by notes on the distribution, phylogeny, classification, and economic importance of the family and the occurrence of

succulence if this is not a general feature of the family as a whole. Also, a key to genera with succulents is included, and special terminology used for genera and species descriptions is discussed. The family concept adopted more or less follows APG III and APG IV, but with the modifications for Asparagales proposed by Nyffeler and Eggli (2010a).

## **Genera and Species**

The entries for genera and species are structured in the following way: names of authors are given in full, with initials added where necessary according to Brummitt and Powell (1992) and IPNI. The literature reference of the original description or combination is followed by information on typification (where available, see below). In the case of genera, important taxonomic literature is then cited. This is followed by information on geographical distribution (including notes on ecology where available) and an explanation of the etymology for generic names. For genera of larger families, their placement within the family is also indicated.

The main part of the entry is made up by the diagnostic description of the taxon, followed by a discussion of its variability, circumscription, and/or application where necessary. It should be noted that the descriptions reflect major variability only but do not usually include all the reported minor variations.

For larger genera, an outline of the accepted formal or informal classification is also given, with individual taxa or groups numbered in sequence. These sequence numbers are subsequently given at the start of each species description to indicate its placement within the genus.

If recent conflicting classifications are available for a given group, this is shortly discussed and the classification adopted is indicated. Further data, for example, on population biology, pollination, and seed dispersal or ethnobotany, are also included. Minor spelling variants of epithets are not indicated; instead, the “corrected” spelling is used throughout for accepted names and synonyms. Major spelling variants are treated as synonyms and are listed accordingly.

## **Infraspecific Taxa**

Infraspecific taxa are given in strict alphabetic order of rank and name (i.e., ranks in the sequence cultivar, forma, subspecies, variety). The typical infraspecific taxon (i.e., the one repeating the species name) is thus not treated first as in many handbooks but in its appropriate alphabetical sequence.

## **Cultivars, Hybrids**

Cultivars (rank indicated by placing the epithet in simple quotes) are not included on an exhaustive base; only cultivars of exceptional horticultural merit or botanical interest are covered. Cultivars not associated with a species are enumerated immediately following the entry for the genus. Cultivars

associated with a species name are included under that species, either as an entry of their own (and in the same form as subspecies, etc.) or, in the case of cultivars of minor importance, in the form of a short mention in the species discussion. Cultivar nomenclature follows the guidelines of the ICBN/ICN.

Formally named hybrid genera (nothogenera) are covered as genera of their own in the proper alphabetical sequence. The same applies to formally named hybrid species (nothospecies) and infraspecific nothotaxa. Hybrids only known with their hybrid formula are either discussed in the generic entry or mentioned under one or the other of their parent species. Formally named naturally occurring hybrids are usually covered in full including a description. No attempt has been made, however, to include all the numerous named artificial hybrids that originated in cultivation.

### **Phylogenetic Diagrams**

Phylogenetic summary cladograms are provided for all major families as well as for larger genera with a well-established infrageneric phylogeny. The width of the triangles in these cladograms is always proportional to the number of species of the clade, and the proportion of succulent taxa per clade is indicated with a darker shade. The length of the branches leading to each terminal clade has no phylogenetic meaning, that is, branch length does not indicate “phylogenetic distance” and thus is not indicative of the degree of relationships between clades. An asterisk (\*) accompanying a clade name indicates that the entity is paraphyletic.

### **Descriptions**

The descriptions are as compact, concise, and diagnostic as possible. Characters that do not vary for the group concerned are usually not repeated from the family or genus descriptions. In the case of genera further subdivided, information already presented in the group definitions is also not normally repeated in the descriptions of individual taxa.

### **Measurements**

All measurements are given in metric units. Measurements without further qualification *always refer to the long axis* of the organ described (i.e., length, height, etc.); two measurements united with the ×-sign stand for length × width.

### **Terminology**

Special terms used in descriptions are explained when first used; other botanical terminology is not further explained, and the readers are referred to the numerous botanical glossaries, of which Stearn (1992) is cited by way of a most important and useful example.

## Typification

An attempt is made to include typification data (including lecto- and neotypifications) for all accepted names. The type citations include the country and major administrative unit where the type was collected, the collector and collection number, and the herbaria where material is said or known to be deposited. The herbarium acronyms conform to *Index Herbariorum*, Ed. 8 (Holmgren & al. 1990) and its current later electronic version. Where more than one herbarium acronym is given, the first relates to the holotype and the others to isotypes (and similarly to lectotype or neotype and isolectotypes or isoneotypes). Additional information on typification is sometimes added, especially in the case of lecto- or neotypes, but epitypes are usually not cited.

## Nomenclatural Status of Names

For all taxa treated, every attempt has been made to use only valid and legitimate names, but this was not achievable in a small number of cases. In the synonym lists, the nomenclatural status (invalid, illegitimate, rejected, incorrect) is indicated by citing the ICBN or ICN articles violated. In many of these cases, the numbering still follows the “Vienna Code” (McNeill & al. 2006), but for more recent names, the numbering in the “Melbourne Code” (McNeill & al. 2012) is used; this is indicated by preceding the violated articles by “ICN.” Spelling variants are considered as invalidly published according to ICBN/ICN Art. 61.

While invalid names are, strictly speaking, not considered as names in ICBN/ICN (see Art. 6.3), they are nonetheless listed (and flagged accordingly with the violated articles of ICBN/ICN) in the synonymies in this handbook to draw attention to the fact that they are invalid.

## Synonymies

The synonymies given for genera and especially species are as complete as possible and include all names recognized as synonyms. The first synonym(s) – if applicable – is/are the basionym(s) and/or later combination(s) for the accepted name of the entry. All combinations of the same basionym are given in sequence of publication year and are united with the  $\equiv$ -sign to indicate that these are homotypic (nomenclatural) synonyms. Please note that the  $\equiv$ -sign is only used for *combinations* based on the same basionym and does not indicate other homotypic synonyms (e.g., *nomina nova*, which are by definition based on the type of the replaced name). All other synonyms are headed with “incl.” to indicate that they are, with the exception of *nomina nova* as just discussed, taxonomic synonyms (= heterotypic synonyms). Again, groups of combinations based on the same basionym are united with  $\equiv$ -signs. Basionyms are given first and in chronological order.

## Geographical Names

Country names are listed roughly in a North to South and West to East sequence. Every attempt has been made to standardize geographical names (of countries, administrative units, regions, etc.) as far as possible, but there is a

surprising amount of change relating to such names. This is specifically the case for the names of the provinces of the Republic of South Africa, which have changed considerably in the 1990s, especially affecting the former Cape Province, which has been split up into four units (North-West Province, Northern Cape, Western Cape, Eastern Cape). We tried as best as we could to provide the modern names in the distribution information included in the handbook, but it has been impossible to adjust all the data for type localities, where the name “Cape Prov.” is still used in a small number of cases.

Some difficulties were also encountered in a few cases where countries have been amalgamated (as in the case of the former North Yemen and South Yemen) or divided (e.g., Eritrea, formerly part of Ethiopia, or the nations that formerly made up Yugoslavia). Full consistency in all these cases was impossible to achieve.

In order to save space, geographical directions such as North, South, etc., are *always* abbreviated (N, S, etc.). Please note that *SW Africa* indicates “southwestern Africa” and *not* the former Southwest Africa (now Namibia). Similarly, *S Africa* indicates “southern Africa” and *not* the Republic of South Africa, for which the abbreviation RSA is always used.

## Literature References

Literature references are given for all accepted names. Normally, the publication is cited with a full abbreviation according to the standards defined in BPH2 (Bridson & al. 2004) for periodicals (supplemented with those of Eggle (1985) and Eggle (1998) for specialist succulent plant periodicals), while TL2 of Stafleu and Cowan (1976–1988) and supplements (Stafleu and Mennega 1992–2000, Dorr and Nicolson 2008–2009) are followed for book abbreviations (in both cases with some minor exceptions to conserve uniformity). In the running text, literature is cited in the usual way (author(s) and year, sometimes supplemented by a page reference), and full details can be found in the list of references at the end of each family or genus.

## Illustrations

An attempt has been made to cite at least one readily accessible illustration for each species or infraspecific taxon when no illustrations are included in the literature reference for the accepted name. If the name used in the cited publication differs from the accepted name in the handbook, it is indicated (genus name abbreviated to first letter if identical, specific or infraspecific epithet omitted if identical to the accepted name).

## Indication of Authorships of the Handbook Texts

For each family and genus, the authorship of the handbook text is indicated at the start of the entry. If more than one author has contributed species entries for a genus, each species entry has its own indication of authorship when this differs from the authorship of the genus as a whole.



## References

- Bridson, G. D. R. [ & al. 2004], Townsend, S. T., Polen, E. A. & Smith, E. R. (2004) BPH-2. Periodicals with botanical contents. Constituting a second edition of *Botanico-Periodicum Huntianum*. Pittsburgh (US): Hunt Institute for Botanical Documentation, Carnegie Mellon University. 2 vols., 1470 pp.
- Brummitt, R. K. & Powell, C. E. (eds.) (1992) *Authors of plant names. A list of authors of scientific names of plants, with recommended standard forms of their names, including abbreviations*. Richmond (GB): The Board of Trustees of The Royal Botanic Gardens, Kew. 732 pp.
- Dorr, L. J. & Nicolson, D. H. (2008–2009) *Taxonomic literature*. Ruggell (FL): A. R. G. Gantner-Verlag KG. Supplements VII–VIII to Ed. 2; 2 vols.
- Eggl, U. (1985) *A bibliography of succulent plant periodicals*. *Bradleya* 3: 103–119. <https://doi.org/10.25223/brad.n3.1985.a6>.
- Eggl, U. (1998 [‘1995’]) *Bibliography of succulent plant periodicals*. *Bibliografie casopisu o sukulentních rostlinách*. *Friciana* 60: 139 pp.
- Eggl, U. (2008) *Sukkulenten*. Stuttgart (DE): Eugen Ulmer. Ed. 2, 392 pp., ill., keys.
- Eggl, U. & Nyffeler, R. (2009) Living under temporarily arid conditions – succulence as an adaptive strategy. *Bradleya* 27: 13–36. <https://doi.org/10.5167/uzh-28825>.
- Geesink, R. [ & al. 1981], Leeuwenberg, A. J. M., Ridsdale, C. E. & Veldkamp, J. F. (1981) *Thonner’s analytical key to the families of flowering plants*. Den Haag (NL): Leiden University Press. 231 pp.
- Holmgren, P. K. [ & al. 1990], Holmgren, N. H. & Barnett, L. C. (1990) *Index Herbariorum*. Part I: The herbaria of the world. New York (US): New York Botanical Garden. Ed. 8; 693 pp. Current electronic version: <http://sweetgum.nybg.org/science/ih/>
- IPNI: The International Plant Name Index, accessible at: <http://www.ipni.org/>
- McNeill, J. [ & al. 2006], Barrie, F. R., Burdet, H. M., Demoulin, V., Hawksworth, D. L., Marhold, K., Nicolson, D. J., Prado, J., Silva, P. C., Skog, J. E., Wiersema, J. H. & Turland, N. J. (eds.) (2006) *International Code of Botanical Nomenclature (Vienna Code)*. Ruggell (FL): A. R. G. Gantner Verlag KG.
- McNeill, J. [ & al. 2012], Barrie, F. R., Buck, W. R., Demoulin, V., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Marhold, K., Prado, J., Prud’homme van Reine, W. F., Smith, G. F., Wiersema, J. H. & Turland, N. J. 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code)*. Königstein (DE): Koeltz Scientific Books.
- Nyffeler, R. & Eggl, U. (2010a) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>.
- Nyffeler, R. & Eggl, U. (2010b) Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data. *Taxon* 59: 227–240. <https://doi.org/10.1002/tax.591021>.

- Ogburn, R. M. & Edwards, E. J. (2010) The ecological water-use strategies of succulent plants. *Advances Bot. Res.* 55: 179–225. [https://doi.org/10.1016/S0065-2296\(10\)55004-3](https://doi.org/10.1016/S0065-2296(10)55004-3).
- Rowley, G. D. (1980) Name that succulent. Keys to the families and genera of succulent plants in cultivation. Cheltenham (GB): Stanley Thornes (Publishers) Ltd. 268 pp., ill., keys.
- Stafleu, F. A. & Cowan, R. S. (1976–1988) Taxonomic literature. Utrecht (NL): Bohn, Scheltema & Holkema, etc. Ed. 2; 7 vols.
- Stafleu, F. A. & Mennega, E. A. (1992–2000) Taxonomic literature. Königstein (DE): Koeltz Scientific Books. Supplements I–VI to Ed. 2; 6 vols.
- Stearn, W. T. (1992) Botanical Latin. Newton Abbot (GB): David & Charles Publishers. Ed. 4; 560 pp.

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# List of Abbreviations and Symbols

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## Symbols

- ≡ Mathematical “equal,” used for homotypic synonyms  
† Dagger symbol, used for lost type specimens and to indicate death dates  
∅ Diameter symbol, used in descriptions  
× Mathematical multiplication symbol, used to connect measurements of length × width and used to indicate hybrid status  
± Plus-minus symbol, used to indicate approximate values  
\* (Beneath a taxon name) indication of a paraphyletic taxon

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## General Abbreviations

Art.	Article of ICBN/ICN
BG	Botanical Garden
C	central
clono	clonotype, i.e., a herbarium specimen derived from the type gathering after the publication of the protologue, and not a “true” type in the sense of botanical nomenclature
cult.	cultivated
cv.	cultivar
<b>Distr</b>	distribution
Distr.	District
E	East, eastern
e.g.	for example
epi	epitype (nomenclatural type)
esp.	especially
<b>Etym</b>	etymology
excl.	excluding
fa.	forma (botanical rank)
fig., figs.	figure, figures
fl.	“floruit,” i.e., lived
Gr.	Greek
Herb.	herbarium
holo	holotype (nomenclatural type)
Hort., hort.	garden, of gardens

<b>I</b>	Illustration
ICBN	International Code of Botanical Nomenclature (“Vienna Code,” 2006)
ICN	International Code of Nomenclature for Algae, Fungi, and Plants (“Melbourne Code,” 2012)
ill., ills.	illustration, illustrations; illustrated
illeg.	illegitimate (nomenclatural concept)
in sched.	“in schedis,” i.e., in the herbarium
incl.	including
ING	Index Nominorum Genericorum
inval.	invalid (nomenclatural concept)
KG, KGW	Karoo Garden, Worcester, RSA
l.c.	“loco citato,” i.e., at the place cited
lecto	lectotype (nomenclatural type)
<b>Lit</b>	literature
ms.	manuscript
Mt., Mts.	mountain, mountains
mybp	million years before present
N	North, northern
NBG	National Botanical Garden, RSA
NE	North-East, north-eastern
neo	neotype (nomenclatural type)
nom.	“nomen,” i.e., botanical name
NW	North-West, north-western
p., pp.	page, pages
p.a.	“per annum,” i.e., per year
p.p.	“pro parte,” i.e., partly
pers. comm.	personal communication
pl.	plate
pp.	pages
Prov.	Province
publ.	published
q.v.	“quod vide,” i.e., which see
RSA	Republic of South Africa
S	South, southern
s.a.	“sine anno,” i.e., without year
s.l.	“sensu lato,” i.e., in a wide sense
s.n.	“sine numero,” i.e., without (collection) number
s.s.	“sensu stricto,” i.e., in the strict/narrow sense
SE	South-East, south-eastern
Sect.	section (botanical rank)
SEM	Scanning electron microscope
Ser.	series (botanical rank)
spp.	several species
ssp.	subspecies (botanical rank)
Subgen.	subgenus (botanical rank)
Subsect.	subsection (botanical rank)

Subser.	subseries (botanical rank)
SUG	Stellenbosch University Botanical Garden
SW	South-West, south-western
syn	syntype (nomenclatural type)
t., tt.	“tabula,” i.e., illustration plate/plates
unpubl.	unpublished
USA	United States
var.	variety (botanical rank)
W	West, western
WCSP	World Checklist of Selected Plant Families. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet: <a href="http://apps.kew.org/wcsp/">http://apps.kew.org/wcsp/</a>

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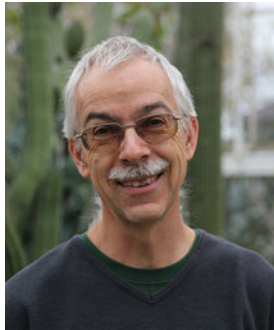
### Abbreviations in Plant Descriptions

<b>Anth</b>	Anther, anthers
<b>Ar</b>	Areole, areoles
<b>Ax</b>	Axil, axils
<b>Bo</b>	Body, i.e., the plant body of a cactus, etc.
<b>Br</b>	Branch, branches
<b>Bra</b>	Bract, bracts
<b>Bri</b>	Bristle, bristles
<b>Ca</b>	Carpel, carpels
<b>Cal</b>	Calyx
<b>Cap</b>	Capitulum (of Asteraceae)
<b>Ci</b>	Interstaminal corona (of Apocynaceae)
<b>Cn</b>	corona
<b>Cs</b>	Staminal corona (of Apocynaceae)
<b>Cy</b>	Cyathium (of Euphorbiaceae)
<b>Fil</b>	Filament, filaments
<b>Fl</b>	Flower, flowers
<b>Fr</b>	Fruit, fruits
<b>Gl</b>	Gland, glands
<b>Gy</b>	Gynostegium (of Apocynaceae)
<b>Ha</b>	Hair, hairs
<b>Inf</b>	Inflorescence, inflorescences
<b>Int</b>	Internode, internodes
<b>ITep</b>	Inner tepal, inner tepals
<b>L</b>	Leaf, leaves
<b>Nec</b>	Nectary, nectaries
<b>NGl</b>	Nectary gland, nectary glands
<b>NSc</b>	Nectary scale, nectary scales
<b>OTep</b>	Outer tepal, outer tepals
<b>Ov</b>	Ovary, ovaries
<b>Pc</b>	pericarpel
<b>Ped</b>	Pedicel, pedicels

<b>Per</b>	Perianth
<b>Pet</b>	Petal, petals
<b>Phy</b>	Phyllaries (of Asteraceae capitula)
<b>Poll</b>	Pollinia
<b>R</b>	Root, roots
<b>Rec</b>	receptacle
<b>Ri</b>	Rib, ribs
<b>Ros</b>	Rosette, rosettes
<b>Sc</b>	Scale, scales
<b>Se</b>	Seed, seeds
<b>Sep</b>	Sepal, sepals
<b>Sp</b>	Spine, spines
<b>SpS</b>	Spine shield (in Euphorbiaceae)
<b>St</b>	Stamen, stamens
<b>Sti</b>	stigma
<b>Sty</b>	Style, styles
<b>Tep</b>	Tepal, tepals
<b>Tu</b>	Tubercle, tubercles (of cactus bodies, etc.)

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## About the Editors



**Dr. Urs Eggli** studied botany at the University of Zürich and produced a monographic study of the genus *Rosularia* (*Crassulaceae*) for his Ph.D. Subsequently he became scientific assistant at the Sukkulenten-Sammlung Zürich, Switzerland, where he continues to curate the herbarium and is responsible for public education, special exhibits, and all aspects of information dissemination. His main focus of interest is the diverse biological aspects of succulent plants. Dr. Eggli is an expert in the classification of succulents, especially of the families *Crassulaceae* and *Cactaceae*, and a specialist of nomenclature. He traveled widely to study succulent plants in habitat, especially in Latin America. His numerous publications cover a diversity of aspects of the biology of succulent plants. Since 1995 he is editor of the annual *Repertorium Plantarum Succulentarum*. During 2001–2003 he edited four volumes of the first edition of the present series, and in 2005 he translated and revised a monograph of the *Cactaceae*. Dr. Eggli was awarded the Cactus d'Or by the International Organization for Succulent Plant Study in 2015.



**Dr. Reto Nyffeler** studied biology at the University of Zürich. In 1997 he received a doctor's degree with a Ph.D. thesis on the systematics of the tribe *Notocactae* (*Cactaceae*) from South America. Subsequently, he spent 4 years as a postdoctoral student at Harvard University and Stanford University and conducted during that stay the first comprehensive molecular phylogenetic study of *Cactaceae*. Since 2002 he is curator for the vascular plant collections at the United Herbaria of the University and ETH Zurich, and he is a lecturer for plant systematics at the

Department of Systematic and Evolutionary Botany, University of Zurich. His research focuses on the systematics of succulent plants and on the history of botany. During the past two decades he published several papers on succulents from different plant families in collaboration with Dr. Urs Egli.



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# Introduction to the Classification of Monocotyledons

R. Nyffeler and U. Eggli

## General Remarks

Succulents of the Monocotyledons (“monocots”, subclass Liliidae or superorder Lilianae) contribute in an important manner to the overall plant diversity in many arid and semi-arid regions. Generally, they are easily recognized on the basis of their characteristic parallel-veined leaves often in rosettes or as geophytic bulbs. Prominent and landscape-dominating representatives are shrubby to arborescent monocots such as the “kokerboom” (*Aloe dichotoma*, Asphodelaceae) in the Namib desert of SW Africa, or tall-growing and branched *Yucca* species, e.g. the “Joshua tree” (*Yucca brevifolia*, Agavaceae), which form open forests in parts of the Mojave desert and surroundings in California, United States.

The Monocotyledons comprise almost 25% of the total existing vascular plant biodiversity, i.e. c. 70,000 species. Overall, about 10%, i.e. ±6460 monocot species, are recognized as succulents, present in five of the eleven orders commonly recognized today (APG 2009, 2016, Christenhusz et al. 2016). Molecular phylogenetic studies of the

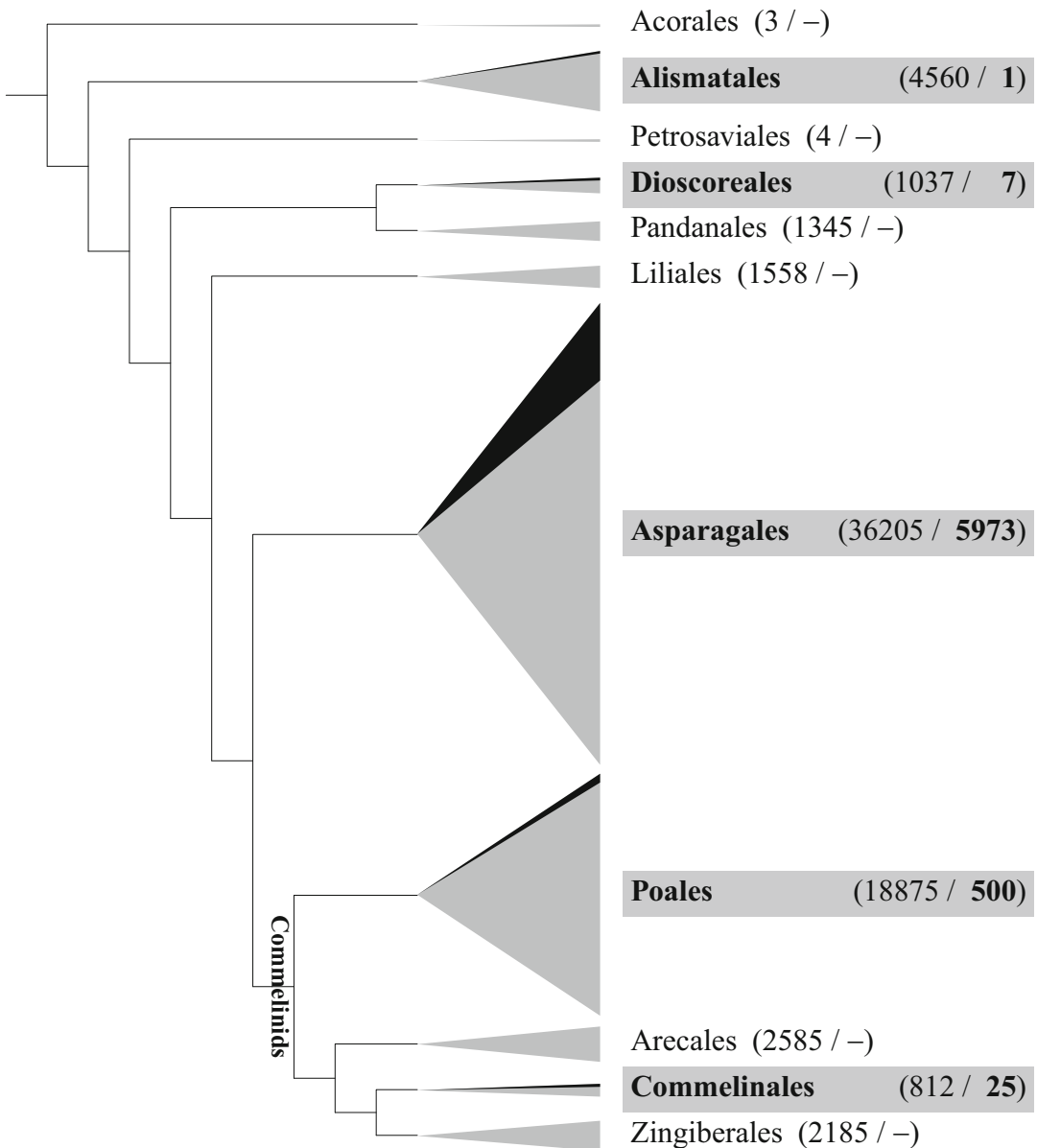
past three decades have provided a well-founded “backbone” of relationships among the distinct clades recognized as orders (e.g., Givnish & al. 2006, Moore & al. 2010, Soltis & al. 2011). Our current knowledge on the phylogenetic relationships among the monocot orders and their share of succulent representatives is illustrated in Fig. 1.

## Family Classification in the Order Asparagales

There is unanimous agreement about the circumscription of the monophyletic order Asparagales in all recent phylogenetic studies (Chase & al. 2000, Fay & al. 2000). This order, comprising in total some 36,000 species of which some 16% are succulent, includes several species-rich distinct succulent lineages. However, their classification into families is still dealt with controversially, as they include most of the former “Liliaceae” and relatives as recognized by Cronquist (1981) and other authors in the era before molecular phylogenetic studies. Relationships among lineages in the order Asparagales are reconstructed in rather stable form (Bogler & al. 2006, Pires & al. 2006, Seberg & al. 2012, Steele & al. 2012) and consensus is reached (e.g., Judd & al. 2016) concerning relative relationships among the major clades, similar to the relationships illustrated in Fig. 2. The order includes a grade of families referred to as “lower Asparagales”, including Orchidaceae and

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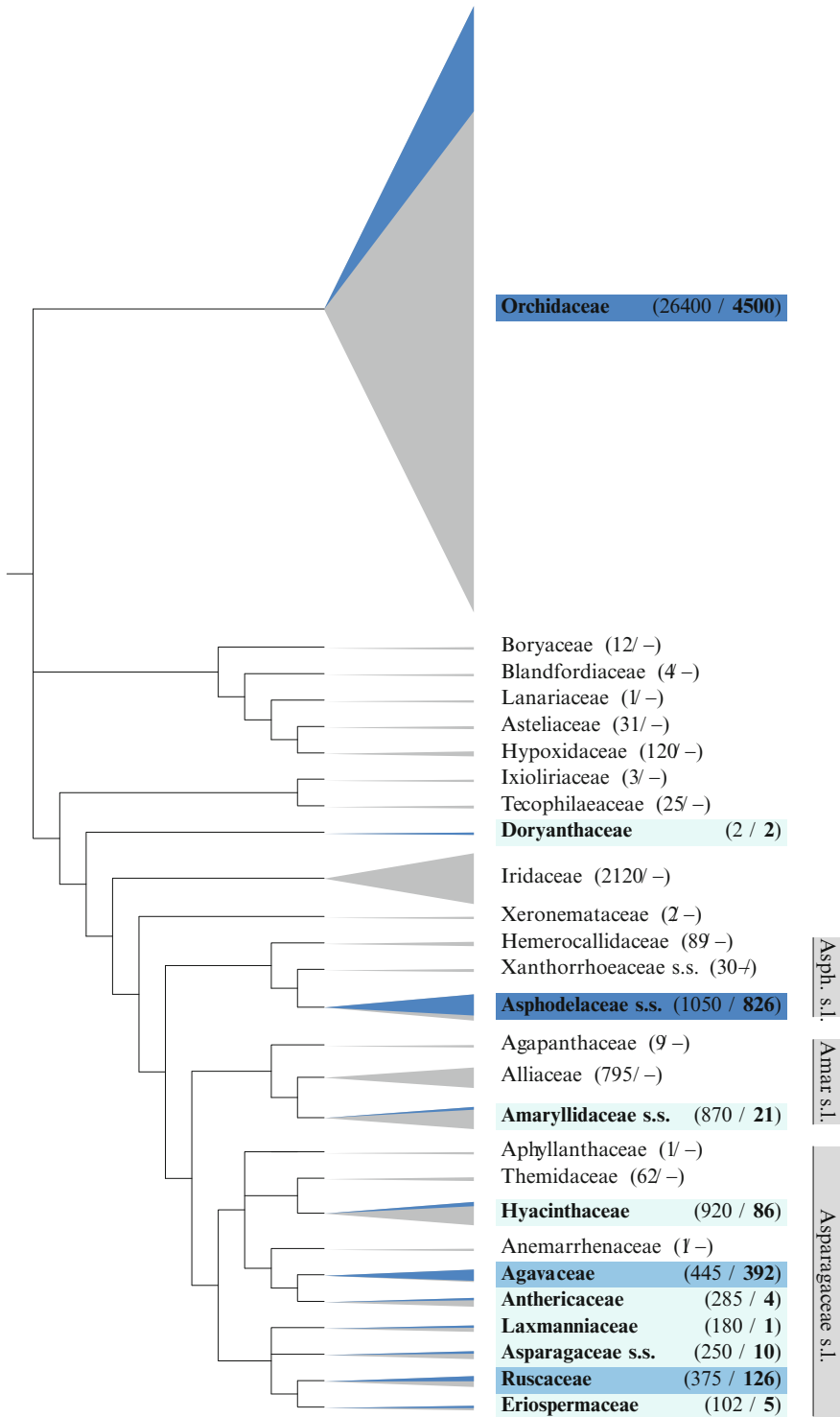


**Fig. 1** Summary phylogeny of the monocot orders following APG (2009, 2016). The numbers to the right of the ordinal names are the total species number and the number of succulent species. The widths of the triangles are proportional to the number of species per order. The proportion of succulents is illustrated by the black part of each triangle.

Except for the order Asparagales, all other orders only comprise a few dozen succulent species, with the only exception of the Poales where the bromeliads (family Bromeliaceae) contribute almost 500 species of succulents. (Copyright: U. Eggli)

Iridaceae, and a well-supported clade of “higher Asparagales” consisting of the broadly circumscribed families Asphodelaceae s.l. (changed for nomenclatural reasons from the previously used

Xanthorrhoeaceae s.l.), Amaryllidaceae s.l. and Asparagaceae s.l. However, no final consensus has been reached for the classification into families, largely due to different concepts of



**Fig. 2** Summary phylogeny of the Asparagales (data from Judd & al. 2007, Mabberley 2008, Nyffeler & Eggli 2010, and Stevens (2001 onwards, accessed Dec. 2017). Family

concepts of APG (2016) are indicated to the right of the shaded boxes. The shading of the boxes relates to the proportion of succulent species in the families. (Copyright: U. Eggli)

**Table 1** Comparison of family names used in this series (based on Nyffeler & Eggli 2010) with the family names proposed by APG (2009, 2016), and the subfamily names proposed by Chase & al. (2009)

Nyffeler & Eggli 2010, used in this Handbook	AGP IV (2016), Christenhusz & al. (2016)	Subfamilies following Chase & al. (2009)
Asphodelaceae s.s. (1)	Asphodelaceae s.l. (3)	Asphodeloideae
Amaryllidaceae s.s.	Amaryllidaceae s.l.	Amaryllidoideae
Agavaceae	Asparagaceae s.l.	Agavoideae
Anthericaceae	Asparagaceae s.l.	Agavoideae
Asparagaceae s.s.	Asparagaceae s.l.	Asparagoideae
Eriospermaceae	Asparagaceae s.l.	Nolinoideae
Hyacinthaceae	Asparagaceae s.l.	Scilloideae
Ruscaceae (2)	Asparagaceae s.l.	Nolinoideae

Notes: (1) incl. Aloaceae; (2) incl. Dracaenaceae, Nolinaceae; (3) previously, e.g. APG (2009) Xanthorrhoeaceae s.l.

inclusiveness at the rank of subfamilies versus families in this order. Hence, we identify the different concepts of inclusiveness relative to each other as *sensu lato* (s.l.) versus *sensu stricto* (s.s.).

Nyffeler & Eggli (2010) have discussed the different options at length, and the situation has not changed during the past half decade (see Nordal & Sletten BJORÅ 2016). The main point for discussion remains the number of families to accept, and their diagnostic circumscriptions. Traditional concepts such as the vast family Liliaceae s.l., or the utilization of superior versus inferior ovaries as basis for classificatory decisions, have been found to be not congruent with inferred phylogenetic relationships and these characters are no longer considered as providing valid concepts. While APG (1998) recognized almost 30 families for the Asparagales as a whole, subsequent discussions about the practicability of having so many families for the “higher Asparagales” led to a “lumping” proposal to recognize only the three widely circumscribed families Asphodelaceae (previously called Xanthorrhoeaceae), Amaryllidaceae and Asparagaceae (APG 2003, 2009, repeated by APG 2016; see Christenhusz & al. 2015 for a history of the APG process and the rationale for the preferred lumping). Hence, and applying these circumscriptions, APG recognizes today 14 families for the order Asparagales. Adherents of this reduction in the number of families and the concomitant wide circumscriptions claim that this results in a gain in practicability, esp. for teaching purposes. On the other side, the proposed radical changes in family circumscriptions are disruptive

in comparison with the traditional “splitting” concepts. It should be noted that the discussion does not concern neither the topology of the phylogenetic backbone, nor accepting non-monophyletic taxa above the rank of species, but merely affects at what level family names are attached to clades. Since the “lumping” approach of APG (2009, 2016) does not result in a gain of information, and because the alleged gains in practicability remain to be clearly identified, we here follow the traditional (splitting) concept, in line with the considerations of Schmid (2013), and in parallel with the recently updated edition of “Plant systematics: a phylogenetic approach” by Judd & al. (2016; Eriospermaceae not covered). Additional support for the recognition of at least some of the traditionally accepted families is discussed by Seberg & al. (2012) and Nordal & Sletten BJORÅ (2016). Our decision keeps all links to previous literature and concepts intact, without concessions to phylogenetic relationships. For clarity, Table 1 lists the two classificatory approaches side-by-side, and also provides the subfamily names suggested by Chase & al. (2009).

## References

- APG [Angiosperm Phylogeny Group] (1998) An ordinal classification for the families of Flowering Plants. *Ann. Missouri Bot. Gard.* 85: 531–553. <https://doi.org/10.2307/2992015>
- APG [Angiosperm Phylogeny Group] (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot.*

- J. Linn. Soc. 141: 399–436. <https://doi.org/10.1046/j.1095-8339.2003.t01-1-00158.x>.
- APG [Angiosperm Phylogeny Group] (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>.
- APG [Angiosperm Phylogeny Group] (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181(1): 1–20. <https://doi.org/10.1111/boj.12385>
- Bogler, D. J. [ & al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of Agavaceae based on *ndhF*, *rbcL*, and its sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>.
- Chase, M. W. [ & al. 2000], Bruijn, A. Y. de, Cox, A. V., Reeves, G., Rudall, P. J., Johnson, M. A. T. & Eguarte, L. E. (2000) Phylogenetics of Asphodelaceae (Asparagales): An analysis of plastid *rbcL* and *trnL-F* DNA sequences. *Ann. Bot. (Oxford)*, n.s. 86: 935–951. <https://doi.org/10.1006/anbo.2000.1262>.
- Chase, M. W. [ & al. 2009], Reveal, J. L. & Fay, M. F. (2009) A subfamilial classification for the expanded Asparagalean families Amaryllidaceae, Asparagaceae and Xanthorrhoeaceae. *Bot. J. Linn. Soc.* 161(2): 132–136. <https://doi.org/10.1111/j.1095-8339.2009.00999.x>.
- Christenhusz, M. J. M. [ & al. 2015], Vorontsova, M. S., Fay, M. F. & Chase, M. W. (2015) Results from an online survey of family delimitation in angiosperms and ferns: Recommendations to the Angiosperm Phylogeny Group for thorny problems in plant classification. *Bot. J. Linn. Soc.* 178(4): 501–528. <https://doi.org/10.1111/boj.12285>.
- Christenhusz, M.J.M. [ & al. 2016], Fay, M. F. & Chase, M. W. (2016). *Plants of the World. An Illustrated Encyclopedia of Vascular Plants*. Chicago (US): University of Chicago Press.
- Cronquist, A. (1981). *An integrated system of classification of flowering plants*. New York (US): Columbia University Press.
- Fay, M. F. [ & al. 2000], Rudall, P. J., Sullivan, S., Stobart, K. L., Bruijn, A. Y. de, Reeves, G., Qamaruz-Zaman, F., Hong, W.-P., Joseph, J., Hahn, W., Conran, J. V. & Chase, M. W. (2000) Phylogenetic studies of Asparagales based on four plastid DNA regions. In: Wilson, K. L. & Morrison, D. A. (eds.): *Monocots: Systematics and evolution*. Melbourne (AU): CSIRO.
- Givnish, T. J. [ & al. 2006], Pires, J. C., Graham, S. W., McPherson, M. A., Prince, L. M., Patterson, T. B., Rai, H. S., Roalson, E. H., Evans, T. M., Hahn, W. J., Millam, K. C., Meerow, A. W., Molvray, M., Kores, P. J., O'Brien, H. E., Hall, J. C., Kress, W. J. & Sytsma, K. J. (2006) Phylogenetic relationship of Monocots based on the highly informative plastid gene *ndhF*: Evidence for widespread concerted convergence. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 28–51. <https://doi.org/10.5642/aliso.20062201.04>.
- Givnish, T. J. [ & al. 2018], Zuluaga, A., Spalink, D., Soto Gomez, M., Lam, V. K. Y., Saarela, J. M., Sass, C., Iles, W. J. D., Lima de Sousa, D. J., Leebens-Mack, J., Pires, J. C., Zomlefer, W. B., Gandolfo, M. A., Davis, J. I., Stevenson, D. W., dePamphilis, C., Specht, C. D., Graham, S. W., Barrett, C. F. & Ané, C. (2018) Monocot plastid phylogenomics, timeline, net rates of species diversification, the power of multi-gene analyses, and a functional model for the origin of monocots. *Amer. J. Bot.* 105 (11): 1–23. <https://doi.org/10.1002/ajb2.1178>.
- Judd, W. S. [ & al. 2007], Campbell, C. S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J. (2007) *Plant systematics: A phylogenetic approach*. Ed. 3. Sunderland (US): Sinauer Associates.
- Judd, W. S. [ & al. 2016], Campbell, C. S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J. (2016) *Plant systematics: A phylogenetic approach*. Ed. 4. Sunderland (US): Sinauer Associates.
- Mabberley, D. J. (2008) *Mabberley's Plant-Book. A portable dictionary of plants, their classification and uses*. Ed. 3. Cambridge (GB): Cambridge University Press
- Moore, M. J. [ & al. 2010], Soltis, P. S., Bell, C. D., Burleigh, J. G. & Soltis, D. E. (2010) Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. *Proc. Nation. Acad. Sci. USA* 107(10): 4623–4628. <https://doi.org/10.1073/pnas.0907801107>.
- Nordal, I. & Sletten Bjørå, C. (2016) Family delimitation in flowering plants, should we bother? - A case study of Asparagales. *Symb. Bot. Upsal.* 38: 41–48.
- Nyffeler, R. & Egli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.25223/brad.n28.2010.a1>
- Pires, J. C. [ & al. 2006], Maureira, I. J., Givnish, T. J., Sytsma, K. J., Seberg, O., Petersen, G., Davis, J. I., Stevenson, D. W., Rudall, P. J., Fay, M. F. & Chase, M. W. (2006) Phylogeny, genome size, and chromosome evolution of Asparagales. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 287–304. <https://doi.org/10.5642/aliso.20062201.24>.
- Schmid, R. (2013) Considerations for flora writers in adopting the new phylogenetic classifications. *Taxon* 62: 206–207. <https://www.jstor.org/stable/24389345>
- Seberg, O. [ & al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jorgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ill. <https://doi.org/10.3732/ajb.110468>.
- Soltis, D. E. [ & al. 2011], Smith, S. A., Cellinese, N., Wurdack, K. J., Tank, D. C., Brockington, S. F., Refulio-Rodriguez, N. F., Walker, J. B., Moore, M. J., Carlswald, B. S., Bell, C. D., Latvis, M., Crawley, S., Black, C., Diouf, D., Xi, Z., Rushworth, C. A., Gitzendanner, M. A., Sytsma, K. J., Qiu, Y.-L., Hilu, K. W., Davis, C. C., Sanderson, M. J., Beaman, R. S.,



- Olmstead, R. G., Judd, W. S., Donoghue, M. J. & Soltis, P. S. (2011) Angiosperm phylogeny: 17 genes, 640 taxa. *Amer. J. Bot.* 98(4): 704–730. <https://doi.org/10.3732/ajb.1000404>.
- Steele, P. R. [ & al. 2012], Hertweck, K. L., Mayfield, D., Mckain, M. R., Leebens-Mack, H. & Pires, J. C. (2012) Quality and quantity of data recovered from massively parallel sequencing: Examples in Asparagales and Poaceae. *Amer. J. Bot.* 99(2): 330–348. <https://doi.org/10.3732/ajb.1100491>.
- Stevens, P. F. (2001+) Angiosperm Phylogeny Website, Version 12, July 2012 [and more or less continuously updated since]. St. Louis (US): Missouri Botanical Garden. <http://www.mobot.org/MOBOT/research/APweb/>

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**Part I**

**The Family Agavaceae**





# Agavaceae

J. Thiede and U. Eggli

**Including** *Funkiaceae* Horaninov (*nom. illeg.*, Art. 18.3).

**Including** *Yuccaceae* J. Agardh.

**Including** *Hesperocallidaceae* Traub.

**Including** *Hostaceae* B. Mathew.

**Including** *Chlorogalaceae* Doweld & Reveal.

Small to often large perennial **Ros** plants or (sometimes bulbous) herbs, or shrubs or trees, **Ros** monocarpic, either unbranched and plant monocarpic, or branched and whole plant polycarpic, terrestrial, very rarely epiphytic; stems none or short (then not rarely caespitose), or  $\pm$  arborescent (then mostly  $\pm$  branching), in part with secondary thickening growth (*Furcraea*, *Yucca*), partly with spreading or thick and upright rhizomes (*Yucca* p.p., *Agave* Subgen. *Manfreda* p.p., herbaceous non-succulent taxa); **L** spirally arranged in **Ros**, dorsiventral, lanceolate, linear or subulate, often broadest near the base or the middle and gradually tapering towards the tip, deciduous or more commonly evergreen and then usually thick and succulent, tough and fibrous or  $\pm$  thin and weak (*Agave* Subgen. *Manfreda*,

herbaceous non-succulent taxa), tip often a hard pungent spine (*Yucca*, *Agave* s.s.) or a  $\pm$  soft (more rarely hard) point (*Beschorneria*, *Furcraea*, *Agave* Subgen. *Manfreda*) or not differentiated, margins entire, hardened in most perennial taxa but soft in herbaceous taxa, or with horny marginal teeth (these often on prominences), or filiferous; **Inf** terminal, mostly large, 0.5–13 m, with few or numerous bracts, determinate and mostly complex much-branched panicles with cymose lateral part-**Inf** consisting of monochasial units; peduncle mostly present, more rarely short to nearly none; peduncular **Bra** mostly  $\pm$  similar to rosette leaves, diminishing in size upwards; floral **Bra** present; **Ped** normally present; **Fl** bisexual, 3-merous, actinomorphic or slightly zygomorphic, pendent or spreading, or  $\pm$  upright (*Agave*), anthesis diurnal and / or nocturnal; **Tep** 3 + 3, mostly whitish to yellow or greenish, rarely  $\pm$  reddish, pinkish or brownish, or lavender or blue, **Tep**  $\pm$  spreading or connivent to form a tube-like structure (*Beschorneria*, *Hesperaloe* p.p.), or fused for part of their length and forming a tubular to campanulate tube (*Agave*), sometimes abruptly widened or urceolate in the upper part; **St** 3 + 3, inserted at or somewhat above the base of the free tepals or within the perianth tube; **Fil** mostly long and slender-filiform, rarely short, sometimes widened basally (*Furcraea*) or apically (*Yucca*), mostly glabrous, sometimes puberulent (*Yucca* p.p.); **Anth** dorsifixed, 2-theccous, small to large, sagittate to hastate (*Yucca*, etc.) or oblong to linear (*Agave*, etc.), long or short,

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dehiscing introrsely with longitudinal slits; pollen primarily sulcate, rarely bisulcate (*Agave* Subgen. *Manfreda* p.p.), mainly released in monads, rarely also in tetrads (*Beschorneria*, *Furcraea*); **Ov** inferior (*Agaveae*) or superior (all other clades), 3-locular, each locule with 2 to several to mostly many ovules; **Nec** septal; **Sty** rather long and simple or apically with 3 free and short branches (*Yucca*); **Sti** mostly single and either capitate or 3-lobed or on 3 style branches (*Yucca*), surface dry or wet; **Fr** mostly loculicidal capsules, rarely septicidal capsules or berry-like (*Yucca* p.p.), with several to many seeds; **Se** various but mostly flat and plate-like, crescent-shaped or semicircular, but sometimes less compressed (*Yucca*), or globose, ovoid or pear-shaped (*Chlorogaleae*, *Schoenolirion*), black (due to phytomelans). — **Cytology**:  $x = 30$  in the *Agavoideae* (bimodal, with 25 short and 5 long chromosomes) and *Hosta* (bimodal, with 4 large, 2 medium and 24 small chromosomes), or variable ( $n = 12, 15, 16, 17, 18, 26, 30, 48?$ ) in the other clades (chromosomes all of equal length, or bimodal in *Hesperocallis*).

**Order:** Asparagales

**Important Literature:** Krause (1930: outdated synopsis); Schulze (1984: palynology, classification); Dahlgren & al. (1985: classification); Eguiarte & al. (1994: classification); Bogler & Simpson (1995: molecular phylogeny); Bogler & Simpson (1996: molecular phylogeny); Verhoek-Williams (1998: synopsis); Bogler & al. (2006: molecular phylogeny); Givnish & al. (2006: molecular phylogeny); Good-Avila & al. (2006: molecular phylogeny); Graham & al. (2006: molecular phylogeny); Rocha & al. (2006: molecular phylogeny & pollination); Smith & al. (2008: molecular phylogeny); Kim & al. (2010: molecular phylogeny); Seberg & al. (2012: molecular phylogeny); Steele & al. (2012: molecular phylogeny); Matiz & al. (2013: photosynthesis); Halpin & Fishbein (2013: molecular phylogeny *Chlorogaloideae*); Archibald & al. (2015: molecular phylogeny *Chlorogaloideae*); Heyduk & al. (2016: molecular phylogeny & photosynthesis); McKain & al. (2016: molecular phylogeny).

**Distribution:** S Canada, USA, Mexico (= distribution centre), C America to Panama, Caribbean Region, Colombia, Venezuela, Peru, Bolivia, E Asia (*Hosta*); widely cultivated throughout the world in suitable climates and often also naturalized.

The *Agavaceae* s.l. are a family of 12 genera and some 445 species. Most are adapted to semi-arid or arid conditions, and the majority are xeromorphic and somewhat to distinctly succulent rosette plants of semidesertic regions and drylands.

**Classification:** The genera placed in *Agavaceae* s.s. have a complicated classification history (Nyffeler & Eggli 2010). Up to the 1950ies, *Agave* and the closely related genera with inferior ovaries were placed in *Amaryllidaceae*, while *Yucca* and superficially similar genera with superior ovaries were classified in *Liliaceae*. At times, superficially similar xeromorphic taxa such as *Dracaena* or *Nolina* (now placed in *Ruscaceae* s.l.) were also included in *Agavaceae*, e.g. by Hutchinson (1934), Matuda & Piña Luján (1980), Rowley (1987) or Verhoek-Williams & Hess (2002).

In traditional classifications (e.g. Verhoek-Williams (1998)), *Agavaceae* s.s. are composed of 8 genera of mostly xerophytic to succulent species. In contrast to this narrow circumscription, already the early molecular phylogenies of Eguiarte & al. (1994), Bogler & Simpson (1995), Eguiarte (1995) and Bogler & Simpson (1996) showed a close relationship of *Agavaceae* s.s. with *Hosta* (traditionally classified as monogeneric *Hostaceae*; not succulent, Kubitzki (1998)), either as sister group, in a basal unresolved position, or nested within.

The inclusion of *Hosta* is also supported by cytological data (Tamura 1995) as well as embryological (Cave 1948), serological (Chupov & Kutivina 1981) and palynological data (Schulze 1984). *Hesperocallis* (monotypic *Hesperocalidaceae*; not succulent, from North America, treated as anomalous genus in *Hostaceae* by Kubitzki (1998: 260)) and *Chlorogalum* and related genera (traditionally classified as *Hyacinthaceae* subfam. *Chlorogaloideae*, Speta (1998)) are also associated with *Agavaceae* s.l. in various recent molecular phylogenies. According to the molecular phylogenies of

Seberg & al. (2012) and Steele & al. (2012). *Agavaceae* should be treated in a wide sense and include not only *Hosta*, but also *Anemarrhena* (monotypic *Anemarrheneaceae*; not succulent, from China and Korea, see Conran & Rudall (1998)), *Behnia* (monotypic *Behniaceae*; not succulent, from SE Africa, see Conran (1998a)) and *Herreria* (bitypic *Herreriaceae*; not succulent, from S America and Madagascar, see Conran (1998b)), although support for the various topologies is low. The most recent well-sampled study is that of Archibald & al. (2015). These authors found the *Chlorogaloideae* as unambiguous (though not monophyletic in the traditional circumscription) part of *Agavaceae*, confirming the earlier expressed views as well as the results of Pfosser & Speta (1999). *Behnia* and *Herreria*, however, remain unplaced in that phylogeny, and for the time being should either be included in an expanded *Anthericaceae*, or probably best be accepted as separate families in sister-group position (Petersen & al. 2006: Fig. 2).

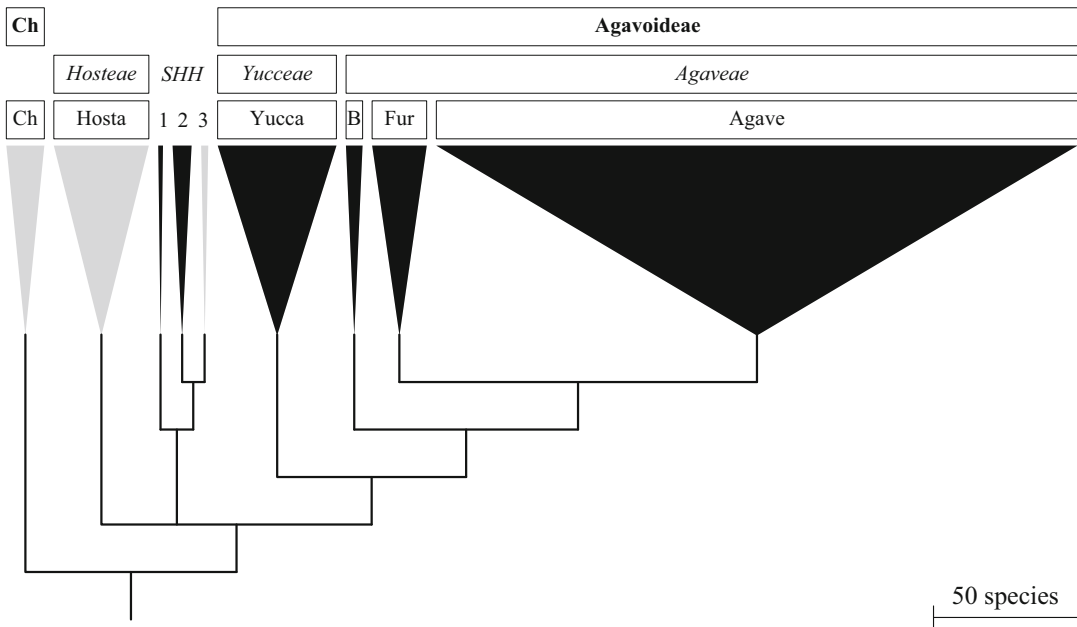
Whether the *Anthericaceae* should also be treated as part of *Agavaceae* s.l. has not yet been fully clarified. While Graham & al. (2006), Givnish & al. (2006) and Kim & al. (2010) prefer to include them in a further enlarged *Agavaceae* s.l., Pfosser & Speta (1999), Good-Avila & al. (2006), Bogler & al. (2006) and Smith & al. (2008) stress the lack of support for this and prefer to treat the *Anthericaceae* as separate family in sister-group position to *Agavaceae* s.l. This is also the position followed in this handbook.

There is no doubt that the *Agavaceae* s.l. belong to the higher core Asparagales, together with *Asparagaceae* s.s., *Anthericaceae*, *Hyacinthaceae* and *Ruscaceae*, to name just the families with succulent representatives. The families of the higher core Asparagales have recently been merged and treated as *Asparagaceae* s.l. (Janssen & Bremer 2004, Graham & al. 2006), and this classification is that advocated by APG (2009), and confirmed by APG (2016). *Asparagaceae* s.l. in that circumscription would be diagnostically circumscribed by racemose inflorescences (vs. umbellate inflorescences in the lower core Asparagales). Within the framework of such a classification, *Agavaceae* s.l. would be classified at the rank of subfamily as

*Agavoideae*. However, support for some of the proposed relationships is either low or unconfirmed in recent molecular phylogenies (e.g. Kim & al. (2010)). Moreover, accepting *Asparagaceae* in the very broad sense of APG does not provide improved insights into the phylogeny of the order, but is unnecessarily disruptive to established traditional classifications (Nyffeler & Egli 2010). Therefore, and in line with these authors and the recent textbook by Judd & al. (2016), *Agavaceae* in their new expanded circumscription is here treated as independent family. While Judd & al. (2016) also include the *Anthericaceae*, we maintain that support for this placement is insufficient, and accept *Anthericaceae* as separate family in this Handbook.

*Agavaceae* s.l. is sister to *Aphyllanthaceae* + *Themidaceae* according to Seberg & al. (2012), while Steele & al. (2012) found just *Aphyllanthaceae* (monotypic, not succulent, W Mediterranean) as the more likely sister group. This is confirmed by the plastid phylogenomic study of Givnish & al. (2018) who also found *Aphyllanthes* as most likely sister of *Agavaceae* (as *Agavoideae*, including *Anthericaceae*), but support is low. The clade age of the expanded *Agavaceae* has been estimated at a mere  $\pm 14.5$  mybp but could also be  $23.7 \pm 9.7$  mybp (Smith & al. 2008a). The monocot-wide plastid phylogenomic study of Givnish & al. (2018) found an age of 24.51 mybp for the split of the expanded *Agavaceae* from *Anthericaceae* (including *Herreria*). This is much younger than the age of  $\pm 35$  mybp given by Wikström & al. (2001) for the split of *Agave* from (*Behniaceae* + *Anthericaceae*). The major radiations in *Agave* (starting 7.8–10.1 mybp) and *Yucca* (starting 13–18 mybp) of crown-group *Agavaceae* (Good-Avila & al. 2006, Rocha & al. 2006) fall into a time of increasing desertification of North America. The origin of the family in its presently wide circumscription is supposed to have been in W North America (Bogler & al. 2006).

**Classification of crown group *Agavaceae*:** The crown group of *Agavaceae* is co-extensive with the “Agave+”-clade of Archibald & al. (2015) and is largely congruent with *Agavaceae* s.s. as covered in the first edition of this Handbook.



**Fig. 1** Summary phylogeny of *Agavaceae* s.l. mainly based on Archibald & al. (2015) (445 species total). Ch = *Chlorogaloideae*, 1 = *Hesperoyucca*, 2 = *Hesperaloe*;

3 = *Schoenolirion*; B = *Beschorneria*, Fur = *Furcraea*; SHH = SHH clade. (Copyright: U. Eggli)

Archibald & al. (2015) show this clade in a trichotomy with *Hosta* on the one hand, and their SHH-clade (*Hesperaloe* and *Hesperoyucca* plus the non-succulent *Schoenolirion*). – Fig. 1.

Although the various molecular phylogenies cited above are not in full agreement about the topology of the genera that make up the “Agave+”-clade, there are good indications that *Yucca* is the sister of an *Agave*-clade that is composed of *Beschorneria* as sister to *Agave* + *Furcraea*. The remaining genera traditionally accepted in *Agavaceae*, i.e. *Manfreda*, *Polianthes* and *Prochnyanthes*, are all derived from within *Agave* s.s. (Bogler & al. 2006, Rocha & al. 2006). They cannot be separated from *Agave* s.s. on molecular grounds, and if they were accepted as separate genera, several clades within *Agave* s.s. would have to be recognized as separate genera as well to attain a monophyletic classification. Such a classification appears clearly unwarranted before the background of the frustratingly low sequence variation for *Agave* (Bogler & al. 2006) and the segregate *Manfreda* (Ritchie 2014, almost no variation at all amongst 19 specimens studied).

In addition, *Manfreda* can be successfully hybridized with *Agave* (= ×*Mangave*) (Klein 2010) and *Polianthes* (= ×*Polifreda*) (Lindstrom 2006a, Lindstrom 2006b, Ritchie & Lindstrom 2014). We interpret this as additional support for subsuming these genera under *Agave*. The mesomorphic characters exhibited by the species of *Manfreda*, *Polianthes* and *Prochnyanthes* have thus evolved secondarily from more arid-adapted evergreen taxa. The study of McKain & al. (2016) arrives at the same topology, but is overall of limited value since only single terminals were analyzed.

*Agavaceae* s.l. can thus conveniently be classified into the following monophyletic clades – Fig. 1:

- **Chlorogaloideae** Lotsy 1911 (= “core Chlorogaloideae” of Archibald & al. (2015); incl. *Hesperocallidaceae* Moore & Reveal 2012); Bulbous herbs; **L** keeled; **Inf** (double) racemes; **Tep** white, greenish or blue; **Ov** superior, with 2 or numerous (*Hesperocallis*) ovules per locule; **Sti** 3-lobed; **Se** pear-shaped to globose or ovoid; n = 15, 17, 18, 24 (*Hesperocallis*), 26, 30, bimodal in

*Hesperocallis* (5–6 large, 18–19 small chromosomes). — 16 species (not succulent) in the 4 genera *Camassia*, *Chlorogalum*, *Hastingsia* and *Hesperocallis* from N America.

- **Hosta-clade** (= *Hosteae* Traub 1972; = *Hostaceae* B. Mathew 1988): Rhizomatous, usually deciduous herbs; **L** linear-lanceolate to cordate-ovate, often long-petiolate, distinctly veined; **Inf** bracteate racemes, often  $\pm$  secund; **Tep** white, lavender or blue; **Fil** declinate; **Ov** superior; **Se** flattened, winged;  $x = 30$ , bimodal with 4 large, 2 medium and 24 small chromosomes. — Only genus *Hosta* ( $\pm 40$  species, not succulent) from Japan, China, Korea and Russia.
- **SHH-clade** (Archibald & al. 2015): **Ov** superior; **Sti**  $\pm$  capitate to slightly lobed. — This clade is morphologically heterogeneous:
  - *Schoenolirion*: Perennial shortly rhizomatous herbs with or without bulb; **L** grass-like, flat, without keel; **Inf** to 1.5 m; **Tep** white or yellow; **Se**  $\pm$  globose;  $x = 12, 15, 16, 24(?)$ . — 3 species (not succulent) from N America.
  - *Hesperaloe* + *Hesperoyucca*: Perennial xerophytes with or without (*Hesperoyucca*) rhizomes and with monocarpic rosettes; **L** few to very numerous, tough, more or less to distinctly succulent, fibrous, rounded or keeled on both faces; **Inf** to 4.5 m, racemose-paniculate; **Tep** greenish-white, white, red to salmon or yellow; **Se** flat;  $x = 30$ , bimodal. — Composed of the genera *Hesperaloe* and *Hesperoyucca*, treated below in this Handbook.
- **Agavoideae** = “*Agave* + clade” of Archibald & al. (2015): Mostly evergreen and **L** mostly fibrous and succulent, rarely hardly succulent and xerophytic, or herbaceous-succulent and  $\pm$  deciduous; **Ov** superior or inferior. — Divisible in 2 subclades:
  - Tribe *Yuceae* Bartlett 1930 (incl. subfam. *Yuccoideae* Kosteletzky 1831; incl. *Yuccaceae* J. Agardh 1858): **L** xeromorphic, fibrous, not strongly succulent (except *Y. endlichiana*); **L** margins mostly filiferous, rarely serrulate; **Fl** pendent, actinomorphic; **Tep** free; **Ov** superior; **Anth** sagittate to

hastate. — Only genus: *Yucca*, treated below in this Handbook.

- Tribe *Agaveae* (incl. tribe *Poliantheae* Hutchinson 1934): **L** mostly xerophytic, evergreen and succulent, rarely deciduous and herbaceous and soft; **L** margins entire and often with teeth, or rarely filiferous; **Fl** pendent or  $\pm$  upright, actinomorphic or slightly zygomorphic; **Tep** free or  $\pm$  fused to form a tube; **Ov** inferior; **Anth** oblong to linear. — Consists of the genera *Agave*, *Beschorneria* and *Furcraea*, all treated below in this Handbook.

**Cytology:** The striking bimodal karyotype (McKelvey & Sax 1933) with  $x = 30$  represents a major distinguishing feature for *Agavaceae* s.s. Similar, but less pronounced bimodal karyotypes are present in *Hesperocallis* ( $x = 24$ ) and *Hosta* ( $x = 30$ ), but not in the other members of the *Agavaceae* s.l. According to McKain & al. (2012) the bimodal karyotype is due to two independent palaeopolyploidization events (identified as whole-genome duplication by McKain & al. (2016)), one predating the last common ancestor of *Agave* and *Hosta*, the other in the lineage that includes *Anthericaceae*. Subsequently, the bimodal karyotype was lost twice independently, once in the *Hesperocallis* - *Chlorogalum* - *Camassia* clade, once in *Schoenolirion*. Polyploidy is common esp. in species of *Agave* subgen. *Agave*. Ploidy ranges from diploid to octoploid, including (sterile) triploids (e.g. *A. angustifolia* var. *letonae*) and pentaploids (e.g. *A. sisalana*) (Robert & al. 2008). Polyploidization, at least in *Agave*, is likely of a comparatively young age (Robert & al. 2008) and probably linked to increased vegetative propagation and/or selected for by the conditions of an increasingly arid and harsh environment. Robert & al. (2008) did not find any dysploid changes, and early chromosome counts that deviate from the basal  $x = 30$  are likely observation errors.

**Succulence:** Leaf succulence in varying degrees prevails in the family, but stem succulence in the form of thickened rhizomes, pachycaulous stems, or subterranean corms, also occurs. The strongly succulent leaves of many *Agave* species show



well-developed tissue succulence, visible in cross sections as a narrow peripheral band of chlorenchyma, and voluminous chlorophyll-free water storage parenchyma (hydrenchyma) with interspersed scattered fibrous vascular bundles (see Müller (1909) for illustrations). The demarcation between chlorenchyma and hydrenchyma is not very strict. Already Bray (1903) found the hydrenchyma to contain air spaces, which cause the whitish colour of this tissue.

The massive trunks of stem-forming *Yucca* species such as *Y. gigantea* are reminiscent in architecture to those of *Beaucarnea* (*Ruscaceae*) and consist of numerous vascular bundles dispersed in a matrix of ground tissue. Within the outer cortex, a secondary thickening meristem develops (Fisher 1975, Stevenson 1980, Carlquist 2012: 113).

**Physiology:** Crassulacean Acid Metabolism (CAM) is almost always present in *Agave* s.s., *Furcraea* and *Hesperaloe*. *Yucca* is heterogenous with respect to photosynthetic pathway, with constitutive CAM in the species of sect. *Yucca*, and C3 in the species of the other sections (Nobel 1988, Gibson 1996: 118, Sayed 2001, Heyduk & al. 2016). *Agave amica* (*Polianthes tuberosa*) and *Beschorneria* appear to use the C3 pathway (Heyduk & al. 2016). Data for *Hesperoyucca* is ambiguous: Winter & Smith (1996) report CAM, but Heyduk & al. (2016) indicate C3. The non-succulent species of the former *Chlorogaloideae*, *Hosta* and the SHH-clade also use the C3 pathway (Heyduk & al. 2016). Heyduk & al. (2016) argue for 3 independent origins of CAM. Olivares & Medina (1990) report that CAM signature varies over the length of the leaves as well as between the leaves of a rosette in *Furcraea acaulis* (as *F. humboldtiana*); CAM is least pronounced in the vertically upright youngest leaves, and in the leaf base of older leaves.

**Chemistry:** Steroidal saponins are probably universally present throughout the *Agavaceae* s.l., sometimes in considerable concentrations. Simmons-Boyce & Tinto (2007) and Sidana & al. (2016) present an overview of steroidal saponins and saponinins found in species of *Agave*,

*Furcraea* and *Yucca*. The most common compound classes are furastanes, furospirostanes, and spirostanes. Some of these compounds show considerable biological activity, including anti-cancer effects, and some are used as starting material for the biosynthesis of steroidal hormones.

**Ecology:** Many species of *Agave* and *Yucca* as well as *Hesperoyucca* are landscape-dominating elements throughout the arid and semi-arid regions of Mexico and the SW, S, and SE USA. Some species form vast populations locally and these are a spectacular sight when mass flowering occurs.

Pollination systems vary from very specialized to generalist. The most striking specialized pollination system is found in *Yucca* and *Hesperoyucca*, with a closely knit mutualistic relationship between the pollinating yucca moths and *Yucca*, sometimes described as “nursery pollination” (Svensson & al. 2011). Althoff (2016) and the chapter on *Yucca* in this Handbook provide overviews of extant knowledge.

In *Agave*, bats and hawkmoths during the night as well as hummingbirds and other birds and/or bees during the day are known as pollinators, depending on the species. The floral syndromes displayed are not always predictive of the main pollinators (e.g. Silva-Montellano & Eguiarte (2003a) for *A. lechuguilla*, Riffell & al. (2008a) and Riffell & al. (2008b) for the generalist pollination systems of *A. palmeri* and *A. chrysantha*). Flowering *A. palmeri* form a veritable “nectar corridor” and its geographical range closely overlaps the range of its migratory bat pollinators. In C Mexico, *Agave* and bats appear to mutualistically depend on each other, while in N Mexico and SW USA, the interdependence is less strict (Riffell & al. 2008b).

**Ethnobotany:** Many species esp. of *Agave* and to a lesser extent of *Yucca* have been used for food, beverage and fibre since prehistoric times by numerous local ethnic groups. The use of these plants can be dated back for at least 9000 years (Gentry 1982: 5) and has continued for centuries among many different and unrelated cultures (Hodgson 2001: 14–51).

Gentry (1982: 3–24) termed the intimate relationship between these cultures and the plants “man-*Agave* symbiosis”.

There is evidence that some species of *Agave* (e.g. *A. parryi*) were extensively cultivated in prehistorical times for both food and fibre (Parker & al. 2014), leading to domestication of selected variants. Indeed, many relict populations continue to exist at ancient dwelling sites, and domestication of *Agave* probably started several 1000 years BCE. *A. murphyi* is one of several ancient cultigens, and clones persist at prehistorically inhabited sites as “living archaeological assemblages preserved in their cultural landscape for more than five centuries after their presumed cultivation” (Hodgson 2001).

Several species of *Agave* are used to manufacture distilled alcoholic beverages, and are the basis of the Mexican pulque, mezcal and tequila industries. Enormous areas are devoted to this purpose: Chagoya-Méndez (2004) (cited from Martínez-Gutiérrez & al. (2013)) report an area of 15.500 hectares just for the Mexican state of

Oaxaca, planted with *A. angustifolia* and yielding an annual 2.9 million litres of mezcal.

A number of species of *Agave* and *Furcraea* continue to be important sources of fibre, and are cultivated in large-scale plantations up to today in suitable climates throughout the world. Another commodity obtained from species of *Agave* is agave syrup.

**Horticulture:** Numerous taxa of *Agavaceae* s.s. have considerable horticultural potential (see Starr (2012) and Moore (2016) for *Agave*, Boeuf (2007) and Ondrovic & Ondrovic (2016) for *Yucca*, as well as the more general works on the horticultural use of perennial succulent monocots by Irish & Irish (2000) or Jacquemin (2000) and Jacquemin (2001)). Many species such as *A. americana* are frequently planted as ornamentals in broad-scale landscaping in suitable frost-free regions, esp. with Mediterranean climates. Numerous cultivars are available in the trade, including variously variegated forms (for *Yucca*, see, e.g. Boeuf & al. (2010)). Numerous species

**Key to the genera with succulents**

<b>1a</b>	<b>L</b> margins often filiferous, rarely serrulate but never toothed; <b>Fl</b> pendent, actinomorphic; <b>Tep</b> free; <b>Anth</b> sagittate to hastate; <b>Ov</b> superior	2
<b>1b</b>	<b>L</b> margins entire and without or with (often strong) teeth, rarely filiferous; <b>Fl</b> pendent or ± upright, actinomorphic or slightly zygomorphic; <b>Tep</b> free or usually forming a ± long tube; <b>Anth</b> oblong to linear; <b>Ov</b> inferior	4
<b>2a</b>	<b>Ros</b> stemless or with short to massive stem and then arborescent; <b>L</b> margins entire or filiferous, <b>L</b> epidermis without papillate cells; <b>Fl</b> usually white or whitish and wax-like; <b>Fil</b> free, apically swollen and outcurved, sometimes puberulent; <b>Sty</b> thickened with 3 short branches; <b>Sti</b> 3 with 2 lobes each (S Canada to Guatemala)	<i>Yucca</i>
<b>2b</b>	<b>Ros</b> stemless; <b>L</b> margins filiferous or finely serrulate, <b>L</b> epidermis with papillate cells over the veins; <b>Fil</b> adnate to the base or lower parts of the tepals, not swollen, straight, glabrous; <b>Sty</b> short and slender; <b>Sti</b> distinctly capitate and fringed with papillae	3
<b>3a</b>	Habit ± grass-like with succulent leaves; <b>Ros</b> few-leaved; <b>L</b> margins filiferous; <b>Tep</b> connivent and <b>Fl</b> therefore narrowly campanulate, whitish to reddish (S USA (Texas), N and C Mexico)	<i>Hesperaloe</i>
<b>3b</b>	Habit <i>Yucca</i> -like; <b>Ros</b> many-leaved; <b>L</b> margins finely serrulate; <b>Tep</b> openly spreading, whitish (SW USA, NW Mexico)	<i>Hesperoyucca</i>
<b>4a</b>	<b>L</b> margins entire or toothed; <b>Fl</b> pendent, actinomorphic; <b>Tep</b> (almost) free; <b>Fil</b> filiform or basally swollen; <b>Sty</b> swollen and with 3 basal ridges, distally abruptly narrowed	5
<b>4b</b>	<b>L</b> margins entire or toothed, or filiferous; <b>Fl</b> ± upright, actinomorphic or slightly zygomorphic; <b>Tep</b> basally fused to form a ± long tube; <b>Fil</b> filiform; <b>Sty</b> basally not swollen (S USA to Colombia and Venezuela, Caribbean region)	<i>Agave</i>
<b>5a</b>	Plants polycarpic; <b>L</b> margins entire or minutely denticulate; <b>Tep</b> free but connivent and forming a tube-like structure, reddish to yellowish; <b>Fil</b> filiform (Mexico)	<i>Beschorneria</i>
<b>5b</b>	Plants monocarpic or polycarpic when branched; <b>L</b> margins mostly toothed; <b>Tep</b> openly spreading, whitish to greenish; <b>Fil</b> basally swollen (Mexico to Bolivia, Caribbean region)	<i>Furcraea</i>

have become naturalized outside their native occurrence, and today form an important feature of the landscape, often together with species of *Opuntia* (esp. *O. ficus-indica*, *Cactaceae*), which has a similar New-World origin.

## References

- Althoff, D. M. (2016) Specialization in the *Yucca*-*Yucca* Moth obligate pollination mutualism: A role for antagonism? *Amer. J. Bot.* 103(10): 1803–1809, map, ills. <https://doi.org/10.3732/ajb.1600053>.
- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>.
- APG (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181(1): 1–20. <https://doi.org/10.1111/boj.12385>.
- Archibald, J. K. [ & al. 2015], Kephart, S. R., Theiss, K. E., Petrosky, A. L. & Culley, T. M. (2015) Multilocus phylogenetic inference in subfamily *Chlorogaloideae* and related genera of *Agavaceae* — Informing questions in taxonomy at multiple ranks. *Molec. Phylogen. Evol.* 84: 266–283, ills., map. <https://doi.org/10.1016/j.ympev.2014.12.014>.
- Boeuf, T. (2007) *Yucca* & Co. Winterharte Wüstengärten in Mitteleuropa anlegen und pflegen. Berlin (DE): Medemia.
- Boeuf, T. [ & al. 2010], Heim, A. & Weissbeck, S. (2010) *Faszination bunt. Die Welt der panaschierten Yuccas*. Münster (DE): Natur und Tier-Verlag GmbH.
- Bogler, D. J. & Simpson, B. B. (1995) A chloroplast DNA study of the *Agavaceae*. *Syst. Bot.* 20(2): 191–205. <http://www.jstor.org/stable/2419449>
- Bogler, D. J. & Simpson, B. B. (1996) Phylogeny of *Agavaceae* based on ITS rDNA sequence variation. *Amer. J. Bot.* 83(9): 1225–1235. <http://www.jstor.org/stable/2446206>
- Bogler, D. J. [ & al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on ndhF, rbcL, and ITS sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>.
- Bray, W. L. (1903) The tissues of some plants of the Sotol region. *Bull. Torrey Bot. Club* 30(11): 621–633, ills. <http://biodiversitylibrary.org/page/713368>
- Carlquist, S. (2012) Monocot xylem revisited: New information, new paradigms. *Bot. Rev. (Lancaster)* 78: 87–153, ills. <https://doi.org/10.1007/s12229-012-9096-1>.
- Cave, M. S. (1948) Sporogenesis and embryo sac development of *Hesperocallis* and *Leucocrinum* in relation to their systematic position. *Amer. J. Bot.* 35(6): 343–349. <https://doi.org/10.2307/2437748>.
- Chagoya-Méndez, V. M. (2004) Diagnóstico de la cadena productiva del sistema producto maguey-mezcal. Oaxaca (MX): Secretaría de Agricultura Ganadería, Desarrollo Rural, Pesca y Alimentación SAGARPA, Delegación Oaxaca.
- Chupov, V. S. & Kutiavina, N. G. (1981) [Russian:] Serological studies in the order *Liliales*. *Bot. Zhurn. (Moscow & Leningrad)* 66: 75–81.
- Conran, J. G. (1998a) *Behmiaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 146–148, ills. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_18](https://doi.org/10.1007/978-3-662-03533-7_18).
- Conran, J. G. (1998b) *Herreriaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 253–255, ills. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_33](https://doi.org/10.1007/978-3-662-03533-7_33).
- Conran, J. G. & Rudall, P. (1998) *Anemarrhenaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 111–114, ills. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_12](https://doi.org/10.1007/978-3-662-03533-7_12).
- Dahlgren, R. M. T. [ & al. 1985], Clifford, H. T. & Yeo, P. F. (1985) *The families of the Monocotyledons. Structure, evolution, and taxonomy*. Berlin, Heidelberg (DE) etc.: Springer-Verlag. <https://doi.org/10.1007/978-3-642-61663-1>.
- Eguiarte, L. E. (1995) Hutchinson (*Agavales*) vs. Huber y Dahlgren (*Asparagales*). Análisis moleculares sobre filogenia y evolución de la familia *Agavaceae* sensu Hutchinson dentro de las monocotiledóneas. *Bol. Soc. Bot. México* 56: 45–56. <https://doi.org/10.17129/botsci.1463>.
- Eguiarte, L. E. [ & al. 1994], Duvall, M. R., Learn, G. H. Jr., & Clegg, M. T. (1994) The systematic status of the *Agavaceae* and *Nolinaceae* and related *Asparagales* in the monocotyledons: An analysis based on the rbcL gene sequence. *Bol. Soc. Bot. México* 54: 36–56. <https://doi.org/10.17129/botsci.1427>.
- Fisher, J. B. (1975) Eccentric secondary growth in *Cordylina* and other *Agavaceae* (Monocotyledonae) and its correlation with auxin distribution. *Amer. J. Bot.* 62: 292–302. <https://doi.org/10.1002/j.1537-2197.1975.tb12356.x>.
- Gentry, H. S. (1982) *Agaves of Continental North America*. Tucson (US): University of Arizona Press.
- Gibson, A. C. (1996) Structure-function relations of warm desert plants. Berlin (DE) etc.: Springer. <https://doi.org/10.17129/botsci.1427>.
- Givnish, T. J. [ & al. 2006], Pires, J. C., Graham, S. W., McPherson, M. A., Prince, L. M., Patterson, T. B., Rai, H. S., Roalson, E. H., Evans, T. M., Hahn, W. J., Millam, K. C., Meerow, A. W., Molvray, M., Kores, P. J., O'Brien, H. E., Hall, J. C., Kress, W. J. & Sytsma, K. J. (2006) Phylogenetic relationship of Monocots based on the highly informative plastid gene ndhF: Evidence for widespread concerted convergence. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 28–51. <https://doi.org/10.5642/aliso.20062201.04>.

- Givnish, T. J. [et al. 2018], Zuluaga, A., Spalink, D., Soto Gomez, M., Lam, V. K. Y., Saarela, J. M., Sass, C., Iles, W. J. D., Lima de Sousa, D. J., Leebens-Mack, J., Pires, J. C., Zomlefer, W. B., Gandolfo, M. A., Davis, J. I., Stevenson, D. W., dePamphilis, C., Specht, C. D., Graham, S. W., Barrett, C. F. & Ané, C. (2018) Monocot plastid phylogenomics, timeline, net rates of species diversification, the power of multi-gene analyses, and a functional model for the origin of monocots. *Amer. J. Bot.* 105(11): 1–23. <https://doi.org/10.1002/ajb2.1178>.
- Good-Avila, S. V. [et al. 2006], Souza, V., Gaut, B. S. & Eguiarte, L. E. (2006) Timing and rate of speciation in *Agave* (*Agavaceae*). *Proc. Nation. Acad. Sci. USA* 103(24): 9124–9129. <https://doi.org/10.1073/pnas.0603312103>.
- Graham, S. W. [et al. 2006], Zgurski, J. M., McPherson, M. A., Cherniawsky, D. M., Saarela, J. M., Horne, E. F. C., Smith, S. Y., Wong, W. A., O'Brien, H. E., Biron, V. L., Pires, J. C., Olmstead, R. G., Chase, M. W. & Rai, H. S. (2006) Robust inference of Monocot deep phylogeny using an expanded multigene plastid data set. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 3–21. <https://doi.org/10.5642/aliso.20062201.02>.
- Halpin, K. M. & Fishbein, M. (2013) A chloroplast phylogeny of *Agavaceae* subfamily *Chlorogaloideae*: Implications for the tempo of evolution on serpentine soils. *Syst. Bot.* 38(4): 996–1011, ills., map. <https://doi.org/10.1600/036364413X674850>.
- Heyduk, K. [et al. 2016], McKain, M. R., Lalani, F. & Leebens-Mack, J. (2016) Evolution of a CAM anatomy predates the origins of Crassulacean Acid Metabolism in the *Agavoideae* (*Asparagaceae*). *Molec. Phylogen. Evol.* 105: 102–113, ills. <https://doi.org/10.1016/j.jympev.2016.08.018>.
- Hodgson, W. C. (2001) *Food plants of the Sonoran Desert*. Tucson (US): University of Arizona Press.
- Hutchinson, J. (1934) *The families of flowering plants*. Vol. 2. London (GB): MacMillan.
- Irish, M. & Irish, G. (2000) *Agaves, Yuccas and related plants. A gardener's guide*. Portland (US): Timber Press.
- Jacquemin, D. (2000) *Les succulentes ornementales. Agavacées pour les climats méditerranéens. Beschneria [sic!], Calibanus, Cordylina, Dasyllirion, Doryanthes, Dracaena, Furcraea, Hesperaloe, Nolina, Phormium, Yucca*. Marly-le-Roi (FR): Editions Champflour.
- Jacquemin, D. (2001) *Les succulentes ornementales. Agavacées pour les climats méditerranéens. Agave, Manfreda, Polianthes, Prochnyanthes, Sansevieria*. Marly-le-Roi (FR): Editions Champflour.
- Janssen, T. & Bremer, K. (2004) The age of major monocot groups inferred from 800+ rbcL sequences. *Bot. J. Linn. Soc.* 146(4): 385–398. <https://doi.org/10.1111/j.1095-8339.2004.00345.x>.
- Judd, W. S. [et al. 2016], Campbell, C. S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J. (2016) *Plant systematics: A phylogenetic approach*. Ed. 4. Sunderland (US): Sinauer Associates.
- Kim, J.-H. [et al. 2010], Kim, D.-K., Forest, F., Fay, M. F. & Chase, M. W. (2010) Molecular phylogenetics of *Ruscaceae sensu lato* and related families (Asparagales) based on plastid and nuclear DNA sequences. *Ann. Bot.* (Oxford), n.s. 106: 775–790. <https://doi.org/10.1093/aob/mcq167>.
- Klein, D. (2010)  $\times$ *Mangave* 'Bloodspot' und  $\times$ *Mangave* 'Macho Mocha'. *Kakt. and Sukk.* 61(8): 211–215, ills.
- Krause, K. (1930) *Liliaceae*. In: Engler, A. & Prantl, K. (eds.): *Die natürlichen Pflanzenfamilien*, ed. 2, 15a: 227–385, key, ills. Leipzig (DE): W. Engelmann.
- Kubitzki, K. (1998) *Hostaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 256–258, ills. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_34](https://doi.org/10.1007/978-3-662-03533-7_34).
- Lindstrom, J. T. (2006a) Intergeneric hybrids between *Polianthes* and *Manfreda*. In: Ranney, T. G. (ed.): *Plant breeding and evaluation section, SNA Research Conference 51*: 599–601. <http://sna.org/Resources/Documents/06resprocsec12.pdf>
- Lindstrom, J. T. (2006b) Plant profile. *Manfreda maculosa* (L.) Salisb. ex Rose  $\times$  *Polianthes tuberosa* L. Arkansas Re-Leaf Newsletter. 7: 2.
- Martínez-Gutiérrez, G. A. [et al. 2013], Íñiguez-Covarrubias, G., Ortiz-Hernández, Y. D., López-Cruz, J. Y. & Bautista Cruz, M. A. (2013) Tiempos de apilado del bagazo del maguey mezcalero y su efecto en las propiedades del compost para sustrato de tomate. *Revista Int. Contam. Amb.* 29(3): 209–216. <http://proyecteuclid.redalyc.org/articulo.oa?id=37028276007>
- Matiz, A. [et al. 2013], Miotto, P. T., Yepes Mayorga, A., Freschi, L. & Mercier, H. (2013) CAM photosynthesis in Bromeliads and Agaves: What can we learn from these plants? In: Dubinsky, Z. (ed.): *Photosynthesis*; pp. 91–134. Rijeka (HR): InTech. <https://doi.org/10.5772/56219/>.
- Matuda, E. & Piña Luján, I. (1980) *Las plantas mexicanas del género Yucca*. Toluca (MX): Miscelanea Estado de México.
- McKain, M. R. [et al. 2012], Wickett, N., Zhang, Y., Ayyampalayam, S., McCombie, W. R., Chase, M. W., Pires, J. C., dePamphilis, C. W. & Leebens-Mack, J. (2012) Phylogenomic analysis of transcriptome data elucidates co-occurrence of a paleopolyploid event and the origin of bimodal karyotypes in *Agavoideae* (*Asparagaceae*). *Amer. J. Bot.* 99(2): 397–406, ills. <https://doi.org/10.3732/ajb.1100537>.
- McKain, M. R. [et al. 2016], McNeal, J. R., Kellar, P. R., Eguiarte, L. E., Pires, J. C. & Leebens-Mack, J. (2016) Timing of rapid diversification and convergent origins of active pollination within *Agavoideae* (*Asparagaceae*). *Amer. J. Bot.* 103(10): 1717–1729. <https://doi.org/10.3732/ajb.1600198>.
- McKelvey, S. D. & Sax, K. (1933) Taxonomic and cytological relationships of *Yucca* and *Agave*. *J. Arnold Arbor.* 14: 76–81. <https://www.jstor.org/stable/43780651>
- Moore, J. (2016) *Aloes & Agaves in cultivation*. Solana Beach (US): Solana Succulents.
- Müller, C. (1909) Beiträge zur vergleichenden Anatomie der Blätter der Gattung *Agave* und ihrer Verwertung für



- die Unterscheidung der Arten. Bot. Zeitung (Leipzig) 67: 93–139, ills., tt. IV–V. <https://biodiversitylibrary.org/page/33628820>
- Nobel, P. S. (1988) Environmental biology of agaves and cacti. Cambridge (GB) etc.: Cambridge University Press.
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>.
- Olivares, E. & Medina, E. (1990) Carbon dioxide exchange, soluble carbohydrates and acid accumulation in a fructan accumulating plant: *Fourcroya humboldtiana* Trel. *J. Exp. Bot.* 41(226): 579–586. <https://doi.org/10.1093/jxb/41.5.579>.
- Ondrovic, R. & Ondrovic, S. (2016) *Yucca*. Vorkommen, Bestimmen und Pflegen aller Arten aus Nordamerika. Remagen-Oberwinter (DE): Verlag Kessel.
- Parker, K. C. [et al. 2014], Trapnell, D. W., Hamrick, J. L. & Hodgson, W. C. (2014) Genetic and morphological contrasts between wild and anthropogenic populations of *Agave parryi* var. *huachucensis* in south-eastern Arizona. *Ann. Bot. (Oxford)*, n.s. 113(6): 939–952, ills., map. <https://doi.org/10.1093/aob/mcu016>.
- Petersen, G. [et al. 2006], Seberg, O., David, J. I. & Stevenson, D. W. (2006) RNA editing and phylogenetic reconstruction in two monocot mitochondrial genes. *Taxon* 55(4): 871–886. <https://doi.org/10.2307/25065682>.
- Pfossner, M. F. & Speta, F. (1999) Phylogenetics of *Hyacinthaceae* based on plastid DNA sequences. *Ann. Missouri Bot. Gard.* 86(4): 852–875. <https://doi.org/10.2307/2666172>.
- Riffell, J. A. [et al. 2008a], Alarcón, R., Abrell, L., Davidowitz, G., Bronstein, J. L. & Hildebrand, J. G. (2008) Behavioral consequences of innate preferences and olfactory learning in hawkmoth—flower interactions. *Proc. Nation. Acad. Sci. USA* 105(9): 3404–3409, ill. <https://doi.org/10.1073/pnas.0709811105>.
- Riffell, J. A. [et al. 2008b], Alarcón, R. & Abrell, L. (2008) Floral trait associations in hawkmoth-specialized and mixed pollination systems. *Commun. Integr. Biol.* 1(1): 6–8, ill. <https://doi.org/10.4161/cib.1.1.6350>
- Ritchie, W. (2014) An assessment of CBOL plant DNA barcodes in the genus *Manfreda* Salisb. (*Asparagaceae*) for utility in species identification and phylogenetic studies. *Bradleya* 32: 172–179, ill. <https://doi.org/10.25223/brad.n32.2014.a9>.
- Ritchie, W. & Lindstrom, J. T. (2014) *×Polifreda* ‘Lindstrom’, a cross between False Aloe and Mexican Tuberose. *J. Environm. Hort.* 32(1): 51–53, ill. <http://hrijournal.org/doi/full/10.24266/0738-2898.32.1.51>.
- Robert, M. L. [et al. 2008], Lim, K. Y., Hanson, L., Sanchez-Teyer, F., Bennett, M. D., Leitch, A. R. & Leitch, I. J. (2008) Wild and agronomically important *Agave* species (*Asparagaceae*) show proportional increases in chromosome number, genome size, and genetic markers with increasing ploidy. *Bot. J. Linn. Soc.* 158(2): 215–222, ill. <https://doi.org/10.1111/j.1095-8339.2008.00831.x>.
- Rocha, M. [et al. 2006], Good-Ávila, S. V., Molina-Freaner, F., Arita, H. T., Castillo, A., García-Mendoza, A., Silva-Montellano, A., Gaut, B. S., Souza, V. & Eguiarte, L. E. (2006) Pollination biology and adaptive radiation of *Agavaceae*, with special emphasis on the genus *Agave*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 329–344, maps. <https://doi.org/10.5642/aliso.20062201.27>.
- Rowley, G. D. (1987) Caudiciform and pachycaul succulents. Pachycauls, bottle-, barrel- and elephant-trees and their kin: A collector’s miscellany. Mill Valley (US): Strawberry Press.
- Sayed, O. H. (2001) Crassulacean Acid Metabolism 1975–2000, a check list. *Photosynthetica* 39(3): 339–352. <https://doi.org/10.1023/A:1020292623960>.
- Schulze, W. (1984) Beiträge zur Taxonomie der Liliifloren: XII. Der Umfang der *Agavaceae*. *Wiss. Z. Friedrich-Schiller-Univ. Jena, Math.-Naturwiss. Reihe* 32(6): 965–979, ills., maps.
- Seberg, O. [et al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ill. <https://doi.org/10.3732/ajb.1100468>.
- Sidana, J. [et al. 2016], Singh, B. & Sharma, O. P. (2016) Saponins of *Agave*: Chemistry and bioactivity. *Phytochemistry* 130: 22–46. <https://doi.org/10.1016/j.phytochem.2016.06.010>.
- Silva-Montellano, A. & Eguiarte, L. E. (2003a) Geographic patterns in the reproductive ecology of *Agave lechuguilla* (*Agavaceae*) in the Chihuahuan Desert. I. Floral characteristics, visitors, and fecundity. *Amer. J. Bot.* 90(3): 377–387, map, ill., diags. <https://doi.org/10.3732/ajb.90.3.377>.
- Simmons-Boyce, J. L. & Tinto, W. F. (2007) Steroidal saponins and sapogenins from the *Agavaceae* family. *Nat. Prod. Commun.* 2(1): 99–114.
- Smith, C. I. [et al. 2008], Pellmyr, O., Althoff, D. M., Balcázar-Lara, M., Leebens-Mack, J. & Segraves, K. A. (2008) Pattern and timing of diversification in *Yucca* (*Agavaceae*): Specialized pollination does not escalate rates of diversification. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 275: 249–258. <https://doi.org/10.1098/rspb.2007.1405>.
- Speta, F. (1998) *Hyacinthaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 261–285, ill., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_35](https://doi.org/10.1007/978-3-662-03533-7_35).
- Starr, G. (2012) *Agaves. Living sculptures for landscapes and containers*. Portland (US)/London (GB): Timber Press.
- Steele, P. R. [et al. 2012], Hertweck, K. L., Mayfield, D., McKain, M. R., Leebens-Mack, H. & Pires, J. C. (2012) Quality and quantity of data recovered from massively

- parallel sequencing: Examples in Asparagales and Poaceae. *Amer. J. Bot.* 99(2): 330–348. <https://doi.org/10.3732/ajb.1100491>.
- Stevenson, D. W. (1980) Radial growth in *Beaucarnea recurvata*. *Amer. J. Bot.* 67(4): 476–489. <http://www.jstor.org/stable/2442287>
- Svensson, G. P. [ & al. 2011], Pellmyr, O. & Raguso, R. A. (2011) Pollinator attraction to volatiles from virgin and pollinated host flowers in a *Yucca* / moth obligate mutualism. *Oikos* 120(10): 1577–1583. <https://doi.org/10.1111/j.1600-0706.2011.19258.x>.
- Tamura, M. N. (1995) A karyological review of the orders *Asparagales* and *Liliales* (*Monocotyledoneae*). *Feddes Repert.* 106(1–2): 83–111. <https://doi.org/10.1002/fedr.19951060118>.
- Verhoek-Williams, S. (1998) *Agavaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 60–70, ills., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_8](https://doi.org/10.1007/978-3-662-03533-7_8).
- Verhoek-Williams, S. & Hess, W. J. (2002) *Agavaceae*. In: Flora of North America north of Mexico; 26: 413–465, ills., keys. New York (US: NY)/Oxford (GB): Oxford University Press.
- Wikström, N. [ & al. 2001], Savolainen, V. & Chase, M. W. (2001) Evolution of the Angiosperms: Calibrating the family tree. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 268: 2211–2220. <https://doi.org/10.1098/rspb.2001.1782>.
- Winter, K. & Smith, J. A. C. (eds.) (1996) *Crassulacean Acid Metabolism. Biochemistry, ecophysiology and evolution*. Berlin (DE) etc.: Springer. <https://doi.org/10.1007/978-3-642-79060-7>.





## Agave AGAVACEAE

J. Thiede

**Agave** Linné (Spec. Pl. [ed. 1], 323, 1753). **Type:** *Agave americana* Linné [lectotype, designated by Britton & P. Wilson, Sci. Survey Puerto Rico, 5: 156, 1923 (fide ING)]. — **Agavoideae** — **Lit:** Trelease (1913: synopsis West Indies); Trelease (1915: synopsis Guatemala); Berger (1915: general synopsis); Hummelinck (1936: synopsis Caribbean); Hummelinck (1938: synopsis Caribbean); Gentry (1972: monograph Sonora); Verhoek-Williams (1975: revision Subgen. *Manfreda*); Gentry (1982: monograph USA, Mexico, C America); Piña Luján (1985: synopsis Subgen. *Manfreda*); Piña Luján (1986: synopsis Subgen. *Manfreda*); McVaugh (1989: Fl. Novo Galiciana); Hummelinck (1993: synopsis Caribbean); Lott & García-Mendoza (1994: Fl. Meso-america); Solano Camacho (2002: revision *Polianthes*); Heller (2006: ill. synopsis cultivated taxa); Castillejos-Cruz (2009: revision *Manfreda*); Solano & Ríos-Gómez (2011: key to Sect. *Polianthes* in Jalisco); Solano & al. (2014: anatomy *Polianthes*); Castro-Castro & al. (2015: key to Sect. *Polianthes* in Nueva Galicia); Guillot Ortiz (2015: key to naturalized taxa in Spain); Mottram (2015: nomenclature infrageneric names); Sidana & al. (2016: review steroidal saponins); Castro-Castro & al. (2016: key to *Polianthes*, flower ills.); Boeuf & al. (2017: ill. synopsis); Thiede &

al. (2019: sectional classification). **Distr:** S USA, Mexico, C America to Panama, whole Caribbean region, Colombia, Venezuela; cultivated worldwide in tropical and subtropical to frost-free temperate climates and often naturalized. **Etym:** Gr. ‘Agave’, daughter of Kadmos and sister of Semele in Gr. mythology, also the mother of Pentheus, who she murdered in an outburst of fury; also Gr. ‘agavos’, stately, noble, illustrious; for the stately nature of many species, but also for the ferocious leaf margin teeth present in many species.

**Incl.** *Polianthes* Linné (1753). **Type:** *Polianthes tuberosa* Linné [typification by inference, only element included].

**Incl.** *Pothos* Adanson (1763) (*nom. illeg.*, Art. 53.1). **Type:** not typified.

**Incl.** *Tuberosa* Heister ex Fabricius (1769) (*nom. illeg.*, Art. 52.1). **Type:** *Polianthes tuberosa* Linné.

**Incl.** *Bonapartea* Willdenow (1814) (*nom. illeg.*, Art. 53.1). **Type:** *Bonapartea juncea* Willdenow.

**Incl.** *Littaea* Tagliabue (1816). **Type:** *Littaea geminiflora* Tagliabue.

**Incl.** *Bravoia* Lexarza (1824). **Type:** *Bravoia geminiflora* Lexarza [typification by inference, only element included].

**Incl.** *Coetocapnia* Link & Otto (1828). **Type:** *Coetocapnia geminiflora* Link & Otto [typification by inference, only element included].

**Incl.** *Robynsia* Drapiez (1841) (*nomen rejiciendum*, Art. 56.1). **Type:** *Robynsia geminiflora* Drapiez

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[typification by inference, only element included].

**Incl.** *Ghiesbreghtia* Roezl (1861) (*nom. illeg.*, Art. 53.1). **Type:** not typified.

**Incl.** *Manfreda* Salisbury (1866). **Type:** *Agave virginica* Linné.

**Incl.** *Allibertia* Marion (1882) (*nom. illeg.*, Art. 53.1). **Type:** *Allibertia intermedia* Marion [typification by inference, only element included].

**Incl.** *Prochnyanthes* S. Watson (1887). **Type:** *Prochnyanthes viridescens* S. Watson.

**Incl.** *Leichtlinia* H. Ross (1893). **Type:** *Agave protuberans* Engelm ex Baker [typification by inference, only element included].

**Incl.** *Delpinoa* Ross (1897). **Type:** *Delpinoa gracillima* Ross [typification by inference, only element included].

**Incl.** *Pseudobravoa* Rose (1899). **Type:** *Bravoa densiflora* B. L. Robinson & Fernald.

**Incl.** *Runyonia* Rose (1922). **Type:** *Runyonia longiflora* Rose [typification by inference, only element included].

**Incl.** ×*Mangave* D. Klein (2010). **Type:** not typified.

**Incl.** ×*Polifreda* W. Ritchie (2014). **Type:** *Polyfreda* ‘Lindstrom’.

Perennial xerophytic **Ros** plants, mostly **L** succulents, mono- or polycarpic but individual rosettes always monocarpic, terrestrial (very rarely epiphytic); **R** tough and fibrous, sometimes fusiformly thickened (Subgen. *Manfreda*), shallowly radiating; **Ros** acaulescent or stems short, rarely elongated (e.g. *A. attenuata* ssp. *dentata*), mostly thick, solitary or branched, sometimes rhizomatous (esp. in Subgen. *Manfreda*); **Ros** small to very large; **L** mostly long-lived, predominantly succulent and xeromorphic, more rarely ± soft and annual (Subgen. *Manfreda* p.p.), ± thick and fibrous, linear to lanceolate to ovate, usually rich in steroidal sapogenins, tip a terminal ± strongly developed **Sp** or a soft point (Subgen. *Manfreda*); **L** margins entire, minutely to strongly toothed (then teeth partly on prominences of the **L** margin), or filiferous; **Inf** paniculate, small to up to 12 m tall (= complete **Inf**, i.e. peduncle and floriferous part); part-**Inf** cymose, consisting of monochasial units, either ± short-stalked and

mostly with few (often paired) flowers (Subgen. *Littaea*), or long-stalked, often several times compound, with many ± densely arranged flowers (Subgen. *Agave*), or without a stalk and paired to single flowers (Subgen. *Manfreda*); **Inf** sometimes bulbiferous, esp. in species of anthropogenic origin; peduncular **Bra** ± similar to rosette leaves, diminishing in size upwards; **Ped** long to short or nearly none (esp. Subgen. *Manfreda*); **Fl** diurnal and/or nocturnal, actinomorphic or (slightly) zygomorphic (Subgen. *Manfreda* p.p., rarely in Subgen. *Littaea*), nearly always proterandrous (proterogynous in *A. polianthiflora*); **Per** tubular to campanulate, usually yellow or greenish to brownish, more rarely reddish, rarely white or pink (Subgen. *Manfreda* p.p.); **Tep** basally usually fused and forming a perianth tube, much varying in length, lobes of varying length; **St** usually exerted, but included in Sect. *Polianthes*; **Fil** usually filiform, normally ± long, rarely ± short, inserted in the tube or at the mouth of the tube or at the tepal base; **Anth** versatile, oblong, pollen released in monads, sulcate (rarely bisulcate); **Ov** inferior, thick-walled, 3-locular, with numerous axile ovules in 2 rows per locule, often constricted above to a ± conspicuous neck; septal **Nec** present; **Sty** elongate, filiform, tubular, not yet fully expanded at anthesis; **Sti** 3-lobed, papillate-glandular; **Fr** dehiscent loculicidal capsules, apically often beaked (i.e. narrowly elongated); **Se** flattened, black. — **Cytology:** x = 30, with multiples present.

The genus includes ±265 species (plus several naturally occurring or artificial hybrids) of leaf succulents (only some species of Subgen. *Manfreda* are weakly succulent) of considerable ethnobotanical, economical, ecological, and horticultural importance. Many of its species are landscape-dominating elements esp. in the Mexican semi-arid and arid biomes.

**Classification History:** *Agave* taxonomy is difficult due to the complex nomenclature with many old names of uncertain application and many poorly or even undocumented names of horticultural origin. Additional difficulties are caused by the pronounced variability and plasticity of

many taxa, including possible hybridization and introgression.

Haworth (1812: 70–72) published a first rudimentary infrageneric classification of *Agave* based on leaf colour with 2 groups “*Foliis glaucis*” vs. “*Foliis viridibus, vel virescentibus*”. Salm-Dyck (1834: 7–8) classified *Agave* into 3 informal groups: *Caulescentes*, *Acaules*, and *Herbaceae* (which includes 2 species of Subgen. *Manfreda*) and later (Salm-Dyck 1859: 86–87) recognized 5 unranked taxa (“§”) based on leaf characters. In a subsequent publication, Salm-Dyck (1861) amended the classification and used the rank of section for these groupings, which is apparently the first formally ranked classification of the genus. Jacobi (1864: 498–501) proposed a classification based on leaf characters into 4 major unranked groupings (“Hauptgruppen”), the largest of which (*Keratacanthae*) is subdivided into 7 subgroups. Koch (1865) was apparently the first to use inflorescence types and proposed an informal classification into 2 divisions (“Abtheilungen”) (“*Agavae paniculatae*” and “*Agavae spicatae*”), subdivided into groups (“Gruppen”) based on leaf characters.

Engelmann (1875: 296–297) provided apparently the first formal classification of *Agave* based on inflorescence types, proposing 3 sections: *A. Sect. Singuliflorae* with solitary flowers (conforming to the modern Subgen. *Manfreda*), *A. Sect. Geminiflorae* with long and narrow ‘subspicate’ panicles (conforming to Subgen. *Littaea*), and *A. Sect. Paniculatae* with broad panicles (conforming to Subgen. *Agave*). Baker (1877a: 171), Baker (1877b: 808), and Baker (1888a: 164) subdivided *Agave* into 3 subgenera based on inflorescence types corresponding to Engelmann’s 3 sections: *A. Subgen. Euagave* (= *Agave*), *A. Subgen. Littaea*, and *A. Subgen. Manfreda*. In a simultaneous alternative classification based on leaf characters, he (Baker 1877b: 808, Baker 1888a: 164–166) divided *Agave* into 4 series, 3 of which are subdivided into 13 informal groups. Terracciano (1885) recognized 2 subgenera, *Cladagave* (conforming to Subgen. *Agave*), and *Aplagave* (conforming to Subgen. *Manfreda* + Subgen. *Littaea*), the latter further subdivided into Engelmann’s *Sect. Singuliflorae*

and *Sect. Geminiflorae*, both further divided into subsections.

Berger (1898) first largely followed Baker’s classification. In his later monograph, Berger (1915) recognised 3 subgenera (*Manfreda*, *Littaea*, *Euagave* (= *Agave*)) and subdivided Subgen. *Littaea* into 7 formal sections, while Subgen. *Euagave* was divided into 18 informal “Reihen”. Berger’s classification became rather influential because it was adopted in Jacobsen’s handbooks (e.g., Jacobsen 1954: 78–89). Trelease (1913), in his monograph of the Caribbean species, established 7 informal groups widely used up to today.

The highly influential monograph of the continental North American species of the genus by Gentry (1982) recognized 2 subgenera only (*Littaea* and *Agave*), thus excluding *Manfreda* from *Agave* s.s. Both subgenera are subdivided into informal groups “tantamount to sections” (Gentry 1982: xi); these were mainly taken from Baker and Trelease or also established as new, and were and are widely used. Several of these informal groups were formalized at sectional rank e.g. by Ullrich (1993b: 53, 56: *Sect. Crenatae*) and Starr & Webb (2015).

For the treatment of *Agave* in the first edition of this handbook, the present author converted molecular phylogenetic results that showed *Manfreda*, *Polianthes* and *Prochnyanthes* to be nested within *Agave* s.s. into a revised, monophyletic circumscription of *Agave* s.l. that included *Manfreda*, *Polianthes* and *Prochnyanthes* in *Agave*, together classified as *A. Subgen. Manfreda*. Hochstätter (2015), in his *Agave* (s.s.) compilation, published many new names at sectional, series and subseries rank (many of the latter seem superfluous when there is only one series within a section or one subseries within a series). Mottram (2015) provided an annotated checklist of the infrageneric taxa of *Agave*.

**Classification:** The circumscription of the infrageneric groupings applied in the first edition of this handbook is largely retained, but names at formal sectional rank for all infrageneric taxa are used. This classification applies, whenever available, names at sectional rank published earlier by

Salm-Dyck (1861), Engelmann (1875), Bentham in Bentham & Hooker (1883), Berger (1915), Ullrich (1992), Ullrich (1993b), Webb & Starr (2015), and Hochstätter (2015), including 3 sectional names recently published as new (Sect. *Conicae*, Sect. *Intermediae*, Sect. *Hibernicae*). Thiede & al. (2019) provide the necessary new combinations for those groupings for which no formal name at sectional rank has previously been published, and also provides typifications and a synopsis of the infrageneric classification of *Agave*.

[1] Subgen. *Littaea* (Tagliabue) Baker 1888 (≡ *Littaea* Tagliabue 1816): **Inf** with ± short-stalked to nearly sessile part-**Inf** mostly with few, mostly geminate (= paired) **Fl**, or **Fl** 3–4 (–8), rarely more or rarely single ('spicate' **Inf**):

[A] 'Weakly armed group'; **L** margins entire, serrulate, filiferous or with weak teeth:

[a] **L** margins firm, not filiferous, **L** surface without white marks left by the central bud, striate, not soft, **L** margins finely serrulate; **Tep** tube well-developed; **Ov** without neck:

[1a] Sect. *Juncineae* Salm-Dyck 1861 (≡ Group *Striatae* Baker 1877 ≡ Subsect. *Striatae* (Baker) A. Terracciano 1885 ≡ Sect. *Schoenagave* A. Berger 1915; incl. Abteilung *Loriformes* Jacobi 1864 ≡ Sect. *Chonanthagave* A. Berger 1915): Plants perennial, often forming large clumps; **L** numerous, narrow, linear, hard, not softly succulent, usually striate, margins finely serrulate; **Fl** geminate; **Tep** forming a well-developed tube often longer than the lobes; **Ov** half-inferior, without neck, merging into a well-developed tepal tube; **Fil** usually inserted in the middle of the tube, rarely higher up, frequently at 2 levels. — 9 species in NE, C and S Mexico.

Some species appear to flower repeatedly from "lateral" inflorescences which are actually likely terminal on rudimentary lateral rosettes. Molecular data (Bogler & Simpson 1996, Bogler & al. 2006, Gil-Vega & al. 2007) show

that Sect. *Juncineae* is the earliest branch-off in *Agave* s.l. and sister to the remainder of the genus. Such a basal position coincides with its plesiomorphic morphological features, esp. as seen in *A. dasyliroides* (see the section on the phylogeny below, and under *A. dasyliroides*).

[b] **L** not striate, margins firm, not filiferous, softly succulent, surface without white marks left by the central bud, margins smooth or irregularly serrulate; **Tep** tube short or none; **Ov** with a neck:

[1b] Sect. *Inermes* Salm-Dyck 1861 (≡ Sect. *Anoplagave* A. Berger 1915 ≡ Group *Amolae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1); incl. Abteilung *Margine integerrimae* Jacobi 1864 (*nom. inval.*, ICN Art. 21.2 Ex. 2 & 32.1c); incl. Ser. *Yuccifoliae* A. Terracciano 1885 ≡ Sect. *Yuccifoliae* (A. Terracciano) B. Ullrich 1996; incl. Group *Serrulatae* Baker 1877; incl. Ser. *Nizandensae* B. Ullrich 1991 ≡ Sect. *Nizandensae* (B. Ullrich) B. Ullrich 1991): **L** soft, margins entire, unarmed, **terminal Sp** usually present, rarely soft or absent; **Inf** with densely arranged **Fl**; **Tep** tube shallow, much shorter than the lobes; **Fil** usually inserted at the mouth of the tepal tube. — 10 species in N, C and S Mexico (mainly Sierra Madre Occidental).

[1c] Sect. *Choritepalae* Hochstätter 2015 (incl. Group *Choritepalae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1)): **L** soft to fleshy-leathery, without (*A. bracteosa*, *A. ellemeetiana*) or with **terminal Sp** (*A. guiengolensis*, *A. gypsicola*); **Inf** dense; **Tep** tube (nearly) lacking and **Tep** arising from a discoid receptacle, or very short; **Fil** inserted on the receptacle or at the base of the tube. — 4 species from N and S Mexico (Oaxaca).

Regarded as artificial by Ullrich (1990b), and this is corroborated by the AFLP data of Gil-Vega & al. (2007) where the 3 studied taxa are not forming a monophyletic group.

[c] **L** margins filiferous (i.e. decomposing into white threads), **L** surface with white marks left by the central bud:

[1d] Sect. *Littaea* (Tagliabue) Bentham 1883 (≡ *Littaea* Tagliabue 1816; ≡ Sect. *Xysmagave* A. Berger 1915; incl. Group *Filiferae* Baker 1877 ≡ Subsect. *Filiferae* (Baker) A. Terracciano 1885): **Ros** small to medium-sized, 20–50 (–200) cm Ø; **L** numerous, narrow, unarmed, filiferous; **Fl** usually geminate, campanulate, 30–55 mm, **Tep** tube usually much (rarely slightly) shorter than the lobes; **Fil** usually inserted at the rim of the tube (rarely slightly below). — 8 species in N and C Mexico (mainly Sierra Madre Occidental).

[1e] Sect. *Parviflorae* Hochstätter 2015 (≡ Group *Parviflorae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1)): **Ros** mostly small, compact, 12–60 (–80) cm Ø, solitary or freely suckering; **L** numerous, short (6–15 to very rarely exceeding 30 cm), narrow, unarmed, filiferous; **Fl** small, 13–42 (–50) mm; **Tep** forming a distinct tube; **Fil** shortly exerted, inserted usually deep in the tube. — 4 species from the N Sierra Madre Occidental (Mexico) and adjacent Arizona (USA). Starr & Devender (2011) supply a key to the species of the group.

[B] ‘Strongly armed group’: **L** margins generally with large teeth (except some species of Sect. *Micracanthae* and Sect. *Heteracanthae*):

[a] Plants mainly polycarpic; stems branched; **Tep** tube deep, lobes 1–2× as long as the tube:

[1f] Sect. *Micracanthae* Salm-Dyck 1861 (incl. Abtheilung *Subcarinatae* Jacobi 1864; ≡ Abtheilung *Aloideae* Jacobi 1868; ≡ Sect. *Anacamptagave* A. Berger 1915; incl. Group *Polycephalae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1)): **Ros** usually surculose; **L** few, 13–36, broad, softly succulent, fleshy, margins usually with small, weak and closely set teeth or denticles; **terminal Sp** weak and flexible to strong; **Tep** tube often ±3-angled

and ± grooved, lobes 1–3× as long as the tube; **Ov** often ±3-angled and ± grooved. — 9 species from NE to E-C and S Mexico. A mostly mesophytic and predominantly tropical group. Many (or even all) species appear to flower repeatedly from “lateral” inflorescences which are actually likely terminal on rudimentary lateral rosettes. See Cházaro Basáñez & Vázquez-García (2013: 59) for a key.

[b] Plants mainly monocarpic; stems simple; **Ros** often surculose; **Tep** tube shallow, lobes 2–6× as long as the tube (except *A. pelona*):

[1g] Sect. *Heteracanthae* Salm-Dyck 1861 (≡ Sect. *Geminiflorae* Engelman 1875; incl. Abtheilung *Marginatae* Jacobi 1864 ≡ Group *Marginatae* Baker 1877 ≡ Subsect. *Marginatae* (Baker) Terracciano 1885 ≡ Sect. *Pericamptagave* A. Berger 1915; incl. Sect. *Brachysolenagave* A. Berger 1915; incl. Sect. *Becholdiae* Hochstätter 2015): **L** stiff and straight, usually with conspicuous and continuous horny margins and with conspicuous marginal teeth; **Fl** usually small with short, ± openly funnel-shaped **Tep** tube, lobes 3–8 (–10) × as long as the shallow tube, frequently involute around the filaments during or only after anthesis. — 25 species from the S USA (S New Mexico, S Texas), Mexico and Guatemala.

[1h] Sect. *Urceolatae* Hochstätter 2015 (≡ Group *Urceolatae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1)): **L** with small or weakly attached **marginal teeth**; **Ros** usually small and in small tight clusters; **Tep** lobes broadly overlapping, ± 2.5–3× as long as the short, broadly funnel-shaped **Tep** tube. — 1 species (*A. utahensis*) in the USA (NW Arizona, S Utah, Nevada, S California).

[2] Subgen. *Agave*: **Inf** with long-stalked, often several times compound part-**Inf** with many ± densely arranged flowers (‘umbellate’ part-**Inf**).

[A] ‘Large-sized group’: Plants medium-sized to (very) large; **Ros**  $\pm 1$ –2.5 m tall; **L**  $\pm 1$ –2.5 m. — Continental Species:

[a] **L** generally not ensiform but lanceolate to ovate, much less than 10 $\times$  longer than wide; **Fr**  $\pm$  oblong:

[2a] Sect. *Agave* ( $\equiv$  Sect. *Macracanthae* Salm-Dyck 1861 (*nom. inval.*, ICN Art. 22.1 & Ex. 2)  $\equiv$  Abteilung *Carnosae* Jacobi 1864 (*nom. inval.*, ICN Art. 22.1 & Ex. 2)  $\equiv$  Sect. *Paniculatae* Engelmann 1875 (*nom. inval.*, ICN Art. 22.1 & Ex. 2)  $\equiv$  Group *Americanae* Baker 1877 (*nom. inval.*, ICN Art. 22.1 & Ex. 2)  $\equiv$  Subsect. *Americanae* (Baker) A. Terracciano 1885 (*nom. inval.*, ICN Art. 22.1 & Ex. 2)  $\equiv$  Reihe *Americanae* A. Berger 1915 (*nom. inval.*, ICN Art. 22.1 & Ex. 2); incl. Abteilung *Subcoriaceae* Jacobi 1864): **Ros** medium-sized to large, (freely) surculose; stems short; **L** light glaucous-grey to pale green, **marginal teeth** well-developed; **Inf** axis with smaller chartaceous **Bra**; fertile part of the **Inf** usually linear to long-oval in outline, part-**Inf** several times compound, not crowded; **Fl** yellow, rather slender; **Tep** tube furrowed, lobes (much) longer than the tube, not wilting until after anthesis; **Fil** inserted mostly at or near mid-tube, rarely at the mouth. — 7 mainly cultivated species.

[2b] Sect. *Salmianae* (A. Berger) Verloove & Thiede in Thiede & al. 2019 ( $\equiv$  Reihe *Salmianae* A. Berger 1915;  $\equiv$  Group *Salmianae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1)): **Ros** large, massive, usually closely and freely surculose; stems short, thick; **L** light green to green, mostly very large, very thick towards the base; **Inf** axis with large appressed imbricate fleshy **Bra**; **Inf** pyramidal to ellipsoid in outline, part-**Inf** widely branching, several times compound; **Fl** large, succulent; **Tep** tube broad, thick-walled, lobes longer than or  $\pm$  as long as the tube,

dimorphic, becoming incurved when wilting after anthesis; **Fil** inserted at, above or below mid-tube, usually at 2 levels. — 3 mainly cultivated species.

[2c] Sect. *Sisalanae* Thiede & Gideon F. Smith 2019 ( $\equiv$  Unterreihe *Sisalanae* A. Berger 1915 (*nom. illeg.*, ICN Art. 53.1)): **Ros** medium to large, usually freely surculose; stems short to elongate; **L** without marginal teeth, or teeth reduced to prickles or irregularly arranged; **terminal Sp** small and weak; **Inf** lax, frequently bulbiferous; **Tep** tube as long as wide,  $\frac{2}{3}$  as long as to equalling the lobes; **Fil** inserted at or near mid-tube. — 3 cultivated species. Ullrich (1990) abandoned this group in the sense of Gentry (1982) as an artificial assemblage and rearranged its species in other groups. This is not followed here.

[2d] Sect. *Crenatae* (A. Berger) B. Ullrich 1993 ( $\equiv$  Unterreihe *Crenatae* A. Berger 1915; incl. Group *Crenatae* Gentry 1982 (*nom. illeg.*, ICN Art. 53.3, and *nom. inval.*, ICN Art. 37.1)): **Ros** medium-sized to large, usually solitary, rarely surculose; stems short; **L** green to yellowish-green, young pruinose, usually with clearly visible marks left by the central bud, **L** margins deeply crenate and undulate, **marginal teeth** large, irregular in size and spacing, frequently with small interstitial teeth, on distinct prominences; **Inf** tall, narrow; **Tep** red or purple in bud, yellow at anthesis, lobes 2.5–5 $\times$  as long as the tube; **Fil** inserted at, above or below mid-tube. — 7 species mainly from the Mexican Sierra Madre Occidental and the Trans-Mexican Volcanic Belt.

[2e] Sect. *Campaniflorae* (Trelease) R. H. Webb & G. D. Starr 2015 ( $\equiv$  Group *Campaniflorae* Trellease 1912b  $\equiv$  Reihe *Campaniflorae* A. Berger 1915): **Ros** small to large, rather open, mostly solitary (except var. *capensis*); stems short; **L** rather softly succulent, 35–150 cm, green,



margins not horny, **marginal teeth** usually 4–7 mm, uniform in size and spacing; **Fl** campanulate; **Tep** tube thin-walled, deep, broad (15–22 mm), **Tep** red to purplish in bud, opening (orange-) yellow, lobes 1.5–2× as long as the tube; **Fil** deeply attached in the tube. — 1 species (*A. aurea*) from Baja California (Mexico).

[2f] Sect. *Umbelliflorae* (Trelease) R. H. Webb & G. D. Starr 2015 (≡ Group *Umbelliflorae* Trellease 1912 ≡ Reihe *Umbelliflorae* A. Berger 1915): Stems commonly branching from **L** axils, frequently developing long branching stems resulting in fragmented clones; **L** broad and short (<70 cm), mostly bright (glaucous) green; **Inf** stout and broad, compact, part-**Inf** large, ± globular ('umbellate'), subtended by large succulent sheathing **Bra**; **Fl** large, fleshy. — 2 species in the USA (SW California) and Mexico (N Baja California).

[b] **L** ensiform, linear, patulous, 10–20× as long as wide; **Tep** lobes drying reflexed on the tube; **Fr** broadly ovoid:

[2g] Sect. *Rigidae* (Baker) R. H. Webb & G. D. Starr 2015 (≡ Group *Rigidae* Baker 1877 ≡ Subsect. *Rigidae* (Baker) A. Terracciano 1885 ≡ Reihe *Rigidae* A. Berger 1915; incl. Abteilung *Canaliculatae* Jacobi 1864; incl. Group *Sisalanae* Trellease 1913; incl. Group *Tequilanae* Trellease 1916): **Ros** small to large, surculose; stems short to elongate; **L** linear, ensiform, narrow, rigid, usually patulous, 10–20× as long as wide, margins nearly straight; **Inf** with relatively few part-**Inf**, open, frequently bulbiferous; **Fl** greenish to yellow, lobes ±2× as long as the tube; **Fr** broadly ovoid. — 14 species, mainly in Mexico, 1 in the S USA (Florida), 1 also in C America, some cultivated only.

In the first edition of this handbook, this group was treated as *Viviparae* for nomenclatural reasons (see under *A. vivipara*) and was merged with Group *Sisalanae* following Ullrich (1990d).

Here, Sect. *Rigidae* and Sect. *Sisalanae* are re-instated in the sense of Gentry (1982: 551, 619) (as Groups).

[B] 'Small-sized group': Plants mostly small to medium-sized; **Ros** ±0.4–1 m tall; **L** ±0.2–1 m. — Continental species:

[a] Plants generally surculose; flowering period spring to summer; **Tep** tube deep, lobes short, strongly dimorphic, outer lobes conspicuously larger; **Fil** usually inserted at 2 levels:

[2h] Sect. *Ditepalae* Hochstätter 2015 (≡ Group *Ditepalae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1); incl. Group *Applanatae* Trellease 1912b; incl. Sect. *Hodgsoniae* Hochstätter 2015): **Ros** small to large, single or sparingly surculose; **L** mostly light glaucous, **marginal teeth** well-developed; **Inf** open; **Bra** scarious, reflexing, persistent; **Tep** leathery, usually yellow or orange, often reddish in bud; **Tep** tube deep, mostly ± as long as or longer than the lobes, rarely shorter, lobes dimorphic, usually short, tips usually red, rarely yellow; **Fil** usually inserted unequally at ± mid-tube; **Fr** long oblong. — 17 species in N, C and S Mexico and the S USA (Arizona, New Mexico).

This section includes many pre-Columbian cultivar species, mainly from Arizona.

[b] As in [a], but **Tep** tube shallow or deep, lobes much longer than the tube, subequal; **Fil** generally inserted all on the same level:

[2i] Sect. *Deserticolae* (Trellease) R. H. Webb & G. D. Starr 2015 (≡ Group *Deserticolae* Trellease 1912b ≡ Reihe *Deserticolae* A. Berger 1915): **Ros** small to medium-sized, usually ± caespitose; stems none or short; **L** glaucous-grey to greenish-yellow; **marginal teeth** weak and easily detached; **Inf** narrow, part-**Inf** short; **Fl** small, 30–60 mm, yellow(ish) to green(ish); **Tep** tube very short and broad to long, lobes 1–5× as long as the tube. — 7 species from the

- USA (SE California, Arizona) and Mexico (mainly Baja California, also Sonora) (Sonoran Desert Region).
- Without close relationship to any other Group except Sect. *Conicae* and Sect. *Intermediae*.
- [2j] Sect. *Conicae* R. H. Webb & G. D. Starr 2015: **Ros** medium-sized, solitary; **Ros** solitary; **L** green or grey-green; **Inf** conical, part-**Inf** conspicuous. — 4 species from Mexico (Baja California and Baja California Sur) (Sonoran Desert Region). Formerly placed in Sect. *Deserticolae* but differing in the shape of the inflorescences.
- [2k] Sect. *Intermediae* R. H. Webb & G. D. Starr 2015: **Ros** medium-sized, solitary or caespitose; **L** dark grey-green to blue-green; **Inf** short, cylindrical, rather broad, part-**Inf** conspicuous; **Fl** with long tepal tube. — 2 species from Mexico (Baja California Sur) (Sonoran Desert Region). Considered intermediate between Sect. *Deserticolae* and Sect. *Umbelliflorae*.
- [2l] Sect. *Parryanae* Hochstätter 2015 (≡ Group *Parryanae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1)): **Ros** small to medium-sized, compact, suckering sparingly or prolifically with vigorous rhizomes; **L** short, broad, closely imbricate, glaucous-grey to green, **marginal teeth** conspicuously larger towards the leaf tip; **Inf** peduncle strong, with large, irregularly reflexing bracts, fertile part usually deep, with 15–40 part-**Inf**; **Tep** red to purplish in bud, tube well-developed, shorter than the lobes; **Fr** rather small, strong-walled, ovoid to oblong. — 4 species from the S USA (California to SW Texas) and Mexico (Central Mexican Plateau to Guanajuato).
- [2m] Sect. *Hibernicae* Hochstätter 2015 (incl. Group *Parrasanae* Alsemgeest & Roosbroeck 2012 (*nom. inval.*, ICN Art. 29.1)): Plants medium-sized; **Ros** compact, mostly solitary, or clustering; **L** broad, yellowish-green to glaucous-green; **Inf** developing during winter, protected by large bracts clasping the young inflorescence, flowers in spring. — 3 species from N & C Mexico. Formerly included in Sect. *Parryanae*.
- [c] Plants not surculose; flowering period winter to early spring:
- [2n] Sect. *Marmoratae* (A. Berger) Thiede & Gideon F. Smith 2019 (≡ Reihe *Marmoratae* A. Berger 1915; ≡ Group *Marmoratae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1)): **Ros** small to large, usually solitary; **L** few, usually grey-green, often cross-zoned and scabrous, margins often repand, **terminal Sp** small; **Fl** mostly small, 28–50 (–70) mm, bright yellow or orange-yellow to orange, tube short. — 9 species from C and S Mexico and Sonora.
- [2o] Sect. *Guatemalenses* (Trelease) B. Ullrich 1992 (≡ Group *Guatemalenses* Trellease 1916; incl. Group *Atravirentes* Trellease 1916; incl. Reihe *Scolymoides* A. Berger 1915; incl. Group *Hiemiflorae* Gentry 1982 (*nom. inval.*, ICN Art. 37.1) ≡ Sect. *Hiemiflorae* Hochstätter 2015): **Ros** small to medium-sized, rarely gigantic, generally solitary; **Inf** narrow, part-**Inf** on short to medium-sized stalks; **Fl** small to medium-sized, in lax or mostly tightly ball-like clusters; **Tep** lobes longer than the tube; **Fl** inserted above mid-tube. — 13 species from E-C and S Mexico and C America (Guatemala to Costa Rica).
- Gentry's group name '*Hiemiflorae*' alludes to its flowering period in winter (Lat. 'hiems, hiemis', winter).
- [C] Caribbean and S American species (the sectional characteristics are in need of revision, and many species are insufficiently known):
- [2p] Sect. *Antillanae* (Trelease) Thiede & Gideon F. Smith 2019 (≡ Group *Antillanae* Trellease 1913 ≡ Reihe *Antillanae* A. Berger 1915): **Ros** suckering; **L** fleshy, usually curved, usually green, **marginal teeth** usually rather large, **terminal Sp** usually elongated; panicles several times compound,

freely fruiting, sometimes bulbiferous; **Fl** rather large (40–80 mm); **Se** rather large (6–9 × 4–6 mm). — 16 species mainly from the Greater Antilles.

- [2q] Sect. *Antillares* (Trelease) Thiede & Gideon F. Smith 2019 (≡ Group *Antillares* Trelise 1913 ≡ Reihe *Antillares* A. Berger 1915): **Ros** suckering; **L** fleshy, usually curved, usually green, **marginal teeth** small, **terminal Sp** usually elongated; panicle **Br** rather simple; **Fl** rather small (30–45 mm); **Se** small (5–6 × 4–5 mm). — 7 species: 5 from Cuba, 1 from Puerto, 1 cultivated only. — Not to be confused with Sect. *Antillanae*.
- [2r] Sect. *Bahamanae* (Trelise) Thiede & Gideon F. Smith 2019 (≡ Group *Bahamanae* Trelise 1913 ≡ Reihe *Bahamanae* A. Berger 1915): **Ros** rarely suckering; **L** usually grey, **terminal Sp** elongated; panicles several times compound; **Fl** rather large (40–60 mm); **Se** rather large (7–8 × 4–6 mm). — 6 species from the Bahamas.
- [2s] Sect. *Caribaeae* (Trelise) Thiede & Gideon F. Smith 2019 (≡ Group *Caribaeae* Trelise 1913; incl. Reihe *Caribaeae* A. Berger 1915): **Ros** solitary and not suckering; **L** fleshy, usually curved, usually green, marginal teeth usually small, **terminal Sp** with stout involutely slitted base, above usually short and oblique; panicles several times compound, freely bulbiferous, not always fruiting; **Fl** rather large (40–80 mm); **Se** rather large (6–9 × 4–6 mm). — 2 species from the Lesser Antilles.
- [2t] Sect. *Inaguenses* (Trelise) Hochstätter 2015 (≡ Group *Inaguenses* Trelise 1913 ≡ Reihe *Inaguensis* A. Berger 1915): **Ros** freely suckering; **L** hard and straight, grey; **Fl** rather small (35–50 mm); **Se** small (5 × 4 mm). — 2 species from the Bahamas.
- [2u] Sect. *Viviparae* (Baker) Verloove & Thiede in Thiede & al. 2019 (≡ Group *Viviparae* Baker 1877 ≡ Subsect. *Viviparae* (Baker) A. Terracciano 1885; incl. Group *Vicinae* Thiede 2001 (*nom. inval.*, ICN Art. 37.1)): **Ros** suckering; **L** fleshy, usually curved, usually green, **marginal teeth** usually small, **terminal Sp** elongated, slender;

panicles several times compound, freely bulbiferous, not always fruiting; **Fl** rather large (40–80 mm); **Se** rather large (6–9 × 4–6 mm). — 8 species from the Leeward Antilles, Trinidad, and N South America (Colombia, Venezuela).

In the first edition of this handbook, Trelise's Group *Viviparae* was renamed Group *Vicinae* for nomenclatural reasons (see under *A. cocui*), but it is here re-established in the original sense of Trelise (1913).

- [2v] Sect. *Columbianae* (A. Berger) Thiede & Gideon F. Smith 2019 (≡ Reihe *Columbianae* A. Berger 1915): **Ros** (always?) solitary and not suckering; **L** ± lanceolate, large, curved, **marginal teeth** small. — 2 species from N South America. Possibly closest to Sect. *Caribaeae*.
- [3] Subgen. *Manfreda* (Salisbury) Baker (1888) (≡ *Manfreda* Salisbury 1866; incl. *Polianthes* Linné 1753; incl. *Bravoa* Lexarza 1824; incl. *Allibertia* Marion 1882; incl. *Delpinoa* Ross 1887; incl. *Prochnyanthes* S. Watson 1887; incl. *Leichtlinia* Ross 1893; incl. *Pseudobravoa* Rose 1899; incl. *Runyonia* Rose 1922):
- [A] Rhizomes upright, fleshy, with basal corm and apical bulb; **R** fleshy and fibrous, arising from the base of the rhizome; **L** chartaceous to fleshy, green for one season or slightly longer, ending in a soft point, margins often hyaline, entire, denticulate to papillate, or with soft teeth; **Inf** 'racemes' or 'spikes' with solitary or paired **Fl** at the nodes. — S USA, Mexico, N-C America.
- [3a] Sect. *Herbaceae* Salm-Dyck 1861 (incl. *Manfreda* Salisbury 1866 ≡ Sect. *Singuliflorae* Engelmann 1875; ≡ Sect. *Manfreda* (Salisbury) Bentham 1883 ≡ *Manfreda* Subgen. *Eumanfreda* Rose 1899 (*nom. inval.*, ICN Art. 21.3) ≡ Group *Manfreda* Thiede 2001 (*nom. inval.*, ICN Art. 37.1); incl. *Manfreda* Subgen. *Pseudomanfreda* Rose 1899): Rhizome globose or oblong, large; **Fl** usually solitary at the nodes (paired only in aberrant specimens), scent sweet or unpleasant; **TeP** mostly greenish or brownish (rarely white or pink), tube



short to long; **St** and **Sty** long-exserted; **Sti** trigonous or rarely 3-lobed. — S USA, Mexico, N-C America.

Solano & al. (2017) describe the comparative anatomy of roots, shoots, leaves and peduncle base.

[3a1] Ser. *Brunneae* (Hochstätter) Thiede & Gideon F. Smith 2019 (≡ *Manfreda* Ser. *Brunneae* Hochstätter 2016 (as ‘*Brunneaea*’) ≡ *Manfreda* Sect. *Brunneae* Hochstätter 2016 (as ‘*Brunneaea*’) ≡ *A. brunnea* Subgroup Thiede 2001 (*nom. inval.*, ICN Art. 37.1)): **L** succulent, evergreen, not dying back at the end of the growing season, tip with a short soft point; **L** margins with large to small teeth  $\pm \geq 1$  mm, spaced apart from each other (**L** not fleshy and with a long pungent apical point in *A. hauniensis*). — 9 species in the USA (Texas) and N Mexico.

[3a2] Ser. *Scabraea* (Hochstätter) Thiede & Gideon F. Smith 2019 ≡ *Manfreda* Ser. *Scabraea* Hochstätter 2016 ≡ *Manfreda* Sect. *Scabraea* Hochstätter 2016 ≡ *A. scabra* subgroup Thiede 2001 (*nom. inval.*, ICN Art. 37.1)): **L** thin to semi-succulent, dying back at the end of the growing season; **L** margins entire or minutely papillate; **Ov** not protruding into the tepal tube; **Tep** tube inserted at the tip of the ovary, funnel-shaped, narrowed above the ovary. — 10 species in C and S Mexico. This subgroup is possibly an artificial paraphyletic hold-all of the least specialized species.

[3a3] Ser. *Guttatae* (Hochstätter) Thiede & Gideon F. Smith 2019 (≡ *Manfreda* Ser. *Guttatae* Hochstätter 2016 (as ‘*Guttataea*’) ≡ *Manfreda* Sect. *Guttatae* Hochstätter 2016 (as ‘*Guttataea*’) ≡ *A. guttata* Subgroup Thiede 2001 (*nom. inval.*, ICN Art. 37.1)): **L** thin to semisucculent, dying back at the end of the growing season; **L** margins hyaline, usually minutely erose-denticulate and thus rough to the touch; **Ov** protruding into the tepal tube; **Tep** tube cylindrical, not narrowed

above the ovary; **Fr** with a scar from the tepals in a ring around the shoulder. — 15 species from C and S Mexico and Guatemala.

[3a4] Ser. *Virginicae* (Hochstätter) Thiede & Gideon F. Smith 2019 (≡ *Manfreda* Ser. *Virginicae* Hochstätter 2016 (as ‘*Virginicaea*’) ≡ *Manfreda* Sect. *Virginicae* Hochstätter 2016 (as ‘*Virginicaea*’) ≡ *A. virginica* Subgroup Thiede 2001 (*nom. inval.*, ICN Art. 37.1)): **L** thin to semisucculent, dying back at the end of the growing season; **Fl** slender; **Tep** lobes erect; **Sty** markedly shorter than the stamens; **Sti** 3-lobed, lobes reflexed at maturity. — Only *A. virginica* from the C and SE USA.

[3a5] Ser. *Yucatanae* Thiede & Gideon F. Smith 2019: **Ros** 30–100 cm Ø; **L** with **terminal Sp**; **Inf** panicles or less often racemes (*A. petskinil* p.p.), with 1–5 branches; **Fl** pedicellate, solitary, subtended by a single bracteole. — Only *A. paniculata* and *A. petskinil* from the N Yucatán Peninsula (Mexico).

[B] Rhizomes small or large, upright, fleshy, with basal corm and apical bulb; **R** fleshy and fibrous, arising from the base of the rhizome; **Fl** usually paired at the nodes (solitary in *A. confertiflora*), scent sweet or absent; **Tep** white (sometimes tinged with green) to reddish, tube long; **St** and **Sty** included; **Sti** 3-lobed, lobes reflexed at maturity.

[3b] Sect. *Polianthes* (Linné) Thiede & Gideon F. Smith 2019 (≡ *Polianthes* Linné 1753): Plants medium-sized to small; **L** linear to lanceolate, herbaceous; **Tep** white, pink, red or coral-pink, tube straight or usually with a wide curve, narrow, usually gradually widening above. — 21 species from Mexico.

Feria-Arroyo & al. (2010) assessed the conservation status and extinction risk for 5 species. Castro-Castro & al. (2015) indicate the distributions by state for all species. Solano & al. (2014) describe the comparative anatomy of shoots, leaves and peduncle base.

[3b1] Ser. *Polianthes* (Linné) Thiede & Gideon F. Smith 2019 (≡ *Polianthes* Linné

1753  $\equiv$  *Polianthes* Group Thiede 2001 (*nom. inval.*, ICN Art. 37.1): **Inf** with (2–) 3–8 (–15) flowering nodes; **Fl** sweet-scented; **Ov** erect or spreading; **Tep** white to pink, sometimes pink to red at senescence, with a long, narrow tube, usually ascending at the base and curved outwards to downwards at about the middle, or also curved near the base, usually widening above the curvature up to the  $\pm$  oblique mouth, lobes erect or reflexed to revolute; **St** included, inserted near the mouth of the tepal tube. — 10 species from N and C Mexico.

[3b2] Ser. *Bravoa* (Lexarza) Thiede & Gideon F. Smith 2019 ( $\equiv$  *Bravoa* Lexarza 1824  $\equiv$  *Polianthes* Subgen. *Bravoa* (Lexarza) M. Roemer 1847  $\equiv$  Group *Bravoa* Thiede 2001 (*nom. inval.*, ICN Art. 37.1); incl. *Prochnyanthes* S. Watson 1887): **Inf** with (3–) 4–22 or more flowering nodes; **Fl** unscented (fragrant in *A. bicolor* and *A. multicolor*); **Ov** horizontal or curved downwards; **Tep** pink, pinkish-red, red, or coral-coloured (yellowish-green in *A. bicolor*, white tinged with grey-green or dull green and red in *A. bulliana*, cream to nearly red in *A. multicolor*), with a narrow tube usually ascending at the base and curved downwards at about the middle or lower so that the flowers are  $\pm$  pendent, tube usually widening above the curvature up to the straight to oblique mouth, lobes short, erect or flaring; **St** included (rarely slightly exserted), inserted from near the base of the tube up to near the throat. — 11 species from C and S Mexico.

**Terminology and measurement conventions:**

Leaf margin characters have widely been employed as diagnostic characters, but the terminology used by different authors is often not directly comparable, and lacks standardization even within major works. Here, the leaf margin is described as straight, concave or repand (rather than undulate, which refers to the structure of the leaf along its long axis). The marginal

extensions (“prickles”) are, in accordance with most current literature, termed teeth, and if they are situated on drawn-out parts of the margins, these parts are termed prominences. The teeth itself can show a specially broadened or otherwise characteristic base, and can be straight or curved, etc.

The inflorescences of Agaves are often termed spikes or panicles with umbels, e.g. by Gentry (1982), but as explained in the opening paragraphs, all inflorescences have basically a paniculate architecture, and have cymose-monochasial part-inflorescences. Accordingly, the terms “spike” and “umbel” should be avoided because they are morphologically inappropriate. Measurements for flower length include the ovary, but not the pedicel.

**Phylogeny:** The first molecular phylogenetic sequencing studies of *Agave* (Bogler & Simpson 1996, Bogler & al. 2006, Good-Avila & al. 2006) as well as a phylogeny based on structural features (Hernández-Sandoval 1995) showed that the genera *Manfreda*, *Polianthes* and *Prochnyanthes*, widely recognized in recent treatments (e.g. Verhoek-Williams 1978a, McVaugh 1989, Castro-Castro & al. 2010), are nested within *Agave*, thus rendering *Agave* s.s. paraphyletic. Recent studies (Archibald & al. 2015, Heyduk & al. 2016, Scheinvar & al. 2016, Flores-Abreu & al. 2019) confirm this pattern. The sole study in which *Manfreda*, *Polianthes* and *Prochnyanthes* grouped separate from rather than nested within *Agave* is the molecular AFLP study of Gil-Vega & al. (2007). However, in all phylogenies thus far published, the support values for the nodes are often wanting to moderate only, and none of the studies is based on a broad sampling of taxa and loci.

The samples of Subgen. *Manfreda* show different placements and either together form a clade (Bogler & Simpson 1996, Archibald & al. 2015) or are dispersed over the tree of *Agave* (Good-Avila & al. 2006, Flores-Abreu & al. 2019). In Flores-Abreu & al. (2019), the samples of the *Bravoa* and the *Polianthes* group of Sect. *Polianthes* both form monophyletic clades, but place separate suggesting polyphyly of Sect.

*Polianthes*; the same is true for the samples of Sect. *Manfreda*.

*Agave* [Subgen. *Littaea*] Sect. *Juncineae* (= Group *Striatae* of Gentry (1982)) is the earliest branch-off in *Agave* s.l. and sister to the remainder of *Agave* in the studies of Bogler & Simpson (1996), Bogler & al. (2006) and Archibald & al. (2015), thus principally confirming an earlier hypothesis of Gentry (1982: 241–242) who suggested a basal position for *A. dasylirioides* (of Sect. *Juncineae*).

Eguiarte & al. (2013) summarize available studies on the population genetics of single species or species groups.

**Biogeography:** Distribution patterns of *Agave* (s.s.) are dealt with by Reichenbacher (1985), García-Mendoza (1995), García-Mendoza & Galván (1995), and García-Mendoza (2002). The natural range of *Agave* (s.l.) ranges from the E-C USA (*A. virginica*) and the S USA throughout Mexico, Mesoamerica and the Caribbean to N South America (Colombia and Venezuela). Highest species richness in *Agave* (s.s.) is found in the border region of Puebla and Oaxaca (Tehuacán-Cuicatlán valley), further concentrations are found along the mountains of E and S Mexico (Sierra Madre Oriental, Trans-Mexican Volcanic Belt, Sierra Madre del Sur), in W Durango (Mazatlán-Durango, highway 40), SE Sonora and SW Chihuahua (Hermosillo-Chihuahua, highway 15), W Mexico (Nueva Galicia) and in S-most Baja California. Subgen *Agave* is more diverse in S Mexico, and Subgen. *Littaea* in E Mexico (Reichenbacher 1985, García-Mendoza 1995). Most species occur at altitudes between (500–) 1000 and 2000 (–2500) m, esp. in desert scrub/chaparral and pine-oak forests (García-Mendoza 2002). Subgen. *Manfreda* is most diverse in W Mexico (Nueva Galicia), along the Trans-Mexican Volcanic Belt, and in N Oaxaca (García-Mendoza 1995) (as *Manfreda*, *Polianthes*, *Prochnyanthes*).

**Cytology:** *Agave* has a bimodal karyotype with  $x = 30$  (McKelvey & Sax 1933, Robert & al. 2008). Ploidy ranges from diploid to octoploid, including (sterile) triploids (e.g. *A. angustifolia* var. *letonae*, *A. cantala*) and pentaploids (e.g.

*A. mapisaga*, *A. sisalana*) (Robert & al. 2008). Polyploidy is common in Subgen *Littaea* and even more so in Subgen. *Agave* (Pinkava & Baker 1985). Some species include several ploidy levels (e.g., *A. americana*  $2\times-8\times$ , *A. angustifolia*  $2\times-6\times$ ). The few counts for Subgen. *Manfreda* show di- or tetraploidy (Verhoek-Williams 1975: 78). Polyploidization is probably linked to increased vegetative propagation and/or selected for by an increasingly arid environment (Robert & al. 2008). The same authors argue that polyploidization is of comparatively recent age since genome structure is completely additive.

Robert & al. (2008) did not find any dysploid changes — the early dysploid counts (e.g. Sató 1935) are thus likely observation errors. Many chromosome numbers are reported by Granick (1944), Cave (1964), Pinkava & Baker (1985), Zonneveld (2003), Lv & al. (2009), and Simpson & al. (2011).

**Natural hybridization:** Natural hybrids are common in co-occurring species, and e.g. Gentry (1982) reports many putative hybrids which are usually more or less intermediate between the putative parents. Introgression is assumed in *A. americana* ssp. *protoamericana*, *A. asperrima* ssp. *asperrima*, ssp. *potosiensis* and ssp. *zarcensis*, *A. chrysantha*, and *A. palmeri*, but in *A. pringlei*, the “introgression” hypothesis of Gentry is dismissed. *A. ×saltilloensis* is an introgressive hybrid swarm connecting both parental species (see there). *A. ×arizonica*, *A. ×glomeruliflora*, and *A. ×peacockii* are natural hybrids originally published as new species. *A. doctorensis* and *A. montium-sancticaroli*, both published as new species, appear to represent natural inter-subgeneric hybrids between species of Subgen. *Littaea* and Subgen. *Agave*. *A. ×ajoensis* is a sterile triploid natural hybrid. Several taxa (*A. cerulata* var. *nelsonii*, *A. hauniensis*, *A. nunsaviorum* (both ssp.), *A. ornithobroma*) might have arisen as allopolyploids of hybrid origin, but more evidence is needed.

**Evolution:** The origin of *Agave* s.l. is dated at 7.9–9.8 mybp (Good-Avila & al. 2006), 9.07 mybp (Smith & al. 2008a), and, respectively,

8.67 mybp (Scheinvar & al. 2016). Speciation rates appear to have been significantly elevated between 8 and 6 mybp coincident with an increase of dry conditions in C Mexico, and between 3 and 2.5 mybp, probably driven by the emergence of the bat pollination syndrome (Good-Avila & al. 2006). Possible driving factors in the radiation of and high diversification rate in *Agave* s.l. may be the evolution of monocarpy, changes in physiology and morphology such as funnel-shaped rosettes, etc., and the evolution of a generalist pollination system largely dependent on nectarivorous bats. Flores-Abreu & al. (2019) calculated a younger age of 5–8 mybp, which coincides with the age of the 3 main genera of nectarivorous bats, suggests a shared evolutionary history between plants and pollinators, and gives further support for a potential *Agave*–bat coevolution.

**Succulence:** Species of Subgen. *Littaea* and Subgen. *Agave* mostly have rather tough, rigid, very fibrous leaves with a well-developed voluminous parenchymatous central water-storage tissue; this tissue is undifferentiated or differentiated into palisade-like cells and a spongy mesophyll that frequently contains groups of elongated water-storage cells (Blunden & al. 1973, Nobel 1988: 41). Bray (1903) found the storage tissue of *A. lechuguilla* to contain air spaces. The water storage tissue is usually not strictly delimited from the photosynthetic tissue (Metzler 1924: 58).

Thickened rhizomes are present in many species, and some species have a well-developed trunk with a secondary thickening meristem (Carlquist 2012: 112).

**Physiology:** Crassulacean Acid Metabolism (CAM) is almost always present and constitutive in Subgen. *Agave* and Subgen. *Littaea*; *A. vilmoriniana* exhibits substantial diurnal CO<sub>2</sub> uptake esp. at lower temperatures (Nobel 1988: 46, 99–100) and appears to be the sole exception. Data for Subgen. *Manfreda* are sparse; *A. scabra* and *A. virginica* (as *Manfreda*) both have CAM, whereas *A. amica* (*Polianthes tuberosa*) appears to use the C<sub>3</sub> pathway (Heyduk & al. 2016). CAM originated in the most recent common ancestor of

*Agave* s.l., and *A. amica* exhibits a reversal to the C<sub>3</sub> pathway, which should be confirmed with physiological measurements to rule out an intermediate form of CAM (Heyduk & al. 2016).

Similar as in *Yucca*, roots near the stem (“rain roots”) and at shallow soil depth play an important role in rapid water uptake after rainfalls (Nobel 1988: 38, 67 & seq., North & Baker 2007), likely based on the fact that the internal anatomy continues to appear more reminiscent of young roots with living cortical cells, despite the suberization of the external root tissues (North & Baker 2007). Rapid water uptake occurs close to the stem and in the distal parts of the root system, while the mid-root sections rapidly lose water uptake abilities (North & al. 2004).

64% of the examined species had contractile roots close to the stem (North & al. 2008), 85% in Subgen. *Agave* but only 47% in Subgen. *Littaea*. Contraction is achieved by radial expansion and longitudinal shortening of the cells of the inner and/or middle cortex, accompanied by a lack of suberization (North & al. 2008). Root contraction occurs already in young seedlings, which may be pulled into the soil for up to nearly 60 mm/year (average 34.7 mm/year in the 16 species studied; North & al. 2008).

**Inflorescence development:** Depending on the species, the vegetative phase may last 6–55 years, during which water and carbohydrates are accumulated in stems and leaves (Slauson 2002a: 10). In *A. deserti*, the percentage of flowering rosettes in a population varied from 3.8% in a peak year to only 0.08% in the subsequent year (Nobel 1992) and depends on the number of wet days in the previous 2 years (Nobel 1988: 92). 68% of the energy stored by the plant is diverted into inflorescence development, and the water required by the inflorescence is fully provided by the leaf water reserves (Nobel 1988: 91). The inflorescences may grow over 10 cm per day (Nobel 1988: 91; *A. lechuguilla* inflorescences may grow up to 20 cm per day and may attain full height in 3–4 weeks).

Scattered reports of polycarpic rosettes flowering repeatedly from leaf axils are discussed by Zona (2018), and are dismissed as relating to

aberrant specimens. Some species (from Sect. *Juncineae* and Sect. *Micracanthae*) are described as “polycarpic” or with “lateral” inflorescences, but such inflorescences are in fact likely in a terminal position on underdeveloped rudimentary lateral rosettes. Lev-Yadun (2017) discusses the proper use of the term monocarpic in relation to clonal species that are polycarpic, but with individual monocarpic rosettes.

**Pollination biology:** *Agave* has a broad variation in floral morphology, colour and size. In general, a broad spectrum of diurnal (hummingbirds and other birds, bees and other hymenoptera, other insects) as well as nocturnal flower visitors (nectar- and pollen-feeding bats, sphingids and moths) has been observed. Many studies were carried out on species in the S USA and Mexico; data on Caribbean and Mesoamerican species and for species of Subgen. *Manfreda* are sparse. For further information and references, see the following paragraphs. Reviews are provided by Slauson (2002a) and Rocha & al. (2006).

Subgen. *Agave*: The flowers are robust, of pale colour, pollen (with high protein content) is abundant, and nectar (abundant, with low sugar concentration) is produced mainly at night, which, together with proterandrous flowers and often a smell of ripening fruit, suggests adaptation to bat pollination (chiropterophily; Slauson 2002a: 14, Rocha & al. 2006: 335). First studies suggested that species of Subgen. *Agave* are mainly pollinated by bats (Rocha & al. 2006: 335), but recent studies showed many species to exhibit a broader range of floral visitors (birds, bees, bats, moths; Rocha & al. 2006: 335), suggesting that diurnal and other nocturnal pollinators are more important than previously thought (Slauson 2002a: 18). Several species are assumed to provide, when in bloom, a “nectar corridor” for migrating nectarivorous bats (Slauson 2002a: 16). Some species (e.g. *A. havardiana*, *A. subsimplex*) have a multiple pollinator syndrome with diurnal and nocturnal nectar production and stigma receptivity, and diurnal and nocturnal visitors that may be equally effective. *A. palmeri* and *A. chrysantha* both show floral shifts from nocturnal bat to diurnal pollination, allowing for multiple pollinators where bats are

infrequent and not important for pollination. *A. mckelveyana* occurs outside the range of nectar-feeding bats and is pollinated by hummingbirds and diurnal insects. For Caribbean species, few casual observations are reported only. *A. braceana* and *A. caymanensis* flowers are visited at day by birds, *A. grisea* nectar is exploited and *A. cajalbanensis* is pollinated by a bat.

Subgen. *Littaea*: Floral traits in Subgen. *Littaea* such as smaller floral tubes in a horizontal position, less abundant nectar with high sugar concentration, more attractive flower colours, and a sweet smell are associated with an insect pollination syndrome (Slauson 2002a: 15). Bees are indeed the most common and important pollinators, but bats, hummingbirds, and hawkmoths are also major visitors (Rocha & al. 2006: 335). Most species have a broader pollinator spectrum ensuring fruit set when the main pollinator fails. *A. parviflora* exhibits largely diurnal anther dehiscence and nectar production and is primarily visited by bumblebees. Nectar-feeding bats are the most important flower visitors in *A. difformis*, *A. garciae-mendozae*, *A. horrida* and *A. mitis*, but other pollinators (bees, hummingbirds, or hawkmoths) also occur. In *A. colimana*, bats are the sole observed visitors. *A. schottii* with mainly nocturnal nectar production favouring bat pollination, but a sweet fragrance, low protein content of the pollen, and yellow flowers favouring bee pollination, is possibly undergoing a shift from bat to bee pollination. *A. lechuguilla*, which is mainly pollinated by bees and hawkmoths, shows a latitudinal pattern in flower shape, colour and flower visitors: Flowers tend to be shorter, more open, and colourful in the N part of the range where the number of flower visits and fruit set decreases significantly.

Subgen. *Manfreda*: Species of Subgen. *Manfreda* remain sparsely studied. In Sect. *Manfreda*, seed set in *A. virginica* is mainly effected by nocturnal moths and hawkmoths, less so by bees. *A. scabra* is mainly pollinated by a long-nosed bat, minor pollinators are other bats, hawkmoths, and hummingbirds. In Sect. *Polianthes*, *A. coetocapnia* is visited by insects and hummingbirds; hummingbirds were also observed in *A. neocernua* and might be the usual



flower visitors also in other red-flowering species. For species with fragrant whitish flowers such as the Tuberose *A. amica*, hawkmoth pollination is assumed (Rocha & al. 2006: 334).

**Flowering and fruiting ecology:** Almost all Agaves are proterandrous: During the male phase on the first day(s), the anthers open and shed pollen; during the female phase in the last days, the style elongates, the stigma opens, and copious nectar is produced mainly during the night. *A. polianthiflora* appears to be the sole proterogynous species. Most species are self-incompatible (outbreeding). Only few species are reported to be self-compatible (e.g. *A. garciae-mendozae*, *A. horrida*), but cross-pollination is most effective for fruit set. In *A. colorata*, flowers pollinated by natural pollinators showed a much higher fruit set, more viable seeds and a higher germination rate compared to fruits obtained from self-pollination.

In Subgen. *Littaea*, inflorescences may have between 740 (*A. difformis*) and 3623 flowers (*A. garciae-mendozae*) of which 43.9% (*A. mitis*) to 60% (*A. garciae-mendozae*) develop into fruits. Inflorescences in Subgen. *Littaea* may release from 4000 (*A. striata*) to 142,725 viable seeds (*A. garciae-mendozae*); the seed production in *A. chrysoglossa* is estimated as 500,000–750,000 seeds per plant. In *A. palmeri*, flowering, nectar and pollen production, sugar concentration, and fruit and seed set in burn-damaged plants are as high as in unburned rosettes (Slauson 2002b). Fruit formation in *A. mckelveyana* appears to be resource- (nutrient) limited rather than pollinator- or pollen-limited.

**Seed dispersal and establishment:** In *Agave*, wind dispersal of the light-weight seeds seems to be the primary dispersal mechanism. Field studies showed that successful seedling establishment in *A. deserti* occurred only in 2 out of 29 years; from only 17 seedlings observed in an area with  $\pm 2900$  rosettes, 14 may reach maturity (Nobel 1992). The length of the first drought period is the limiting factor for establishment, with water-stress in the seedling stage as the single most important factor. Most successful seedlings are associated with

protective nurse plants (Nobel 1988: 87–88, 130). For a summary of many further ecological and ecophysiological studies on *A. deserti* see Nobel (1988). Seeds germinate both under light and dark conditions (Pavliscaak & al. 2015: for *A. palmeri*). A germination temperature of 30 °C produces optimal seedling emergence for *A. tequilana* and *A. mapisaga* (Ramírez-Tobías & al. 2016), while optimal germination temperatures of 25 °C were found for 8 further Mexican species (Ramírez-Tobías & al. 2012).

In *A. durangensis*, the seed morphology, germinability and phenolic profiles varied among 3 natural populations, and in *A. potatorum*, seeds from different localities show significant differences in size, weight, and germinability decreases with age.

**Ethnobotany:** The genus *Agave* is of considerable ethnobotanical importance due to its many-fold human uses on a household to industrial level. Agaves were consumed by humans at least 9000 years ago, and artefacts of *Agave* fibre and tools from *Agave* date from the same time (Gentry 1982: 5, 6). Cultivation of *Agave* began at least 6000 years ago (Nobel 1988: 4).

A summary of pre-hispanic culture of *Agave* in Mesoamerica and NW Mexico is provided by Radding (2012); Castetter & al. (1938) review its uses by native Americans in the SW USA, and Stewart (2015) gives an overview of past and possible future uses as beverage, food, sweetener, bioenergy and for fibres. Many data on the uses of single species are given by Bye & al. (1975: SW Chihuahua), Martin & al. (1998: NW Mexico: Río Mayo area), Hodgson (2001b: Sonoran Desert), and Delgado-Lemus & al. (2014: Tehuacán Valley). Colunga-García Marín & al. (2007) list vernacular names for 102 taxa used in Mexico.

The Mescalero Apaches were so named due to their use of *A. parryi* ssp. *neomexicana* for food (as “mescal”). Five species from Arizona (*A. delamateri*, *A. phillipsiana*, *A. sanpedroensis*, *A. verdensis*, *A. yavapaiensis*) occur always or predominantly associated with pre-Columbian living sites of native Americans, and apparently represent cultivars developed by pre-Columbian

people for food or fibre. *A. americana* var. *expansa*, *A. decipiens* and *A. murpheyi* are further pre-Columbian cultigens. *A. parryi* ssp. *parryi* and var. *huachucensis* include ancient anthropogenic populations planted by native Americans that persisted for up to 600 years.

**Domestication:** Uses of *Agave* range from harvesting wild populations or its management to cultivation on a household to plantation (industrial) level. Several species show domestication gradients, such as the different cultivars subsumed under *A. fourcroydes* that show different degrees of similarity with its wild progenitor *A. angustifolia*, and *A. inaequidens* (wild and cultivated) apparently gave rise to *A. hookeri*, which is exclusively cultivated. The domestication syndrome (direction of human selection) includes gigantism (larger leaves and rosettes), greater fibrosity (in fibre plants) or higher sugar contents (in *A. tequilana* landraces), less pronounced thominess, and reduced sexual reproductive capacity (often even sterility) (Colunga-García Marín & al. 1996, Colunga-García Marín & May-Pat 1997, Ramírez-Tobías & al. 2016). *A. tequilana* (used for tequila), *A. fourcroydes* and *A. sisalana* (both used for fibre) are domesticated “species” derived from *A. angustifolia* (*A. tequilana*, *A. fourcroydes*) or of possible hybrid origin involving *A. angustifolia* or *A. kewensis* (*A. sisalana*).

**Alcoholic beverages:** Alcoholic beverages from Agaves include those produced from the sap of living plants, consumed fresh as aguamiel or fermented as pulque, and distilled liquors known as mescal (alternative spelling mezcal) or tequila. Pulque was developed from aguamiel by the Aztecs at the end of the twelfth century and incorporated into religious and mystical ceremonies which were associated with several gods, including Mayahuel, the Aztec goddess of pulque (Gentry 1982: 8). Many *Agave* species are harvested for pulque from natural populations or are cultivated (e.g. *A. americana* s.l., *A. atrovirens* var. *mirabilis*, *A. hookeri*, *A. marmorata*, *A. salmiana* ssp. *salmiana*, *A. weberi*). Further fermented beverages are produced regionally, e.g., “sugui”, a strong alcoholic beverage from baked stems and leaf bases of *A. bovicornuta*, *A. multiflifera* or *A. wocomahi* in NW Mexico. Torres & al. (2015)

provide a list of 37 species that are extracted from natural populations for mescal production. The increased demand for *Agave*-derived alcoholic beverages results in intensified development of agricultural use, which diminishes food availability for pollinators, and concurrently negatively impacts genetic diversity (Trejo-Salazar & al. 2016). According to these authors, a bat-friendly approach would be to allow 5% of the plants to flower — applying such an approach to the whole current total population of *A. tequilana* would feed 2.3 million bats per month. For *A. cupreata*, Torres & al. (2015) suggest to conserve at least 30% of the reproductive plants of a population to ensure natural or assisted population recovery.

The distilled beverage mescal may be produced from any species of *Agave* and is officially produced mainly in Oaxaca and also in Tamaulipas, Durango, Zacatecas, San Luis Potosí, Guanajuato, Guerrero, Puebla and Oaxaca. It includes regional variants such as bacanora in Sonora. Species used include *A. angustifolia*, *A. cupreata*, *A. durangensis*, *A. inaequidens*, *A. lyobaa*, *A. marmorata*, *A. montium-sancticaroli*, *A. potatorum*, and *A. salmiana* ssp. *crassispina*. According to Mexican law, tequila can only be produced in Jalisco from the cultivar ‘Azul’ of *A. tequilana* (see there for details). The landscape around the town of Tequila (Jalisco, Mexico) where *A. tequilana* ‘Azul’ is cultivated in large plantations was declared as UNESCO World Heritage “Agave Landscape and Ancient Industrial Facilities of Tequila” in 2006.

Enormous areas are planted with *Agave* species to meet the demand of the beverage industry – Fig. 1. Alone for Oaxaca, an area of 15,500 hectares is planted with mostly *A. angustifolia*, resulting in a primary production of 2.9 million litres of mescal per year (Chagoya-Méndez 2004 cited in Martínez-Gutiérrez & al. 2013). The stupendous amount of bagass waste of the mescal industry is currently underused but could be employed for soil-less vegetable production (Martínez-Gutiérrez & al. 2013).

**Fibre:** Many *Agave* species are used locally for fibre, e.g. *A. cocui*, *A. ghiesbreghtii*, *A. multiflifera*, and *A. quiotepensis*. For large-scale



**Fig. 1** Enormous areas are devoted to commercial plantations with species and cultivars of *Agave*, such as *Agave* ‘Azul’ for tequila production. (Source: Flickr/Sergio Niebla, CC BY-SA)

fibre production, *A. lechuguilla* is harvested from wild populations, and *A. fourcroydes* and *A. sisalana* are cultivated on industrial level in plantations (see under these species). Fibres and textiles traded in Morocco under the name of “Agave silk” (or “cactus silk”) have nothing to do with *Agave* fibres, and have been found to consist of viscose fibres (U. Egli, pers. comm.).

**Food:** Stems (hearts) are eaten cooked or pit-baked (*A. americana* var. *expansa*, *A. jaiboli*, *A. marmorata*, *A. multiflifera*, *A. pelona*) or made into mescal bread (“mesagoli”, *A. americana* var. *expansa*, *A. multiflifera*, *A. wocomahi*) or sweet food (*A. polianthiflora*). *A. kerchovei* plants are used as food for humans. Flower buds (“cacayas”) are prepared boiled and cooked in various stews (*A. bovicornuta*, *A. durangensis*, *A. graciellae*, *A. gypsicola*, *A. maximiliana* var. *maximiliana*, *A. quioatepecensis*), or also eaten dried (*A. gypsicola*) or in the form of tortillas (*A. bovicornuta*), sometimes washed to remove the bitterness (*A. bovicornuta*). Sometimes, flowers are eaten, too (*A. gypsicola*). (Young) inflorescences (“quiotes”) are cooked and eaten as stew or sweets (*A. graciellae*, *A. gypsicola*, *A. jaiboli*, *A. marmorata*). In recent years, unfermented concentrated juice

(“Agave syrup”) has gained some importance as sweetener.

Giant bugs feeding on inflorescences of *A. triangularis* are also used as food item. Leaf cuticles (“mixiote”) from *Agave* leaves are used to envelop food (Delgado-Lemus & al. 2014: 7), and the illegal removal from leaves of plantation plants negatively affects growth rates (José Jacinto & García Moya 2001). In order to prevent thefts of cuticles, small holes are made into the central leaf bud, which renders the cuticles useless for “mixiote” production, but does not affect leaf unfolding rates (García-Moya & Nobel 1990).

**Animal fodder:** Young or also old plants and inflorescences are used as fodder mainly for cattle and goats (Delgado-Lemus & al. 2014: 7; see also under *A. kerchovei*, *A. quioatepecensis*), sometimes also the flowers (*A. kerchovei*).

**Medicine and poison:** Roasted leaves, leaf infusions, tonics and tinctures are used as anti-inflammatory, analgesic and anticoagulant treatments, and to relieve luxation pains, stomach ache, cold, fever, bronchitis, and for whetting appetite and treating rheumatic and traumatic pains (Delgado-Lemus & al. 2014: 7). *A. paniculata* and *A. petskinil* are used against headache,



species of Sect. *Manfreda* (*A. brunnea*, *A. maculosa*, *A. variegata*, *A. virginica* ssp. *virginica*) are used as antidote against snakebites, and *A. vilmoriniana* is used to stupefy fish.

**Fencing and construction:** Agaves may be used as live fences or hedges (*A. americana* var. *expansa*, *A. ghiesbreghtii*, *A. hurteri*, *A. karatto*, *A. striata* ssp. *striata*, *A. tecta*), also on rock walls (*A. hurteri*), and dried inflorescences may also be used (*A. gypsicola*).

Several species are used as wooden material for supporting roofs, walls and fences. Peduncles are employed as water pipes, leaves for thatching, and fibre cords for tiding house structures (Delgado-Lemus & al. 2014: 7). Large peduncles are used for manufacturing ladders, and thinner, longer peduncles as pole vaults for collecting fruits (Delgado-Lemus & al. 2014: 7). Inflorescence stalks may be used as arrow shafts (*A. polianthiflora*).

**Ritual and religious:** Several species are used for decorating altars (Delgado-Lemus & al. 2014: 7; see also *A. marmorata*) or for curing and death ceremonies (*A. shrevei*). Dried inflorescences of *A. missionum* are used as Christmas tree.

**Ornamental:** Many species are locally planted as ornamentals (Delgado-Lemus & al. 2014: 7). Species of sect. *Polianthes* are locally used as ornamentals (*A. neonelsonii*, *A. rosei*) or harvested for the cut-flower trade (*A. dolichantha*). The “Tuberose” (*A. amica*) has attracted considerable interest from the cut-flower trade.

**Biofuel:** Remains of dead adult large-sized species are used locally as firewood (Delgado-Lemus & al. 2014: 7). For the industrial use for biomass and biofuel production, see Garcia-Moya & al. (2011) and Davis & al. (2011). Under optimal conditions, productivity of *Agave* plantations attains 40 tons dry weight per hectare per year. Mechanized large-scale production is a challenge, however (Stewart 2015). Industrial ethanol production using *Agave* is more costly than using corn or sugar cane as basis (Núñez & al. 2011).

**Chemistry:** Due to high saponin contents, species esp. of Sect. *Manfreda* (*A. brunnea*, *A. hauniensis*, *A. maculosa*, *A. paniculata*, *A. petskinil*), but also *A. cocui* and *A. vilmoriniana*

are used as soap, bath, laundry and shampoo. The chemistry and bioactivities of the steroidal saponins of *Agave* are reviewed by Sidana & al. (2016); for the industrial potential as source of saponins as antinutritional factors and anticancer, antifungal, and anti-inflammatory agents, see Santos-Zea & al. (2012).

For the industrial potential of Agaves as source of polyphenols with anticancer, antioxidant, anti-diabetic, anti-inflammatory, antiparasitical, antimicrobial, and prebiotic activities, see Santos-Zea & al. (2012) and Almaraz-Abarca & al. (2013a).

**Horticulture:** Many *Agave* species are cultivated world-wide esp. in Mediterranean climates, in the arid S USA also for “desert landscaping” (see Starr 2012). Many species are naturalized world-wide; naturalized species near Valencia, Spain, are listed by Guillot Ortiz & Meer (2003a), at the central W coast and SE coast of Portugal by Silva & al. (2015) and Smith & Figueiredo (2008), and in the Cape Floristic Region, RSA, by Smith & Klopper (2007). Species cultivated in (sub-)tropical regions might be threatened by the Agave Snout Weevil (*Scyphophorus acupunctatus*) (see Smith & al. 2012). Control of neophytic *A. americana* on the Canary Islands was most effective combining removal of adults with herbicide spraying of juveniles, but with significant recovery 4 years after the treatment (Arévalo & al. 2015).

In cultivation, variegated cultivars are increasingly popular. Early listings of known variegates are given by Koch (1862) and Trelease (1908b). Many named cultivars and also unnamed examples are shown by Starr (2012), Pilbeam (2013), Starr (2014), and Moore (2016). Keys to variegated and other cultivars grown in Spain are provided by Guillot Ortiz & Meer (2003a) and Guillot Ortiz & al. (2008). In *A. americana*, cultivars with various degrees of variegation are common, and sometimes also naturalized, e.g. in Spain (Guillot Ortiz & Meer 2003a, Guillot Ortiz & al. 2012: as *A. ingens*) or Portugal (Smith & Figueiredo 2008). The origin and genetics of variegated cultivars is dealt with by Zonneveld (2007). Methods for large-scale propagations of

useful *Agave* species are described by Binh & al. (1990).

Artificial *Agave* hybridisation started in 1865 with *A.* × *hybrida* (see there). Trelease (1914) listed the interspecific hybrids known at that time. Hybrids between species of Subgen. *Agave* and Subgen. *Littaea* and with and between species of the former genera *Manfreda*, *Polianthes* and *Prochnyanthes* show that crossing barriers within *Agave* s.l. are weak or absent: Examples for crosses of Subgen. *Agave* × Subgen. *Littaea* are *A.* × *engelmannii*, *A.* × *guignardii*, *A.* ‘Blue Flame’ (see under *A. attenuata* ssp. *attenuata*), and *A.* ‘Royal Spine’ (see under *A. macroacantha*), examples for crosses of *Manfreda* × *A.* Subgen. *Agave* or Subgen. *Littaea* (= × *Mangave*) are *A.* × *gonzaloii*, *A.* ‘Bloodspot’ (see under *A. macroacantha* and *A. maculosa*), *A.* ‘Macho Mocha’ (see under *A. variegata*), and *A. spicata* (?). Crosses also exist for *Manfreda* × *Polianthes* (= × *Polifreda*; Lindstrom (2006), Ritchie & Lindstrom (2014); see under *A. virginica* ssp. *virginica*), and *Polianthes* × *Prochnyanthes* (*A.* × *neokewensis*). In the white-flowered Tuberose *A. amica*, modern hybrids were obtained from crossings with other species of Sect. *Polianthes* with other flower colours (see there).

The following species may be hardy outdoors in C Europe in mild climates and/or with rain protection: *A. havardiana*, *A. parryi* and ssp. *neomexicana* (as *A. neomexicana*), *A. utahensis* (Boeuf 2007), and *A.* × *glomeruliflora* (see there).

The following names are of unresolved application but are referred to this genus: *Agave abortiva* A. Terracciano (1885); *Agave aloides* Jacobi (1866); *Agave americana* Grisebach (1864) (*nom. illeg.*, ICN Art. 53.1); *Agave aspera* A. Terracciano (1885) (*nom. illeg.*, ICN Art. 53.1); *Agave attenuata* var. *subdenudata* hort. ex Trelease (1892); *Agave banlan* Perrotet (1824); *Agave baxteri* Baker (1888); *Agave bennetii* hort. ex A. Berger (1915); *Agave bernhardii* Jacobi (1868); *Agave bonnetii* hort. ex A. Berger (1915); *Agave calderonii* Trelease (1923); *Agave caribaea* Verschaffelt (1873); *Agave chloracantha* Salm-Dyck (1842) (*nom. inval.*, ICN Art. 38.1a); *Agave concinna* Lemaire in Hort. Vanhoutte

(1846); *Agave cookei* Woodrow (1899); *Agave cucullata* Lemaire ex Jacobi (1865); *Agave davillonii* Baker (1892); *Agave deamiana* Trelease (1915); *Agave decaisneana* Jacobi (1868); *Agave diacantha* Royle (1855); *Agave elizae* A. Berger (1915); *Agave entea* Hartwich (1897); *Agave erosa* A. Berger (1915); *Agave flaccida* Jacobi (1866) (*nom. illeg.*, ICN Art. 53.1); *Agave fourcroydes* Jacobi (1865) (*nom. illeg.*, ICN Art. 53.1); *Agave fragrantissima* Jacquin (1762); *Agave* × *franzosinii* Hort. Hanbury ex W. Watson (1889) (*nom. inval.*, ICN Art. 32.1c?); *Agave friderici* A. Berger (1912); *Agave galeottei* Baker (1877); *Agave glabra* Karwinsky in M. Roemer (1847); *Agave glaucescens* Otto in M. Roemer (1847) (*nom. inval.*, ICN Art. 32.1c?); *Agave grandibracteata* Ross (1892); *Agave granulosa* Scheidweiler ex K. Koch (1861); *Agave guedeneiryi* Houlllet (1875); *Agave gutierreziana* Trelease (1920); *Agave henriquesii* Baker (1887); *Agave heteracantha* A. Berger (1898) (*nom. illeg.*, ICN Art. 53.1); *Agave horizontalis* Jacobi (1868); *Agave horizontinalis* Baker (1887) (*nom. inval.*, ICN Art. 61.1); *Agave humboldtiana* Jacobi (1866); *Agave inghamii* hort. ex Verschaffelt (1872) (*nom. inval.*, ICN Art. 38.1a?); *Agave inghamii* [?] *longissima* Hort. Whitacker ex A. Berger (1915); *Agave ixtli* K. Koch (1860) (*nom. illeg.*, ICN Art. 53.1); *Agave kellermaniana* Trelease (1915); *Agave killischea* Rafarin (1874); *Agave lamprochlora* Jacobi (1868); *Agave laticincta* Verschaffelt (1868); *Agave leguayana* Baker (1877) (*nom. illeg.*, ICN Art. 53.1); *Agave leguayana* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); *Agave lemairei* Hort. Verschaffelt ex Ill. Hort. (1864); *Agave lempana* Trelease (1925); *Agave lindleyi* Jacobi (1868); *Agave littaeoides* Pampanini (1909); *Agave longisepala* Todaro (1878); *Agave maculata* Regel (1856); *Agave maculata* hort. ex A. Berger (1915) (*nom. illeg.*, ICN Art. 53.1); *Agave malinczii* Hort. Tonel ex K. Koch (1862); *Agave maximowicziana* Regel (1890); *Agave milleri* Salm-Dyck (1834) (*nom. illeg.*, ICN Art. 53.1); *Agave minarum* Trelease (1915); *Agave monostachya* Sessé & Moçño (1894); *Agave monstrosa* Rafarin (1874); *Agave mooreana*

Masters & T. Moore (1874) (*nom. inval.*, ICN Art. 36.1a); *Agave muelleriana* A. Berger (1915); *Agave multiflora* Todaro (1890); *Agave nigra* Bassols (1870) (*nom. inval.*, ICN Art. 38.1a); *Agave nigromarginata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); *Agave nirvana* Herbin & Robins (1968) (*nom. inval.*, ICN Art. 39.1, 40.1); *Agave nissonii* Baker (1874); *Agave ortgiesiana* Todaro (s.a.) (*nom. illeg.*, ICN Art. 53.1)  $\equiv$  *Agave filifera* fa. *ortgiesiana* (Todaro) H. Jacobsen (1954) (*nom. inval.*, ICN Art. 41.4); *Agave pallida* Sartorius ex Jacobi (1865) (*nom. illeg.*, ICN Art. 53.1); *Agave pampaniniana* A. Berger (1915); *Agave paupera* A. Berger (1915); *Agave pavoliniana* Pampanini (1910); *Agave perlucida* Jacobi (1868); *Agave perringea* Rafarin (1874); *Agave planera* Fasio (1903) (*nom. inval.*, ICN Art. 32.1c); *Agave polyacantha* Haworth (1821); *Agave polyacantha* Jacobi (1865) (*nom. illeg.*, ICN Art. 53.1); *Agave potatorum* K. Koch (1860) (*nom. illeg.*, ICN Art. 53.1); *Agave pringlei* hort. ex A. Berger (1912); *Agave prostrata* Martius ex Dragendorff (1898) (*nom. inval.*, ICN Art. 32.1c); *Agave pulcherrima* Otto in M. Roemer (1847); *Agave pulverulenta* Verschaaffelt (1863); *Agave pumila* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); *Agave purpurea* Souza Novelo (1941) (*nom. inval.*, ICN Art. 39.1); *Agave ragusae* Todaro (1897); *Agave regia* Baker (1877); *Agave robusta* Rafarin (1874); *Agave rohanii* hort. ex A. Berger (1915) (*nom. illeg.*, ICN Art. 53.1); *Agave rudis* Lemaire ex Jacobi (1865); *Agave saponifera* H. Grothe (1880); *Agave scolymus* D. Dietrich (1843) (*nom. illeg.*, ICN Art. 53.1); *Agave scolymus* Kunth (1850) (*nom. illeg.*, ICN Art. 53.1); *Agave serrata* Hort. Tonel ex K. Koch (1862); *Agave serrulata* Steudel (1841); *Agave silvestris* hort. ex A. Berger (1915); *Agave smithiana* Jacobi (1866); *Agave sordida* A. Berger (1915); *Agave subinermis* M. Roemer (1847); *Agave taeniata* Hort. Tonel ex K. Koch (1862); *Agave teoxomuliana* Karwinsky ex M. Roemer (1847); *Agave thomsoniana* Jacobi (1866); *Agave toeniata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); *Agave toneliana* Hort. Tonel ex K. Koch (1862);

*Agave toneliana* Baker (1881) (*nom. illeg.*, ICN Art. 53.1); *Agave toneliana* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); *Agave troubetskoyana* Baker (1892); *Agave vandervinnenii* Lemaire (1864); *Agave viridissima* Baker (1877); *Agave vivipara* Salm-Dyck (1859) (*nom. illeg.*, ICN Art. 53.1); *Agave washingtonensis* Rose (1898); *Agave watsonii* J. R. Drummond & C. H. Wright (1907); *Agave weissenburgensis* Wittmack ex Baker (1889) (*nom. inval.*, ICN Art. 61.1?); *Agave wercklei* Trelease (1920); *Agave wiesenburgensis* Wittmack (1885); *Agave wiesenburgensis* Wittmack (1885) (*nom. inval.*, ICN Art. 61.1); *Agave wildringii* Britton (1911); *Agave zuccarinii* Otto (1842); *Polianthes ensifolia* hort. ex Steudel (1840); *Polianthes purpurea* Dean (1874); *Polianthes pygmaea* Jacquin (1793).

**A. abisaii** A. Vázquez & Nieves (Syst. Bot. 38 (2): 321–323, ills., 2013). **Type:** Mexico, Jalisco (*García-Mendoza & al.* 6414 [MEXU, IBUG, MEXU]). — **Distr:** Mexico (S Jalisco); limestone outcrops in tropical dry forests, 640–800 m; flowers February to March. **I:** Vázquez-García & al. (2007b: figs. M5–M8, as *A. gypsophila*); Hochstätter (2015: VI: 25); Meer (2016d).

[2n] **Ros** 0.95–1 × 1.5 m, surculose; **L** 9–11, linear to narrowly lanceolate to obtrullate, generally arching, firm but brittle, guttered, wider above the base, abaxially with a transversal or longitudinal wrinkle at the base, smooth, 80–90 × 9–13 cm, to 7 cm wide and to 3.5 cm thick at the base, light to dark green, not evidently cross-banded, abaxially glaucous at the base; **marginal teeth** firm, closely set, on prominences 3–4 × 2.5–3 mm, teeth mostly curved, 1–3 mm from a broad base 2–5 mm wide, 6–17 mm apart in the middle of the leaf, regularly spaced, dark brown, intervening margin concave, involute, with few denticles; **terminal Sp** conical, firm, 4–5 mm, dark brown, not decurrent; **Inf** 2.5–3 m, paniculate, peduncle with triangular **Bra** to 7.5 cm long at the base, fertile **Inf** part oblong, occasionally with numerous red bulbils, part-**Inf** 13 in the upper 1/3, with 30–38 flowers; **Fl** 28.5–35.5 mm; **Tip** tube funnellform, 2.5–3.5 × 6–8 mm (at the mouth), green, lobes triangular, erect, fleshy, 14–16

**Fig. 2** *Agave acicularis*  
(Etter & Kristen 4130:  
Cuba, ± 40 km SE of  
Cienfuegos, 20 m).  
(Copyright: J. Etter &  
M. Kristen)



× 2.5–4 mm, orange, apex galeate; **Fil** 18–25 mm, inserted 1 mm above the tube base; **Anth** centric, 8–10 mm, yellow; **Ov** 12–16 × 2–3 mm; **Sty** shorter than the filaments; **Sti** capitate; **Fr** oblong, slender, 22 × 10 mm, shortly stipitate, apiculate; **Se** crescent-shaped, thin, flat, membranous, 3–4 × 2–3 mm, black.

The recent study of the *A. gypsophila* group by Vázquez-García & al. (2013) has led to a narrower re-circumscription of *A. gypsophila* and the description of this and 3 further new species (*A. andreae*, *A. kristenii*, *A. pablocarrilloi*). According to the protologue, *A. abisaii* is most similar to *A. gypsophila* s.s. in having rosettes with few smooth green leaves, but differs by having suckering rosettes, linear to narrowly obtrullate leaves with a glaucous base and with transversal or longitudinal wrinkles at the abaxial base, regularly spaced marginal teeth at mid-leaf, orange flowers, red bulbils on the inflorescence, smaller inflorescences with fewer branches, and smaller capsules. Material belonging to *A. abisaii* was formerly placed in *A. gypsophila* by Gentry (1982). Newton (2004: as *A. gypsophila*) provides photographs of the rosette, inflorescence, flowers and bulbils.

**A. acicularis** Trelease (Mem. Nation. Acad. Sci. 11: 34, t. 52, 1913). **Type:** Cuba, Santa Clara (*Britton & al.* 5926 [MO, MEXU, NY]). — **Lit:** Berger (1915: 208); Álvarez de Zayas (1996: 119–121, with ills.); Guillot Ortiz & Meer

(2011: with ill.). **Distr:** C Cuba (Matanzas: Rio San Juan) rocky cliffs and quartzite outcrops in tropical dry forests, 250 m; flowers January to March. **I:** Etter & Kristen (1997+: accessed 2016). – Fig. 2.

[2p] Acaulescent, **Ros** solitary; **L** lanceolate, 90–105 × 8–14 (–16) cm, green to slightly greyish, dull; **marginal teeth** gently upcurved, triangular from a somewhat lenticular base, 1–4 × 1–3 mm, chestnut-brown, 8–20 mm apart, more distant (to 25 mm) in the lower leaf parts and larger (4 mm) and reflexed, occasionally with outcurved point, intervening margin slightly repand; **terminal Sp** stoutly acicular, straight, subtriangularly grooved below the middle, smooth, (5–) 9–20 (–25) × 1.5–3 mm, grey-brown, slightly glossy, not decurrent; **Inf** paniculate, 3–6 m, peduncle with narrow triangular **Bra**, fertile part oblong, part-**Inf** ±25, in the upper ¾ of the inflorescence, 29–33 cm, not known to be bulbiferous; **Ped** 5–11 mm; **Fl** (35–) 38–47 mm; **Tep** yellow, wilting golden-yellow, tube open, 4–6 × 7–8 mm, lobes 11–16 × 4 mm, about ½ as long as the ovary; **Fil** 25–35 mm, inserted slightly below the throat; **Anth** 10–13 mm; **Ov** oblong-fusiform, 25 mm; **Sty** longer than the filaments; **Sti** capitate; **Fr** cylindrical, 35–43 × 15–17 mm, stipitate, apex rostrate; **Se** triangular, 6–7 × 4–5 mm.

Differs from *A. brittoniana* esp. in its narrower lanceolate leaves with non-decurrent terminal spine, and from *A. grisea* in its smaller leaves. Known from one population at the bank of the Río



San Juan only (Álvarez de Zayas 1996) and classified as “Endangered” (Berazaín & al. 2005).

**A. acklinicola** Trelease (Mem. Nation. Acad. Sci. 11: 41, t. 91, 1913). **Type** [syn]: Bahamas, Acklin Island (*Brace* 4442 & s.n. [NY, MO]). — **Lit**: Berger (1915: 204–205); Britton & Millspaugh (1920: 75–76); Correll & Correll (1982: 309); Freid & al. (2014: 210–211, 217). **Distr**: Bahamas (Acklins, Crooked and Mayaguana Island); tropical dry forests. **I**: Hochstätter (2015: VII: 82).

[2r] Acaulescent, **Ros** solitary; **L** rather narrowly lanceolate, fleshy, curved, concave, occasionally somewhat guttered, 180–300 × 15 cm, dull greyish; **marginal teeth** straight or gently curved, rather acuminate deltoid, often from oblique green prominences or with lenticular bases, 1–1.5 mm, 5–10 mm apart, intervening margin nearly straight; **terminal Sp** conical, somewhat flexuously recurved, involutely grooved to or beyond the middle, smooth, 20–25 × 4–6 mm, red-brown, becoming grey, glossy, decurrent; **Inf** paniculate, peduncle thick, with triangular **Bra**, fertile part broadly ovoid; part-**Inf** ±20 in the upper  $\frac{2}{3}$  of the inflorescence, not known to be bulbiferous; **Fl** bright yellow, not further known; **Fr** and **Se** not known.

According to the protologue with the “aspect of *A. bahamana*” (see also the note there).

**A. ×ajoensis** W. C. Hodgson (Novon 11(4): 414–415, ills., 2001). **Type**: USA, Arizona (*Hodgson & al.* 4478 [DES, ORPI]). — **Lit**: Parker (2018a: 21, with ill.). **Distr**: USA (S Arizona); rocky slopes in desert scrub and grasslands, 900–1100 m; flowers late spring to summer. **I**: Pilbeam (2013: 17); Hochstätter (2015: VIII: 65–66).

[1e × 2i] This is the sterile hybrid *A. deserti* ssp. *simplex* × *A. schottii* var. *schottii*. It is known in nature from 1 population with 28 clones in the Ajo Mts. within the Organ Pipe Cactus National Monument in S Arizona only and was first misidentified as *A. schottii* var. *atricha* (= *A. schottii* var. *treleasei*), but differs in being much lighter in colour (Parker 2018a). The hybrid is triploid (2n = 90), while sympatric ssp. *simplex* is diploid (2n = 60) and var. *schottii* is tetraploid (2n = 120) (protologue and Reveal & Hodgson (2002)).

**A. aktites** Gentry (US Dept. Agric. Handb. 399: 148–150, ill., 1972). **Type**: Mexico, Sinaloa (*Gentry* 11470 [US, ARIZ, ASU, MEXU, MICH]). — **Lit**: Gentry (1982: 555–559, with ills.). **Distr**: Mexico (Sonora, N Sinaloa); sand dunes with coastal thorn forests; flowers February to April. **I**: Richter (2011: 76); Pilbeam (2013: 18); Hochstätter (2015: VII: 28).

[2g] Stems broadly globose; **Ros** 40–70 × 60–110 cm, surculose; **L** linear, straight, patulous, unequal within a rosette, broadly clasping at the base, convex below, nearly flat above, smooth or asperous, 40–60 × 2–4 cm, bluish-glaucous-grey, sometimes with transverse zonal pattern; **marginal teeth** generally antrorse, with slender flexuous tips, 3–5 mm, irregularly spaced, 10–30 or 40–50 mm apart; **terminal Sp** abruptly subulate, usually broad at the base and flattened above, 12–20 mm, dark brown to greyish; **Inf** 1.8–4 m, paniculate, narrow, part-**Inf** 10–15 in the upper  $\frac{1}{4}$ – $\frac{1}{3}$  of the inflorescence, short, small; **Fl** 64–70 mm; **Tep** pale greenish (Gentry) or light yellow (Etter & Kristen 1997+), sticking together and not opening properly, quickly wilting, tube cylindrical to globose, narrowly grooved, 14–16 × 12–16 mm, thick-walled below the filaments, lobes long-linear, soon infolding and becoming spatulate with broadly rounded hooded tips, unequal, the outer larger, closely overlapping the inner, 21–25 mm; **Fil** 40–50 mm, inserted at wide angles 8–10 mm above the base of the tube; **Anth** slender, extremely excentric, 23–29 mm; **Ov** angulate-cylindrical, 26–31 mm, neck constricted, tapering to the pedicel; **Sty** longer than the stamens after anthesis; **Sti** capitate; **Fr** linear-oblong when still unripe; **Se** unknown. — **Cytology**: 2n = 60 (Palomino & al. 2010).

This is the only Mexican *Agave* growing naturally and regularly in the maritime zone of beach dunes, to which habitat it appears to be narrowly endemic. The widespread *A. angustifolia* is common in the same region, but *A. aktites* can usually be distinguished from it by its smaller size and narrow bluish leaves (Gentry 1982: 558). Palomino & al. (2010) found some evidence for spontaneous heterozygous chromosomal exchange in 2 studied populations, indicating an actively differentiating genome.

**A. albescens** Trelease (Mem. Nation. Acad. Sci. 11: 44, tt. 53, 116, 1913). **Type:** Cuba (Britton 2085 [MO, NY, US]). — **Lit:** Berger (1915: 273); Greulich (2010: with ills.); Kunte (2013: with ills.). **Distr:** SE Cuba; calcareous soils in coastal and near-coastal xerophytic scrub. **I:** Pfendbach (2005: 76); Richter (2010: 39); Richter (2011: 92–93); Kattermann (2012: 12); Pilbeam (2013: 19–21); Rigerszki & al. (2013: 257); Hochstätter (2015: VII: 89, 96); Lodé (2015).

[2q] Acaulescent, **Ros** solitary, rarely suckering at the base; **L**  $\pm$ 30–40, oblong-lanceolate, flattish, slightly rough,  $\pm$ 45  $\times$  15 cm, light grey, dull, passing to glaucous, sometimes transversely banded, margins nearly straight; **marginal teeth** usually straight or gently curved, broadly triangular or acuminate deltoid, 2–3 mm, dark brown,  $\pm$ 10 mm apart, from broad deltoid prominences; **terminal Sp** conical, somewhat recurved, shallowly grooved or involute below the middle, dull, sometimes roughened except at the tip, 15  $\times$  4 mm, blackish chestnut-brown, very shortly decurrent; **Inf** paniculate, 5 m, with  $\pm$ 30 ascending part **Inf** in the upper  $\frac{3}{4}$ ; **Ped** slender, 10 mm; **Fl** 30–35 mm; **Tep** golden-yellow, tube open, 5–6 mm, lobes 12–14  $\times$  4 mm; **Fil** 35 mm, inserted somewhat below the throat of the tube; **Ov** fusiform, 15 mm; **Sty** longer than the filaments; **Fr** and **Se** unknown.

A small species variable in leaf characters. According to the protologue, it differs from the few other grey-leaved Cuban species in the granular roughening of the leaves and the finally purplish-black colour of the terminal spine and marginal teeth. Habitat photographs and cultivated plants indicate that the rosettes are likely surculose (Greulich 2010, Richter 2010, Richter 2011), whereas the protologue describes them as solitary. The species may form natural hybrids with *A. underwoodii* (Richter 2010: 41). It is classified as “Least Concern” in the Cuban Red List (Berazain & al. 2005).

**A. alboaustralis** (E. Solano & Ríos-Gómez) Thiede (Bradleya 33: 83, 2015). **Type:** Mexico, Oaxaca (Solano & Ríos 2516 [MEXU, CHAPA, FEZA, IAMIZ, IEB, OAX]). — **Lit:** Solano &

Ríos-Gómez (2014: as *Polianthes*, with ills.). **Distr:** Mexico (W Oaxaca); in disturbed habitats in black or brown loamy to clayey soils, in juniper, pine-oak and montane cloud forests, 1945–2130 m; flowers August to September. **I:** Hochstätter (2016: II: 5).

$\equiv$  *Polianthes alboaustralis* E. Solano & Ríos-Gómez (2014).

[3b1] Herbaceous; corm cylindrical, 1.5–3.6  $\times$  1–2.2 cm, bulb ovoid, 1.7–4 (–6)  $\times$  1.3–3.5 cm, covered with dry leaf bases; **R** contractile, thickened; **L** 2–6, linear, cartilaginous, apex acute, thickened, 36–63  $\times$  0.4–0.7 cm, upper and lower surface with papillae unevenly distributed over the veins, margins papillose-toothed; **Inf** 94–160 cm, ‘spicate’, internodes becoming shorter towards the distal portion, peduncle with first **Bra** linear, 29–56  $\times$  0.3–0.8 cm, fertile part with 3–7 floral nodes, 7–25 cm; **Ped** none; **Fl** geminate, diffuse to divaricate at anthesis, fragrant, at the base with two bracteoles; **Tep** white at anthesis, white-pink at senescence, tube curved  $\pm$  in the middle, infundibular above the curve and widening to the base of the lobes, broadest part usually with extrafloral nectaries, 40–60  $\times$  4–8 (at the tip) mm, throat symmetrical, lobes extended, broadly ovate, papillose on both faces, margins hyaline, almost equal, 2–6  $\times$  2–3.7 mm, apex cucullate, obtuse to rounded, papillose, pink, purplish, or reddish; **St** included; **Fil** filiform, white, 2–10 mm, inserted  $\pm$ 30–60 mm above the tip of the ovary; **Anth** linear, 5–10  $\times$  1–2 mm, yellow to green-yellowish; **Ov** cylindrical, 4–10  $\times$  1.5–3 mm; **Sty** filiform, 39–45 mm, included at anthesis, white; **Sti** 3-lobate, papillose; **Fr** globose, 16–23  $\times$  10–21 mm, with persisting perianth remains; **Se** ovate-depressed, flat, 5–6  $\times$  4–5 mm, black, dull.

According to the protologue most similar to *A. neonelsonii* (as *Polianthes nelsonii*) and *A. palustris* (as *P. palustris*), but differing by its longer leaves, longer sterile primary bract, and its much longer inflorescence. The species is remarkable for its extrafloral nectaries which are reported for the first time for Sect. *Polianthes*. It is the only species of the section with fragrant white flowers from S of the Trans-Mexican Volcanic Belt.

**A. albomarginata** Gentry (Agaves Cont. North Amer., 129–131, ill., 1982). **Type:** Ex cult. (Gentry 19811 [US 2601938, ARIZ 265547]). — **Lit:** Irish & Irish (2000: 93–94); Puche & Meer (2014: with ills.). **Distr:** Mexico (W & N-C Querétaro); ecology not recorded, presumably desert scrub, 1300–2100 m; flowers June to July; neophyte in Spain. **I:** Hochstätter (2015: IX: 23); Hernández-Sandoval & al. (2016: 203); Martínez & al. (2017: 188).

[1g] Stems short; **Ros** open, freely suckering; **L** 16–30, long lanceolate-linear, straightly ascending, rigid to sinuous, apex long acuminate, convex below, nearly flat above, somewhat keeled towards the base, 100–125 × 4 (near the base)/2.5 cm (in the middle), greyish-green, often with paler mid-stripe, margins thin, horny, somewhat friable, easily separable, white to grey, rarely brown; **marginal teeth** at mid-leaf white like the margin with tips sometimes reddish or light grey, thin, deltoid, recurved, 2–4 mm, remote, 30–50 mm apart, towards the leaf base blunt, 10–20 mm apart, distal 1/3 of the leaf toothless; **terminal Sp** subulate, with a rounded groove above, 15 mm, white or sometimes light grey with dark tip, thinly decurrent; **Inf** 2–4.5 m, ‘spicate’, peduncle with narrowly deltoid chartaceous **Bra**, fertile part slender, laxly flowered, part-**Inf** with 2 or 3 flowers; **Ped** short, thick, bracteolate; **Fl** 30–35 (–40) mm; **Tep** yellow or greenish-yellow, tube broadly funnel-shaped, forming a marked angle relative to the tepal base, 4–5 × 9 mm, lobes strictly erect, equal, 13–14 × 3 mm, pale yellow,

clasping the filaments; **Fil** dorsiventrally flattened, to ±30 mm, greenish-yellow to reddish, inserted at the tube rim; **Anth** excentric, 16–17 mm; **Ov** fusiform, 18–22 mm, neck thick, grooved; **Fr** oblong or obpyriform, 20–30 × 12–14 mm, brown; **Se** semicircular, thickened esp. at the curved rough side, shiny black.

In the protologue, Gentry (1982) cited the specimen at US (2 cross-labelled sheets) as holotype, but the isotype at ARIZ bears the stamp “Gentry Herbarium” and his handwriting “type collection”. According to the protologue perhaps better treated as a var. or ssp. of the closely related *A. lechuguilla*, but more extreme in morphological characters than other variants of the taxon, esp. in its elongate leaves with conspicuous, white, friable margins and a toothless terminal third. Known to Gentry (1982) from cultivation only, the species was subsequently rediscovered in habitat in Querétaro (Magallán Hernández & Hernández Sandoval 2001). Gómez-Bellver & al. (2019: 24–25) report the taxon as local neophyte from Spain.

**A. albopilosa** I. Cabral & al. (Acta Bot. Mex. 80: 52–55, ills., 2007). **Type:** Mexico, Nuevo León (Cabral 1612 [MEXU, ANSM, CFNL, CIIDIR, ENCB, UNL]). — **Lit:** Starr (2012: 40–43, with ills.). **Distr:** Mexico (Nuevo León); steep nearly vertical limestone rocks, 1000–1500 m. **I:** Etter & Kristen (2009a); Richter (2011: 56); Lodé (2011); Janeba (2013); Alsemgeest (2013); Pilbeam (2013: 22); Hochstätter (2015: VII: 5, 15). – Fig. 3.

**Fig. 3** *Agave albopilosa* (Etter & Kristen 4282: Mexico; Nuevo León, Huasteca Canyon, 1600 m). (Copyright: J. Etter & M. Kristen)



[1a] Stems decumbent, with woody rootstock up to  $20 \times 2\text{--}2.5$  cm; **Ros** symmetrical, semi-globose,  $20\text{--}40 \times 15\text{--}36$  cm, caespitose; **L** 100–180, in 15–25 spiral rows, linear-triangular, broadened at the base, narrowing at the apex, slightly concave with dorsal keel, striate on both faces, glabrous,  $14\text{--}23 \times 0.8\text{--}1.4$  (in the middle) cm, yellowish-green to slightly glaucous, margins rigid, slightly curved, serrate; **marginal teeth** none; **terminal Sp** straight to sigmoid, sub-conical,  $3\text{--}6 \times 0.7\text{--}0.9$  (at the base) mm, blackish, 4–6 mm below its base with a ring of white hairs 4–7 mm long; **Inf** straight to inclined, 45–80 cm, ‘spicate’, peduncle  $30\text{--}50$  cm  $\times$  6–9 mm, with linear-triangular **Bra**  $3\text{--}5 \times 0.3\text{--}0.5$  cm, fertile part cylindrical, dense,  $15\text{--}30 \times 4\text{--}8$  cm, with 70–120 flowers; **Fl** usually geminate, slightly campanulate, 22–36 mm; **Top** greenish, with purple tinge, buds greenish-purple, tube 8–10 mm, lobes erect, slightly incurved, 4–5 mm; **St** exserted; **Fil** flattened, 25–30 mm, greenish-yellow according to the protologue but with purple tinge according to photographs, inserted in the middle of the of tube; **Anth** 8–10 mm, yellow; **Ov** shortly oblong, 8–10 mm, green, neck constricted; **Sty** cylindrical, 26–32 mm, greenish; **Sti** slightly 3-lobate; **Fr** oblong, with transversal stripes,  $10\text{--}12 \times 8\text{--}10$  mm, coffee-brown; **Se** semicircular, flattened, thickened at the curved side,  $3\text{--}3.5 \times 1.5\text{--}2$  mm, black, shiny.

Morphologically similar to *A. stricta*, but with fewer leaves with an apical ring of hairs, and smaller flowers and fruits. *A. rzedowskiana* is also similar but lacks the ring of hairs, and has larger flowers. The ring of hairs near the leaf tip just below the terminal spine is unique.

**A. americana** Linné (Spec. Pl. [ed. 1], 1: 323, 1753). **Type:** LINN 443.1 [lecto]. — **Distr:** USA, Mexico; cultivated worldwide in frost-free climates, and locally naturalized.

The lectotype cited above was designated by Howard & Thompson-Mills (1979: 486).

**A. americana** ssp. **americana** — **Lit:** Gentry (1982: 276, 278–281, with ills.); Lott & García-Mendoza (1994: online with ills.); Smith & Mössmer (1996: with ills.); Hodgson (1999a: 3–4); Reveal & Hodgson (2002); Guillot Ortiz &

Meer (2006a: key to cultivars grown in Spain); González-Elizondo & al. (2009: 43–46, with ills.); Hurrell & Delucchi (2009: with ills.); García-Mendoza (2011a: 7–10); Guillot Ortiz & al. (2012: with ills., as *A. ingens*). **Distr:** USA (SE Texas), E Mexico; sandy places in desert scrub, 20–1830 m; flowers June to September; widely cultivated and naturalized in suitable climates. **I:** Curtis’s Bot. Mag. 65: t. 3654, 1938–1939; Irish & Irish (2000: t. 2); Reveal & Hodgson (2002: 18, 19, 60–62); Richter (2011: 70, 120); Pilbeam (2013: 23); Hochstätter (2015: VII: 4).

≡ *Agave americana* var. *americana*; **incl.** *Agave virginica* Miller (1768) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave communis* Gaterau (1789); **incl.** *Agave ramosa* Moench (1794) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Agave spectabilis* Salisbury (1796); **incl.** *Agave theometel* Zuccagni (1806) ≡ *Agave americana* var. *theometel* (Zuccagni) A. Terracciano (1885); **incl.** *Agave milleri* Haworth (1812); **incl.** *Agave variegata* Steudel (1821) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Agave americana* var. *variegata* Hooker (1838); **incl.** *Agave picta* Salm-Dyck (1859) ≡ *Agave longifolia* var. *picta* (Salm-Dyck) Regel (1865) ≡ *Agave mexicana* var. *picta* (Salm-Dyck) J. F. Cels (1865) ≡ *Agave milleri* var. *picta* (Salm-Dyck) van Houtte (1868) ≡ *Agave americana* var. *picta* (Salm-Dyck) A. Terracciano (1885) ≡ *Agave ingens* var. *picta* (Salm-Dyck) A. Berger (1912); **incl.** *Agave altissima* Zumaglini (1864); **incl.** *Agave ornata* Jacobi (1865); **incl.** *Agave fuerstenbergii* Jacobi (1870); **incl.** *Agave americana* fa. *virginica* Voss (1895); **incl.** *Agave salmiana* var. *gracilispina* Roland-Gosselin (1896) ≡ *Agave gracilispina* (Roland-Gosselin) Engelmann ex Trelease (1914); **incl.** *Agave picta* A. Berger (1904) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave americana* var. *marginata* Trelease (1908); **incl.** *Agave americana* var. *medio-picta* Trelease (1908); **incl.** *Agave americana* var. *striata* Trelease (1908); **incl.** *Agave americana* var. *marginata alba* Trelease (1908) (*nom. inval.*, ICN Art. 23.1); **incl.** *Agave americana* var. *marginata aurea* Trelease (1908) (*nom. inval.*, ICN Art. 23.1); **incl.** *Agave americana* var. *marginata pallida* Trelease (1908) (*nom. inval.*, ICN Art. 23.1); **incl.** *Agave celsiana* hort. ex A. Berger (1911) (*nom. illeg.*, ICN Art. 53.1);



**incl.** *Agave ingens* A. Berger (1912); **incl.** *Agave complicata* Trelease ex Ochoterena (1913); **incl.** *Agave melliflua* Trelease (1914); **incl.** *Agave zonata* Trelease (1914); **incl.** *Agave tingens* A. Berger (1915); **incl.** *Agave felina* Trelease (1920); **incl.** *Agave rasconensis* Trelease (1920); **incl.** *Agave subtilis* Trelease (1920)  $\equiv$  *Agave americana* cv. *subtilis* (Trelease) A. Valenzuela & Nabhan (2003)  $\equiv$  *Agave americana* var. *subtilis* (Trelease) A. Valenzuela & Nabhan (2004); **incl.** *Agave subzonata* Trelease (1920); **incl.** *Agave americana* [?] *nairobensis* Herbin & Robins (1968) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Agave cordillerensis* Lodé & Pino (2008).

[2a] Stems none or short, trunks <2 m; **Ros** open or dense, 1–2.5  $\times$  2–3.7 m, freely suckering; **L** 40–70, lanceolate, erect, ascending, or frequently reflexed above the middle, narrowed above the thickened base, usually acuminate, convex below near the base, flat above and somewhat guttered near the base, smooth to slightly asperous, mostly 100–200  $\times$  15–30 cm, 6–10 $\times$  longer than wide, light green to green or glaucous-grey, sometimes variegated yellow or whitish, especially in cultivated forms, sometimes cross-zoned, margins straight or repand to crenate; **marginal teeth** variable, larger teeth (5–) 7–10  $\times$  6–12 mm, brown to pruinose-grey, 20–65 mm apart, from broad low bases, tips slender, straight to flexuous or curved; **terminal Sp** conical or subulate, 20–50  $\times$  4–5 mm, shiny brown to pruinose-grey; **Inf** 5–9 m, paniculate, peduncle green, with triangular chartaceous **Bra** 30–60 cm, fertile part slender, straight, long-oval in outline, rather open, part-**Inf** 15–35, 1.-order stalks 1–1.2 m, in the upper  $\frac{1}{3}$ – $\frac{1}{2}$  of the inflorescence, spreading; **Fl** long-pedicellate, slender, 70–100 mm; **Tep** yellow, tube funnel-shaped, 8–20  $\times$  12–20 mm, lobes oblong unequal, 25–35  $\times$  3–5 mm; **ITep** 2–3 mm shorter than the **OTep**, tip cucullate; **Fil** somewhat flattened, long tapering, 60–90 mm, inserted  $\pm$ 5–10 mm above the tube base, yellowish-green; **Anth** centric to excentric, 30–36 mm, yellow; **Ov** fusiform, 30–45  $\times$  5 mm, greenish, neck grooved, tapering to the narrower base; **Sty**  $\pm$ 90 mm, longer than the stamens after anthesis; **Sti** 3-lobate; **Fr** oblong, 40–80  $\times$  20–25 mm, beak short, shortly stipitate;

**Se** crescent- to tear-shaped, winged for 2 mm, 7–10  $\times$  5–8 mm, shiny. — **Cytology**: 2n = 60, 120, 180, 240; also 20, 44, 96, 81–104, 110, 115, 118, 119, 125, 134, 226 (see esp. Granick (1944), Satô 1935, Lv & al. 2009, Simpson & al. 2011).

The leaves are often reflexed above the middle, and this is a characteristic feature of the species. The flowers exhibit a short tapering ovary that is shorter than the tepals. *A. americana* ssp. *americana* is a very polymorphic taxon cultivated worldwide in many variants, especially in winter-rainfall climates (Gentry 1982: 278). Ssp. *americana* differs from its assumed wild progenitor ssp. *protoamericana* esp. in its longer leaves 6–10 $\times$  longer than wide, and its larger capsules.

Asensi & al. (2016) report the taxon as naturalized in Spain (where it may invade natural communities), Smith & Klopper (2007) for RSA, and Smith & Figueiredo (2008) for Portugal, but it is also naturalized in C & S America, N Africa, Asia, Australia, New Zealand, and on the islands of the Pacific (see references in Hurrell & Delucchi (2009), who also list many uses of the plant). The experimental management control of naturalized plants on the Canary Islands is described by Arévalo & al. (2015).

Cultivars with various degrees of variegation are common, and sometimes also naturalized, e.g. in Spain (Guillot Ortiz & Meer 2003b, Guillot Ortiz & al. 2012: as *A. ingens*) or Portugal (Smith & Figueiredo 2008). The origin and genetics of variegated cultivars is dealt with by Zonneveld (2007). A key to variegated and other cultivars grown in Spain is provided by Guillot Ortiz & Meer (2003b) and Guillot Ortiz & al. (2012).

A review of *A. americana* in American ancient cultures based on earliest Spanish chronicles is given by Pardo (2007). Meer (2011) summarized early European literature on flowering cultivated plants. European historical illustrations of flowering *A. americana* published before 1800 were reviewed by Ullrich (1993d). The very first illustration of an *Agave* was published in 1574 by Rembert Dodoens.

*A. cordillerensis* is a cross-zoned variant recently described from Peru. It represents hardly more than a locally cultivated variant and is therefore synonymized according to Govaerts (2014+).

**A. americana** ssp. **protoamericana** Gentry (Agaves Cont. North Amer., 287–290, ills., 1982). **Type:** Mexico, Nuevo León (*Gentry & Barclay* 20156 [US, ARIZ, MEXU]). — **Lit:** Reveal & Hodgson (2002). **Distr:** USA (Texas); Mexico (Nuevo León, Tamaulipas, San Luis Potosí); sandy places and open slopes in tropical deciduous and thorn forests or desert scrub, 200–1400 m; flowers early spring to early summer. **I:** Richter (2011: 99, 116); Pilbeam (2013: 25); Hochstätter (2015: VII: 7).

[2a] Differs from ssp. *americana*: **L** generally shorter, shortly narrowed above the thick and fleshy base, 80–135 × 17–22 cm, 4–6× longer than wide, light glaucous-grey to pale green, sometimes cross-zoned; **Inf** generally with fewer (15–20) part-**Inf**; **Tep** tube deeply funnel-shaped, longer, 15–20 mm; **Fr** 35–40 mm.

Regarded as the wild progenitor of the many cultivated types of *A. americana* ssp. *americana* according to the protologue. In Mexico, it shows apparent introgression with *A. asperrima* (as *A. scabra*; Gentry 1982: 289). Plants from Starr County, Texas, are smaller than Mexican material but appear to belong here (Reveal & Hodgson 2002).

‘Silver Surfer’ is a cultivar selected from seedlings (Starr 2014: 220, with ill.).

**A. americana** var. **expansa** (Jacobi) Gentry (US Dept. Agric. Handb. 399: 80, 1972). **Type:** not typified. — **Lit:** Bye & al. (1975: 93–94); Gentry (1982: 276, 283–284, with ills.); McVaugh (1989: 132); Reveal & Hodgson (2002); Vázquez-García & al. (2007b: 40–41); Smith & Figueiredo (2011: with ills.). **Distr:** Cultivated only (USA [California, Arizona], Mexico [SW Chihuahua, Jalisco]); sandy places in desert scrub and grasslands, 500–1300 m; flowers late spring to early summer; naturalized in RSA **I:** Pilbeam (2013: 24); Hochstätter (2015: VII: 6, as ssp.).

≡ *Agave expansa* Jacobi (1868) ≡ *Agave americana* ssp. *expansa* (Jacobi) Hochstätter (2015); **incl.** *Agave abrupta* Trelease (1920).

[2a] Differs from ssp. *americana*: Stems forming a short trunk in age, to 60 cm; **L** erect to stiffly spreading, deeply channelled above, glaucous-grey, frequently cross-zoned, margins crenate; **marginal teeth** along the middle of the lamina on several sharply angled low prominences; **terminal Sp** 20–30 mm; **Fl** 70–85 mm; **Fr** and **Se** unknown. — **Cytology:** 2n = 119 (Granick 1944, Simpson & al. 2011).

The wild forms of var. *expansa* are classified as a variant of ssp. *americana* (Reveal & Hodgson 2002). Known only as a cultivar (and better to be named as such) used for the pulque industry, first introduced into W Europe where it was described by Jacobi (Gentry 1982: 283). Var. *expansa* is occasionally cultivated in the warmer regions of the USA and is not naturalized. It has never been found in fruit and reproduction is strictly vegetative. Var. *expansa* likely is an early cultivar developed by pre-Columbian people who established it far to the west of the species’ range in E Mexico (Reveal & Hodgson 2002). It differs from ssp./var. *americana* esp. in its erect, non-reflexed leaves with a shorter terminal spine. In Chihuahua, leaf-bases are eaten pit-baked or prepared as mescal bread (Bye & al. 1975), and in Jalisco, it is used as living fence and for the production of aguamiel and pulque (Vázquez-García & al. 2007b). It is naturalized in RSA (Smith & Figueiredo 2011, Walters & al. 2011: 40–41).

**A. americana** var. **oaxacensis** Gentry (Agaves Cont. North Amer., 285–287, ills., 1982). **Type:** Mexico, Oaxaca (*Gentry & Arguelles* 12260 [US, ARIZ, DES, MEXU]). — **Lit:** García-Mendoza (2011a: 9–10). **Distr:** Cultivated only (Mexico: Oaxaca). **I:** Pilbeam (2013: 26); Hochstätter (2015: VII: 8, as ssp.).

≡ *Agave americana* ssp. *oaxacensis* (Gentry) Hochstätter (2015).

[2a] Differs from ssp. *americana*: **L** not reflexed, spreading, very large, 120–250 × 10–24 cm, glaucous-white, margins nearly straight, without distinct prominences; **marginal teeth** closely set; **Inf** large, 6–10 m; **Fl** large, 95–105 mm.

According to the protologue observed in cultivation only (and thus better treated as a cultivar), esp. in the Oaxaca Valley, but similar plants were also observed elsewhere. Formerly grown for fibre and pulque, but later abandoned (Gentry 1982: 287). Guillot Ortiz & Meer (2004) interpret an old illustration from Valentini (1719) as representing this taxon.

**A. amica** (Medikus) Thiede & Govaerts (Phytotaxa 306(3): 237, 2017). **Type:** BM [Herb. Hermann 3: 34, No. 125]. — **Lit:** McVaugh (1989); Ullrich (1993e: with ills.); both as *Polianthes*. **Distr:** Cultivated only. **I:** Bot. Reg. 1: t. 63, 1815; Curtis's Bot. Mag. 43: t. 1817, 1815–1816; Hochstätter (2016: II: 24); all as *Polianthes tuberosa*.

≡ *Tuberosa amica* Medikus (1790); **incl.** *Polianthes tuberosa* Linné (1753) ≡ *Agave tuberosa* (Linné) Thiede & Eggli (1999) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Crinum angustifolium* Houttuyn (1780); **incl.** *Polianthes gracilis* Link (1821) ≡ *Polianthes tuberosa* var. *gracilis* (Link & Otto) Beurling (1856); **incl.** *Polianthes tuberosa* fa. *plena* Moldenke (1948); **incl.** *Agave polianthes* Thiede & Eggli (2001) (*nom. illeg.*, ICN Art. 52.1).

[3b1] Herbaceous; corm cylindrical, mostly short and broad,  $\pm 1\text{--}1.5 \times 2\text{--}3$  cm, bulb ovoid to conical, to 5–6 cm, covered with dry leaf bases; **R** contractile, thickened; **L** 6–10 in a basal **Ros** from a bulbous base, linear, soft, deeply channelled in the basal  $\frac{1}{2}$ , to  $30\text{--}60 \times 1\text{--}1.5$  cm, bright green, sometimes reddish near the base, sometimes with brown spots on the lower face; **Inf** 60–100 cm, 'spicate', fertile part 14–28 cm, laxly flowered, with up to 15 flowering nodes; **Fl** geminate, mostly sessile, fragrant, 25–40 mm; **Tep** waxy white, base upright or strongly ascending, tube smoothly outcurved from below the middle, funnel-shaped above the curvature, expanding to the very slightly oblique mouth, there 7–8 mm  $\varnothing$ , lobes subequal, elliptic-ovate, obtusely pointed, often  $15\text{--}25 \times 5\text{--}10$  mm; **St** included; **Sty** included, with 3 oblong-ovate recurved lobes 2.5 mm long; **Fr** not described; **Se** poorly produced, not further known. — **Cytology:**  $2n = 60$ ,

120;  $2n = 50$  in double-flowered cultivars (Whitaker 1934, Satô 1935, Verhoek-Williams 1998, Tapia-Campos & al. 2013).

This is the "Tuberosa" or "Nardo", one of the most important cut flowers in (sub-)tropical areas, grown commercially for its fragrant flowers in India, New Zealand, Japan and Mexico, and for the perfume industry in India and France (Barba-Gonzalez & al. 2012). It was already cherished and cultivated as a perfume flower named "Omixochitl" (bone flower) by the Aztecs in pre-conquest times (Trueblood 1973). In Europe, the tuberosa is known since 1594 when Clusius received a specimen which he illustrated in 1601 (Sims 1816). Old European illustrations are discussed by Ullrich (1993e). Especially common is a form with double ('filled') flowers, *Polianthes tuberosa* fa. *plena* Moldenke 1948, which should better be treated as cultivar 'Plena'. The species is at present not known from the wild and already Linné based his description on cultivated material from India. It is most probably of Mexican origin and possibly native to the region around Guadalajara (Jalisco), where its putative ally *A. dolichantha* has recently been rediscovered in the wild (see note there).

Unfortunately, the original species name is pre-occupied in *Agave*, and the replacement name *A. polianthes* unfortunately is predated by *Tuberosa amica*, whose epithet must be taken up for priority reasons.

Modern hybrids with pink, reddish-purple, purple, orange and yellow flowers, obtained from crossings with other species of Sect. *Polianthes*, were bred during the last years in North America, Europe and Asia and are now commercially offered (Huang & al. 2001: with ills., Guillot Ortiz & al. 2006: with ills., Barba-Gonzalez & al. 2012, Datta 2017).

**A. andreae** Sahagún & A. Vázquez (Syst. Bot. 38(2): 323–326, ills., 2013). **Type:** Mexico, Michoacán (*Muñiz-Castro & Padilla-Lepe* 862 [IBUG, GUADA, IEB, MEXU, MICH, MO, WIS]). — **Distr:** Mexico (W Michoacán: Sierra de Coalcomán); limestone outcrops in tropical dry forests, 1400–1435 m; flowers January to

March. **I:** Cházaro Basáñez & al. (2006a); Vázquez-García & al. (2007b: figs. M1, M3); both as *A. gypsophila*; Hochstätter (2016: VI: 26).

[2n] **Ros** 0.8–2.3 × 1.5–3.6 m, solitary or rarely surculose; **L** 20–40, narrowly lanceolate, firm but brittle, concave to channelled with the sides almost perpendicular, smooth on both faces, 90–150 (–210) × 12–14 (–23) cm, to 11.5–15 cm wide and to 4–5.5 cm thick at the base, light green and slightly darker above, glaucous below at the base, not evidently cross-zoned on both faces, margins slightly repand; **marginal teeth** flattened, on prominences 3–4 × 4–5 mm, mostly ascending and curved, mostly 3–5 mm, 30–38 mm apart at mid-leaf, 5–11 mm at the base, dark brown, from broad bases 3–4 mm wide, intervening margin repand with few or no teeth; **terminal Sp** usually short and conical, firm, 15–26 mm, dark brown, not decurrent; **Inf** 5–7.3 m, paniculate, with triangular **Bra** to 15 cm long at the peduncle base, fertile part oblong, occasionally with numerous red bulbils, part-**Inf** 27–36, compact, in the upper 2/3 of the inflorescence; **Fl** 34–40 mm; **Tep** orange, tube somewhat funnel-form, 5–6 × 11–12 mm, lobes triangular, erect, fleshy, 11–13 × 5–7 mm, yellow at the base, orange at the galeate apex; **Fil** firm, 32–36 mm, inserted 2–3 mm above the tube base, orange; **Anth** centric, 14–15 mm, yellow; **Ov** 18–21 × ±4 mm, neck constricted, green; **Sty** shorter than the filaments; **Sti** capitate; **Fr** oblongoid, 32–39 (–45) × 18–19 mm, stipitate, apiculate; **Se** crescent-shaped but curved on one side, flat, membranous, 5–6 × 4 mm, black.

Part of the *A. gypsophila* species group, and recently (together with *A. abisaii*, *A. kristenii* and *A. pablocarrilloi*) separated from a more narrowly circumscribed *A. gypsophila* (Vázquez-García & al. 2013). This is the largest-growing species in the group, and differs from the most similar *A. gypsophila* s.s. by more numerous and ascending leaves, more robust inflorescences, larger flowers, and by occurring at higher elevation.

**A. angustiarum** Trelease (Contr. US Nation. Herb. 23: 139, 1920). **Type** [syn]: Mexico, Guerrero (*Trelease* 17 + 77 [MO, ARIZ [para]]). — **Lit:**

Gentry (1982: 134–135, with ill.); Vázquez-García & al. (2007b: 41–42, t. B [excl. B1–B4 = *A. garciaruii*]); Greulich (2012a: with ill.); Hernández-Vera & al. (2019). **Distr:** Mexico (SE Jalisco, Michoacán, México, Morelos, Puebla, Guerrero, Oaxaca); limestone rock abutments and cliffs in tropical deciduous forests and desert scrub, 600–2300 m; flowers March and October. **I:** Richter (2011: 111); Pilbeam (2013: 27); Hochstätter (2015: IX: 24).

[1g] Stems short; **Ros** open, (0.5–) 0.8–1.2 × <1–2.2 m, mostly solitary, rarely with basal offsets; **L** 20–50, linear to lanceolate, openly spreading, straight, thick, firm, long acuminate, flat to concave above, thickened below, 50–120 × 6–13 cm, olive-green or glaucous-green (both forms occur sympatrically), mostly with a conspicuous light green median stripe above, margins horny, continuous; **marginal teeth** straight or slanted downwards but commonly upcurved, rather slender, flattened, largest somewhat scattered, mostly 2–7 mm, brown to grey, 10–40 mm apart, 3–7 teeth per 10 cm, teeth absent from the topmost 1/4–1/3 of the leaf, intervening margin nearly straight, scarcely 1 mm broad; **terminal Sp** acicular, rounded, very slender, narrowly grooved above, with a conspicuous median protrusion below, 25–45 mm, long decurrent to the upper teeth; **Inf** 1.5–5 m, ‘spicate’, slender, fertile part in the upper 50–60%, rarely bulbiferous; **Ped** 9–11 mm; **Fl** 35–40 mm; **Tep** glaucous greenish-white, cream-yellow, yellow, yellowish-green or reddish, tube very short, 4–5 × 6–7 mm, lobes 16 × 3 mm, clasping the filaments; **Fil** 40–45 mm; **Anth** 14–15 mm, usually yellow, rarely reddish; **Ov** 15 mm, neck narrow; **Sty** slightly shorter than the filaments; **Sti** capitate; **Fr** 8–25 × 5–15 mm, fruit valves straight, apically rounded; **Se** 3–5 × 2–3 mm.

Distinguished by its simple rosettes with long, narrow leaves that are toothless along the long-tapering apex, and the long-protruding spine-base. The taxon may be confused with some forms of *A. kerchovei*, but the latter has larger rosettes with more leaves which are longer, narrowly lanceolate, and more sword-shaped (Gentry 1982). The description by Gentry (1982: 134) is inadequate and omits the variation given in Trelease’s protologue (Greulich 2012a);



Hernández-Vera & al. (2019) provide additional data. Plants of *A. angustiarum* from Nizanda (Oaxaca) placed here by Greulich (2012a) are placed in *A. ghiesbreghtii* by Mexican botanists (e.g. Pérez-García & al. (2001)). The recently published *A. arcedianoensis* from C Jalisco with purple-reddish flowers appears closely related (see there). For differences from the closely related *A. garciaruii* see there. The complex *A. angustiarum* — *A. arcedianoensis* — *A. kerchovi* is in need of a critical study.

**A. angustifolia** Haworth (Synops. Pl. Succ., 72, 1812). **Type** [neo]: Mexico, Oaxaca (*García-Mendoza & Palma* 5654 [MEXU]). — **Distr:** N Mexico to Panama, widespread.

García-Mendoza & Chiang (2003: 86) designated the neotype cited above.

**A. angustifolia** var. **angustifolia** — **Lit:** Trelease (1908a: with ills.); Gentry (1972: 143–148, with ills., as *A. pacifica*); Gentry (1982: 559–564, with ills.); McVaugh (1989: 133–134); Lott & García-Mendoza (1994: online version with ills.); Turner & al. (1995: 41–43, with ills.); García-Mendoza & Chiang (2003: with ills.); Vázquez-García & al. (2007b: 42–44, t. C); González-Elizondo & al. (2009: 45–47, with ills.); García-Mendoza (2011a: 12–14); Franck (2012: 3–6, with ills.). **Distr:** Mexico (widespread from Sonora and Chihuahua to the S), Belize, Costa Rica, Honduras, Nicaragua, El Salvador, Panama; mainly tropical savannas, thorn forests, and tropical deciduous forests at low to middle elevations (to 1500 m, rarely more); flowers March to November; naturalized in Spain and RSA. **I:** Curtis’s Bot. Mag. 85: t. 5097, 1859, as *A. jacquiniana*; Curtis’s Bot. Mag. 97: t. 5893, 1871, as *A. ixtlioides*; Heller (2006: 147, as *A. vivipara*); Richter (2011: 20–21, 119, 123); Pilbeam (2013: 28); Hochstätter (2015: VII: 28, 29). — Fig. 4.

**Incl.** *Agave rigida* Miller (1768) ≡ *Furcraea rigida* (Miller) Haworth (1812); **incl.** *Agave lurida* Jacquin (1790) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave flaccida* Haworth (1812); **incl.** *Agave rigida* Spin (1812) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave jacquiniana* Schultes & Schultes fil. (1829) ≡ *Agave lurida* var. *jacquiniana*



**Fig. 4** *Agave angustifolia* var. *angustifolia* (Eggl & al. 1944a: Mexico; Sonora, Bahia Kino, cultivated). (Copyright: J. Thiede)

(Schultes & Schultes fil.) Salm-Dyck (1861) ≡ *Agave vera-cruz* var. *jacquiniana* (Schultes & Schultes fil.) Ascherson & Graebner (1906); **incl.** *Agave bromeliifolia* Salm-Dyck (1834) ≡ *Agave vivipara* var. *bromeliifolia* (Salm-Dyck) A. Terracciano (1885); **incl.** *Agave ixtli* Karwinsky ex Salm-Dyck (1834); **incl.** *Agave punctata* Salm-Dyck (1834); **incl.** *Agave rubescens* Salm-Dyck (1834) ≡ *Agave angustifolia* var. *rubescens* (Salm-Dyck) Gentry (1982) ≡ *Agave vivipara* var. *rubescens* (Salm-Dyck) P. I. Forster (1992) ≡ *Agave angustifolia* ssp. *rubescens* (Salm-Dyck) Hochstätter (2015); **incl.** *Agave flaccida* Salm-Dyck (1834) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave yxtli* Karwinsky ex G. Don (1839) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave serrulata* Karwinsky ex Otto (1842) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave theoxmulliana* Karwinsky ex M. Roemer (1847); **incl.** *Agave vivipara* Wight (1853) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave*

*elongata* Jacobi (1865); **incl.** *Agave excelsa* Jacobi (1866); **incl.** *Agave flavovirens* Jacobi (1866); **incl.** *Agave houllettii* Jacobi (1866); **incl.** *Agave ixtlioides* Lemaire ex Jacobi (1866); **incl.** *Agave erubescens* Ellemeet (1871); **incl.** *Agave ixtlioides* Hooker fil. (1871) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave cuspidata* Baker (1877); **incl.** *Agave excelsa* Baker (1877) (*nom. illeg.*, ICN Art. 53.1)  $\equiv$  *Agave ixtli* var. *excelsa* (Baker) A. Terracciano (1885); **incl.** *Agave spectabilis* Todaro (1878) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave sobolifera* var. *serrulata* A. Terracciano (1885); **incl.** *Agave rigida* var. *elongata* Anonymous (1893) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave rigida* A. Berger (1898) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave wightii* J. R. Drummond & Prain (1906); **incl.** *Agave aboriginum* Trelease (1907); **incl.** *Agave endlichiana* Trelease (1907); **incl.** *Agave lespinassei* Trelease (1907); **incl.** *Agave zapupe* Trelease (1907); **incl.** *Agave deweyana* Trelease (1909)  $\equiv$  *Agave angustifolia* var. *deweyana* (Trelease) Gentry (1982)  $\equiv$  *Agave vivipara* var. *deweyana* (Trelease) P. I. Forster (1992)  $\equiv$  *Agave angustifolia* ssp. *deweyana* (Trelease) Hochstätter (2015); **incl.** *Agave bergeri* Trelease ex A. Berger (1912) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave donnell-smithii* Trelease (1915); **incl.** *Agave kirchneriana* A. Berger (1915); **incl.** *Agave prainiana* A. Berger (1915); **incl.** *Agave sicifolia* Trelease (1915); **incl.** *Agave pacifica* Trelease (1920); **incl.** *Agave panamana* Trelease (1920); **incl.** *Agave yaquiana* Trelease (1920); **incl.** *Agave owenii* I. M. Johnston (1924); **incl.** *Agave prolifera* Schott ex Standley (1930); **incl.** *Agave costaricana* Gentry (1949); **incl.** *Agave breedlovei* Gentry (1982) (*nom. inval.*, ICN Art. 36.1a); **incl.** *Agave vivipara* var. *bermejo* A. Valenzuela & Nabhan (2003) (*nom. inval.*, ICN Art. 39.1, 40.1).

[2g] Nearly acaulescent or stems to 20–60 (–90) cm; **Ros** radiately spreading, 1–1.5 (–2)  $\times$  1.5–2 m, surculose; **L** 40–70, linear to (very broadly) lanceolate, ascending to horizontal, mostly rigid, hard-fleshy, fibrous, narrowed and thickened towards the base, convex below, flat to concave above, full-grown generally (40–) 60–100 (–130)  $\times$  3.5–5 (–10, larger in cultivation) cm, light green to glaucous-grey, margins straight to repand,

sometimes thinly cartilaginous; **marginal teeth** generally small, (0.5–) 2–5  $\times$  (0.5–) 2–5 mm, rarely longer, commonly reddish-brown or dark brown, evenly and closely spaced or remote, from low narrow bases, tips slender,  $\pm$  curved, 10–35 mm apart; **terminal Sp** variable, conical to subulate, flat to shallowly grooved above, (15–) 20–35 mm, dark brown to blackish, greying with age, not or thinly decurrent; **Inf** 2.5–5 m, paniculate, open, peduncle green to brownish, somewhat waxy, with quick-drying narrow triangular **Bra** 7–15 cm, fertile part in the upper  $\frac{1}{2}$ – $\frac{1}{3}$ , oblong, with 9–15 (–20) horizontally spreading to ascending part–**Inf** 25–35 cm long, sometimes (freely) bulbiferous, bulbils leafy; **Ped** 2–3 mm; **Fl** (40–) 50–65 (–80) mm; **Tep** green, brownish-green, yellowish-green to yellow, tube funnellform to slightly urceolate, grooved, (4–) 7–16 (–20)  $\times$  8–10 mm, lobes oblong, unequal, (15–) 18–25  $\times$  2–5 mm, rapidly infolding, at first erect, soon wilting, drying reflexed against the tube, outer broadly overlapping the inner at the base, obtuse to rounded, tip slightly cucullate; **Fil** slender, flattened, 35–45 (–50) mm, inserted in the middle to the upper  $\frac{1}{4}$  of the tube, yellowish or with purple dots; **Anth** centric or excentric, (15–) 20–30 mm, yellow(ish); **Ov** small, angulate-cylindrical, somewhat ribbed, tapering at the base, 20–30  $\times$  3–5 mm, neck short, slightly grooved; **Sty** 50–60 mm, longer than the stamens after anthesis; **Sti** capitate; **Fr** broadly ovoid to oblong, 50–60  $\times$  20–30 mm, dark brown, raggedly beaked, shortly stipitate; **Se** 7–12  $\times$  5–8 mm, hilar notch a long cleft, not winged, dull. — **Cytology**: 2n = 60, 90, 120, 180 (esp. Castorena Sanchez & al. 1991, Palomino & al. 2005, Robert & al. 2008, Simpson & al. 2011: p.p., as *A. rigida*, Gomez-Rodriguez & al. 2013).

According to Wijnands (1983), *A. vivipara* is the oldest name for the widespread continental taxon previously referred to as *A. angustifolia* by Gentry (1982: 559) and others, which was followed in the first edition of this handbook. However, García-Mendoza & Chiang (2003) showed that Wijnands' interpretation is incorrect, and that *A. angustifolia* and *A. vivipara* are distinct species. Consequently, *A. angustifolia* is re-established as circumscribed by Gentry (1982),

and *A. vivipara* is applied to the Caribbean species previously known under that name.

The plants from Panama separated as *A. panamana* (Cseh 1993) merely represent the S-most element in the complex (Lott & García-Mendoza 1994). Smith & Figueiredo (2017) re-studied the taxon and argue that it could be accepted at specific rank, pointing out differences from *A. angustifolia*. *A. angustifolia* var. *rubescens* apparently represents a superfluous separate name for a depauperate form with narrower leaves and shorter narrower teeth, occurring irregularly in shady habitats within the species' range in Mexico (Gentry 1982: 567, García-Mendoza 2011a). Since the leaf and other measurements given by both authors fall well into the range of var. *angustifolia*, it is included in the synonymy here. *A. angustifolia* var. *deweyana* merely represents a "not well marked" (Gentry 1982: 564) cultivar cultivated in Tamaulipas and Veracruz. It is included in the synonymy of var. *angustifolia* by García-Mendoza (2011a) which is followed here, but it might warrant cultivar status. *A. spectabilis* Todaro is placed in the synonymy here based on Gentry (1982: 559) and the original plate, in contrast to its placement in the synonymy of *A. appianata* by Govaerts (2014+).

*A. angustifolia* is by far the most wide-ranging species of the genus and exhibits an extensive range of variation esp. in vegetative features. It is a sun-loving taxon (although also not rarely found with etiolated growth in light shade) occurring in nearly all vegetation types (albeit mainly in the 'tierra caliente') (Gentry 1982: 561).

Zizumbo-Villarreal & al. (2013) report on the local sustainable management of sylvicultural populations of *A. angustifolia* for mescal production in S Jalisco. The genetic variability of wild populations in Sonora was studied by Barraza Morales & al. (2006) and Sánchez-Teyer & al. (2009), and that of landraces in Jalisco by Vargas-Ponce & al. (2009). *A. angustifolia* is the wild progenitor of the cultivated *A. tequilana* (mainly used for alcoholic beverages) and *A. fourcroydes* (mainly used for fibre) (see there).

Variiegated and non-variiegated varieties cultivated in Spain are presented by Guillot Ortiz & Meer (2016b). *A. angustifolia* is naturalized in the

Balearic Islands (Sáez & al. 2016: 103) and in RSA (Steyn & Smith 2000: as *A. vivipara*, Walters & al. 2011: 43–45).

**A. angustifolia** var. **letonae** (F. W. Taylor ex Trelease) Gentry (Agaves Cont. North Amer., 564, ill. (p. 565), 1982). **Type:** El Salvador (*Milner* s.n. [US, ILL]). — **Lit:** Trelease (1925: 393–395, with ills.). **Distr:** Cultivated only (for fibre): Guatemala, El Salvador. **I:** Heller (2006: 153).

≡ *Agave letonae* F. W. Taylor ex Trelease (1925) ≡ *Agave vivipara* var. *letonae* (F. W. Taylor ex Trelease) P. I. Forster (1992) ≡ *Agave angustifolia* ssp. *letonae* (F. W. Taylor ex Trelease) Hochstätter (2015); **incl.** *Agave letonae* var. *marginata* Trelease (1925).

[2g] Differs from var. *angustifolia*: Stems broad; **Ros** robust; **L** nearly white. — **Cytology:** 2n = 120 (Robert & al. 2008).

A robust, nearly white-leaved plant which develops a broad trunk over several years of leaf-cutting. It has been of considerable economic importance for fibre production in El Salvador and has been in minor cultivation in Guatemala (Gentry 1982: 564). It apparently merely represents cultivated selections and should better be named as cultivar. In a molecular study, var. *letonae* clustered independently from *A. angustifolia*, but the result should be viewed with some caution, as the studied plants of *A. angustifolia* and *A. fourcroydes* likewise did not form a common clade (Infante 2006).

**A. angustifolia** var. **marginata** Trelease (in Linsbauer, Wiesner-Festschrift, 343, t. viii, 1908). **Type:** not typified. — **Lit:** Trelease (1908a: 286–287, t. 35). **Distr:** Cultivated only. **I:** Irish & Irish (2000: t. 4); Heller (2006: 147, as *A. vivipara* var. *marginata*); Sáez & al. (2014).

**Incl.** *Agave vivipara* 'Marginata' Hort. ex Gentry ex P. I. Forster (1992).

[2g] Differs from var. *angustifolia*: Stems 30–60 cm; **L** numerous, with narrow white or yellow margins. — **Cytology:** 2n = 60 (Castorena Sanchez & al. 1991, Lv & al. 2009).

This variety is merely a horticultural selection, now widely distributed around the World as an ornamental (Gentry 1982: 564), and sometimes

naturalized (e.g. in Spain, Sáez & al. (2014)). Probably better recognized as cultivar. In a molecular study (Infante 2006), var. *marginata* did not cluster with *A. angustifolia* s.s. (see var. *letonae* above for more details).

**A. angustifolia** var. **nivea** (Trelease) Gentry (Agaves Cont. North Amer., 566, 1982). **Type:** Guatemala, Progreso Dept. (*Trelease* 11 [ILL 00009808]). — **Lit:** *Trelease* (1915: 143–144, t. 22); Standley & Steyermark (1952: 114). **Distr:** Cultivated only (for fibre and fences): Guatemala. **I:** Guillot Ortiz & Meer (2016b: 65).

≡ *Agave nivea* *Trelease* (1915) ≡ *Agave vivipara* var. *nivea* (*Trelease*) P. I. Forster (1992).

[2g] Differs from var. *angustifolia*: Stems short; **L** 130–140 (–200) × 9–10 (–15) cm, characteristically dull bluish-grey, somewhat transversely green-banded; **Inf** unknown.

A long-leaved and short-stemmed plant with characteristic dull bluish-grey leaves, still present at its type locality in Guatemala in 1965 (Gentry 1982: 566), but also cultivated elsewhere (Standley & Steyermark 1952). Possibly better treated as cultivar.

**A. angustifolia** var. **sargentii** *Trelease* (Annual Rep. Missouri Bot. Gard. 22: 99, tt. 100–101, 1912). **Type:** [lecto — icono]: Annual Rep. Missouri Bot. Gard., 22: tt. 100–101, 1912. — **Lit:** Gentry (1982: 567). **Distr:** Cultivated only: Mexico (México, Puebla).

≡ *Agave vivipara* var. *sargentii* (*Trelease*) P. I. Forster (1992) ≡ *Agave angustifolia* ssp. *sargentii* (*Trelease*) Hochstätter (2015).

[2g] Differs from var. *angustifolia*: Stems ±25 cm; **Ros** dwarf; **L** numerous, narrowly oblong-lanceolate, minutely roughened, 25–30 × 2.5–3 cm, greyish-green; **marginal teeth** 1–2 mm, nearly black, glossy; **Inf** ±1 m, part-**Inf** few, bulbiferous; **Fl** 40 mm.

Gentry (1982) designated the lectotype cited above (as “Type”), which makes the later designation by Smith & Figueiredo (2014e: 228) unnecessary.

**A. angustifolia** var. **variegata** *Trelease* (Annual Rep. Missouri Bot. Gard. 19: 287, 1908). **Type:** not

typified. — **Lit:** *Watson* (1899b: as *A. woodrowii*). **Distr:** Cultivated only.

≡ *Agave vivipara* cv. *Variegata* (*Trelease*) P. I. Forster (1992); **incl.** *Agave woodrowii* W. Watson (1899) ≡ *Agave vivipara* var. *woodrowii* (W. Watson) A. Berger (1915) (*nom. inval.*, ICN Art. 41.4) ≡ *Agave angustifolia* fa. *woodrowii* (W. Watson) D. Guillot & P. Van der Meer (2016) (*nom. inval.*, ICN Art. 41.5).

[2g] Differs from var. *angustifolia*: **L** with unusual broad marginal white stripe, remainder of the leaf silvery-grey or milky.

A horticultural selection only, which is reported to have arisen in the Botanical Garden of the College of Science at Poona, India, around 1895 (*Trelease* 1908a: 287, Gentry 1982: 567). Better to be treated as cultivar.

**A. anomala** *Trelease* (Mem. Nation. Acad. Sci. 11: 36, t. 66, 1913). **Type:** Cuba (*Shafer* 1409 [MO, K, US]). — **Lit:** Berger (1915: 211–212); Correll & Correll (1982: 310). **Distr:** Bahamas (Rum Cay and San Salvador [Watling] Island), E Cuba (Holguín: N Holguín, Mayabe [Myabe]); beach coppices (Bahamas) and limestone outcrops (Cuba); flowers December to April. **I:** Richter (2011: 88); Pilbeam (2013: 29); Hochstätter (2015: VII: 66).

[2p] Acaulescent; **Ros** to 1 × 1 m, solitary; **L** ±40, elongate-lanceolate, spreading and arching, guttered, rather gradually pointed, 75–100 × 10 cm, green, not cross-zoned, margins straight; **marginal teeth** none or few and very small towards the base; **terminal Sp** conically subulate, unguicately recurved, smooth, rather dull, openly grooved to ± the middle, 10–30 × 3 mm, reddish to dark brown, shortly decurrent and dorsally immersed into the green tissue; **Inf** at least 4 m, paniculate, fertile part in the upper ½, narrowly oblong, part-**Inf** ascending, not known to be bulbiferous; **Ped** ±10 mm and slender or 40 mm and much stouter; **Fl** 55–60 (–70) mm; **Tep** yellow, tube conical, 8–10 mm, lobes 15–20 × 3–5 mm; **Fil** 25–40 mm, inserted nearly in the throat; **Ov** oblong-fusiform, 25–40 mm; **Sty** longer than the filaments; **Sti** capitate; **Fr** broadly ellipsoid, 30–40 × 15–20 mm, beaked, somewhat stipitate; **Se** 6 × 4 mm.



The species was described based on the type collection only and is the only native Caribbean species that lacks marginal teeth (Trelease 1913: 36). It has apparently hardly ever been recollected, but Richter (2011: 88) shows a plant cultivated in Germany. Pilbeam (2013: 29) and Hochstätter (2015: VII: 66) publish the first habitat photographs. Ullrich (1990d: 107) suggests that it might be identical with the Mexican *A. desmetiana* (see also there); photographs of both species by Pilbeam (2013: 29, 75) and elsewhere are indeed hardly different. Since *A. desmetiana* is placed in Sect. *Sisalanae* (as Group), *A. anomala* is probably better placed in that section. It is classified as “Least Concern” in the Cuban Red List (Berazaín & al. 2005).

**A. antillarum** Descourtilz (Fl. Méd. Antilles 4: 239, t. 284, 1827). **Type:** not typified. — **Lit:** Engelm. (1875: 313–314); Petersen (1893: with ill.); Trel. (1913: 31–32, tt. 41–43 [leaf margin of t. 43 probably of *A. intermixta*]); Berger (1915: 206–207); Álvarez de Zayas (1995: 41). **Distr:** Hispaniola (Haiti, Dominican Republic).

This is the earliest named species of Sect. *Antillaranae*, but the protologue is short and indicates orange flowers. Engelm. (1875) equated it with the short- and red-orange-flowered *Agave* of S Haiti, and he was followed by later authors (Petersen 1893, Trel. 1913: 31). According to Álvarez de Zayas (1995), the differences of the other *Agaves* from Hispaniola (*A. brevipedata*, *A. brevispina*, *A. intermixta*) are very subtle and need a critical revision, since they might be conspecific.

**A. antillarum** var. **antillarum** — **Distr:** Hispaniola (Haiti, Dominican Republic); hillsides, limestone rock outcrops and steep cliff sides, S-exposed places, 340–1400 m; flowers in February and November. **I:** Richter (2011: 15, 89, 90); Pilbeam (2013: 30); Hochstätter (2015: VII: 67).

**Incl.** *Agave vivipara* Lamarck (1783) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave americana* Schomburgk (1835) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave dominicensis* Ruse (1893) (*nom.*

*inval.*, ICN Art. 32.1c); **incl.** *Agave americana* Urban (1903) (*nom. illeg.*, ICN Art. 53.1).

[2p] Acaulescent; **Ros** solitary; **L** lanceolate, gradually acute, somewhat concave, 75–100 × 6–11 cm, bright green, margins typically nearly straight; **marginal teeth** straight or upcurved, narrowly triangular from lenticular bases or acuminate deltoid, hard, sharp, 2–4 mm, deep brown to reddish-brown, 10–30 mm apart; **terminal Sp** conical, nearly straight, involutely grooved near the base, smooth, 15–20 × 3 mm, brown or reddish-brown, dull, decurrent; **Inf** 2.5–5 m, paniculate, peduncle with acute green **Bra**, fertile part narrowly oblong, part-**Inf** ascending, in the upper ¼–½ of the inflorescence, the middle ones longest, to 30 cm, with up to nearly 100 densely clustered flowers, not known to be bulbiferous; **Ped** 5–10 (–25) mm; **Fl** 40–50 mm, fragrant; **Tep** deep orange, tube open, 5–10 mm (Petersen 1893: almost none), yellowish-green, lobes linear-lanceolate, erect-patent, 15–25 (–28) × 4 mm, orange; **Fil** 25–30 mm, inserted in the throat of the tube or a little below; **Anth** ±20 mm, orange before dehiscence; **Ov** oblong-fusiform, triquetrous, 25–40 (–46) mm; **Sty** as long as the filaments; **Fr** narrowly oblong, 38–45 × 15–20 mm, beaked, stipitate; **Se** 5–7 × 3–4 mm, shiny, black.

**A. antillarum** var. **grammontensis** Trel. (Repert. Spec. Nov. Regni Veg. 23: 362, 1927). **Type:** Hispaniola, Haiti (*Ekman* 3355 [US, B, ILL, S]). — **Distr:** Hispaniola (Haiti); hard limestone rocks.

≡ *Agave antillarum* ssp. *grammontensis* (Trel.) Hochstätter (2015).

[2p] Differs from var. *antillarum*: **L** glaucous; **marginal teeth** in the middle of the leaf broadly triangular, larger, 5 mm, 5–10 mm apart, margins between the teeth concave; **Tep** orange, almost cochineal-red within; **Fr** and **Se** unknown.

Apparently never recollected.

**A. apedicellata** Thiede & Egli (Kakt. and Sukk. 50(5): 111, 1999). **Type:** Mexico, San Luis Potosí (*Parry & Palmer* 867 [K, GH, NY, US]). — **Lit:** Rose (1903a: 9, as *Polianthes durangensis*, 10, as *P. sessiliflora* & *P. pringlei*);

McVaugh (1989: 255–258, as *P. pringlei*); Solano & Feria (2007: as *P. sessiliflora*); Cházaro Basáñez & al. (2014: with ills., as *P. pringlei*); Cházaro Basáñez & al. (2015: with ills., as *P. pringlei*). **Distr:** Mexico (Durango, Zacatecas, Aguascalientes, San Luis Potosí, Nayarit, Jalisco, Guanajuato, Michoacán); grasslands, grassy openings and hillsides in oak or pine-oak forest regions, wet meadows and pastures, 800–2470 m; flowers July to October. **I:** Hemsley (1879–1888: t. 86, as *Bravoa sessiliflora*); Barba-Gonzalez & al. (2012: 124, as *P. pringlei* & *P. sessiliflora*); Hochstätter (2016: II: 23, as *P. sessiliflora*); Castro-Castro & al. (2016: 721, as *P. sessiliflora*).

≡ *Bravoa sessiliflora* Hemsley (1880) ≡ *Polianthes sessiliflora* (Hemsley) Rose (1903a); **incl.** *Polianthes durangensis* Rose (1903a); **incl.** *Polianthes pringlei* Rose (1903a); **incl.** *Agave neopringlei* Thiede & Egli (1999).

[3b1] Herbaceous; corm ± (1–) 2.2–3.2 × 1.5–2.5 cm, oblong, bulb 4–6 × 1.2–2.5 cm, narrowly ovoid to conical, completely covered with dried fibrous leaf bases; **R** fleshy, thickened, contractile; **L** drought-deciduous, (1–) 5–15, erect or nearly so, linear to linear-attenuate, grass-like, sometimes 1–6 additional ones a few cm above the peduncle base, upper ones much reduced, sometimes papillose on the veins on the lower face, 10–25 (–45) × (0.1–) 0.3–0.7 (–1) cm, green, margins ± papillose; **Inf** (20–) 25–45 (–65) cm, erect, ‘spicate’, green, peduncle with 2–4 **Bra**, lanceolate-subulate, 1–4 cm, internodes decreasing in size distally, fertile part 8–17 (–20) cm, very lax, with 2–7 remote floral nodes; floral **Bra** ± 0.8–1.2 × 0.2 cm, broadly ovate, acute or shortly acuminate; **Ped** none; **Fl** geminate, fragrant, 54–75 mm; **Tep** white, sometimes (pale) pink, or white inside and pink outside, or sometimes red, or drying purplish, forming a slender tube, ascending from the base, commonly curved outwards in the middle or below, narrowly funnel-shaped above, tube 30–70 × 2.5–4 mm at the base of the lobes, mouth strongly oblique, lobes elliptic to oblong or broadly ovate, subequal, ascending-spreading or finally recurved, erect or finally recurved, (3–) 10–15 × (2.5–) 3–6 mm, apex obtuse or subacute, tip cucullate; **Fil** filiform, 1–2 mm, included, inserted 4–6 mm below the

mouth of the tube; **Anth** linear, (5–) 7–9.5 mm, apex reaching the tip of the lobes; **Ov** fusiform, erect, ± 5–6 × 2–3 mm; **Sty** filiform, not exerted; **Sti** 3-lobed, included; **Fr** broadly ellipsoid, 10–13 × 8–10 mm, weakly stipitate; **Se** flat, 3.5–4 mm.

The second-most widely distributed species of Sect. *Polianthes* and recorded from 64 localities by Solano & Feria (2007). It is characterized by its narrow leaves and white flowers with a long tube curved outwards. *A. neopringlei* (≡ *Polianthes pringlei*) and *Polianthes durangensis* are both placed in the synonymy of this species following A. Castro-Castro (pers. comm. to author, Nov. 2018). *A. dolichantha* has similar white flowers with an oblique mouth, but differs in its longer flowers with much longer filaments. The record from the Balsas basin (Fernández Nava & al. 1998: 2, as *P. pringlei*) needs confirmation. — The original epithet of *Polianthes sessiliflora* is pre-occupied under *Agave*, necessitating the new name published by Thiede & Egli (1999).

**A. applanata** Hort. Tonel *ex* K. Koch (Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 5: 198, 1862). **Type** [neo]: Mexico, Veracruz (*Trelease* 1 [MO]). — **Lit:** *Trelease* (1912b: 86–88, with ills.); Gentry (1982: 421–425, with ills.); Alsemgeest & al. (2005: with ills.); García-Mendoza (2011a: 15, 17, 21); Starr (2012: 44–49, with ills.); Smith & Figueiredo (2013: 54–55). **Distr:** Mexico (Chihuahua, Durango, Zacatecas, Guanajuato, Querétaro, Hidalgo, México, Puebla, Veracruz, Oaxaca). **I:** Alsemgeest & al. (2005); Heller (2006: 63); Klopper & al. (2010: 54); Richter (2011: 14); Pilbeam (2013: 31); Hochstätter (2015: IV: 5). – Fig. 5.

**Incl.** *Agave cinerascens* Jacobi (1864); **incl.** *Agave applanata* var. *major* Jacobi (1866); **incl.** *Agave applanata* var. *subnivea* Jacobi (1866); **incl.** *Agave applanata* var. *spectabilis* A. Terracciano (1885); **incl.** *Agave spatularia* hort. *ex* Alsemgeest & Roosbroeck (2010) (*nom. inval.*, ICN Art. 38.1a).

[2h] Stems short; **Ros** 0.5–1 × 1–2 m (in cultivars 1.2–2 × 2.5–3.5 m), solitary or

**Fig. 5** *Agave applanata*

(Etter & Kristen 3648: Mexico; Querétaro, along the road to Cerro Zamorano, 2600 m). (Copyright: J. Etter & M. Kristen)



sparingly caespitose; **L** 100–200, linear-lanceolate, stiffly erect-spreading, very rigid, hard-fleshy with coarse, abundant fibres, gradually acute, usually widest at or near the base, very openly concave, smooth, 40–60 × 7–10 cm (cultivated material 100–160 × 10–15 cm), mostly glaucous-grey, mature leaves much longer than earlier stages, margins horny throughout or not differentiated in the middle of the lamina; **marginal teeth** nearly straight or frequently curved downwards, very strong, sharp, larger teeth (middle of the leaf) 8–15 mm, dark brown becoming light waxy pruinose, mostly 25–60 (–75) mm apart, smaller (5–8 mm) and more closely spaced (25–35 (–50) mm) in wild forms, abruptly lenticularly widened to 20–30 mm at the base, or confluent throughout to form a slightly concave horny margin ±1 mm wide, which is, like the teeth, sparsely granular; **terminal Sp** very strong, flat or broadly guttered, often somewhat flexuous, 30–70 × 6–14 (at the base) mm, dark reddish-brown becoming greyish with age, long-decurrent along the margin; **Inf** 3.5–8 (–14) m, paniculate, peduncle glaucous-green, with reflexed triangular **Bra** 20–25 cm long, fertile part narrowly oblong, in the upper ½, part-**Inf** numerous, horizontal or slightly ascending, (40–) 65–80 cm; **Ped** 15–20 mm; **Fl** 55–70 (–85) mm, foetid; **Tep** yellow to greenish-yellow, sometimes with brownish or reddish tinge, tube cylindrical, thick-walled,

deeply furrowed from the tepal sinuses, 12–22 × 10–15 mm, lobes linear-lanceolate, thick, unequal, 15–22 × 4–8 mm, **ITep** shorter and narrower, with a narrow prominent keel, apex cucullate, brown; **Fil** flattened, 45–65 mm, inserted in 2 ranks at mid-tube or ± in the upper ½, yellowish-green; **Anth** centric or excentric, 20–30 mm, yellow; **Ov** angularly cylindrical, tapering towards the base, 35–38 mm, greenish; **Sty** 70 mm; **Sti** 3-lobate; **Fr** oblong, 40–50 × 20–25 mm; **Se** 6–7 × 5–7 mm, shiny, with inconspicuous wing.

See Smith & Figueiredo (2013) for the place of valid publication. The neotype cited above was designated by Gentry (1982: 422). This taxon appears to be truly native to Veracruz and adjacent Puebla and is cultivated as a cottage plant elsewhere. It was possibly disseminated to the North by men in (pre-) historic times (Gentry 1982: 424–425). For plants from Guanajuato with rosettes of few broad leaves with especially long terminal spines, resembling *A. applanata*, the invalid name “*A. spatularia*” is used (Alsemgeest & Roosbroeck 2010: 74); Richter (2011: 57, 119, ill.) places these plants under *A. parryi*. In habitat, plants are very similar to some forms of *A. flexispina*. ‘Cream Spike’ is a variegated cultivar (Starr 2012: 49, with ill.); Alsemgeest & al. (2005: 248) show unarmed variegated plants. See also the notes under *A. angustifolia* var. *angustifolia* and *A. potatorum*.





**Fig. 6** *Agave arcedianoensis* (Etter & Kristen 3514; Mexico; Jalisco, Río Santiago Canyon, 1220 m). (Copyright: J. Etter & M. Kristen)

**A. arcedianoensis** Cházaro & al. (in Vázquez-García & al. (eds.), *Agaves Occid. Méx.*, 45–46, ills. (t. EE, pp. lxxiv–lxxv), 2007). **Type:** Mexico, Jalisco (*Vázquez-García & Cházaro Basáñez* s.n. [IBUG]). — **Lit:** Cházaro Basáñez & Valencia (2003: with ills., as *A. impressa*); Greulich (2012a: 32–35); Hernández-Vera & al. (2019: with ills.). **Distr:** Mexico (C Jalisco: endemic to the Santiago Canyon N of Guadalajara); volcanic rock cliffs and ridges in tropical deciduous forests, 1250–1440 m; flowers May to July; only known from the type locality. **I:** Etter & Kristen (2012: 91); Pilbeam (2013: 32); Hochstätter (2015: IX: 25). – Fig. 6.

**Incl.** *Agave colimillensis* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1).

[lg] **Ros** stemless, solitary, symmetrical, to  $0.9 \times 1.5$  m  $\varnothing$ ; **L** many, lanceolate, rigid, fleshy,  $60\text{--}70 \times 10\text{--}12$  cm, dark green, with a

conspicuous yellowish-green mid-stripe above along the whole length, with inconspicuous marks left by the central bud, margins horn-grey; **marginal teeth** numerous, straight or variously curved, size not described, with broad base, greyish to silvery, 20–25 mm apart, partly absent from the upper leaf parts; **terminal Sp** 20–40 mm, dark brown, long-decurrent; **Inf** 1.8–2 m, ‘spicate’, peduncle with many filiform  $\pm$  horizontal **Bra**, fertile part in the upper 70–80%, 15–18 cm  $\varnothing$ ; **Ped** 3–6 mm, thick; **Fl** geminate; **Tep** reddish-purple above, greenish below, tube very short, lobes greenish below, upper  $\frac{2}{3}$  reddish-purple, tips slight recurved; **Fil** long exerted, reddish-purple; **Anth** 14–15 mm, reddish-purple; **Ov** 17–18 mm, greenish, neck with a longer constriction; **Fr** oblong,  $30\text{--}40 \times 16\text{--}22$  mm, beaked, fruit valves spreading, infructescence 18–25 cm  $\varnothing$ ; **Se** unknown.

The protologue description is incomplete, and information taken from published photographs is here added. Similar to *A. angustiarum* according to the protologue but differing in smaller rosettes, more widely spaced marginal teeth, and reddish flowers. The comparison is based on the inadequate data for *A. angustiarum* in Gentry (1982: 134), however, which did not include the complete variation given in Trelease’s protologue. Based on this data, rosette and leaf sizes of *A. arcedianoensis* fall within the range of *A. angustiarum* (see there), and the same is true for the arrangement of the marginal teeth. The reddish-purple flowers therefore appear to remain as sole distinguishing character, as pointed out by Greulich (2012a); reddish flowers are rarely also reported for *A. angustiarum* (Velasco Gutiérrez & al. 1904, MEXU 1375574: “tépalos rojizos”). Hernández-Vera & al. (2019) provide additional morphological data and photographs, pointing out differences from *A. angustiarum* esp. in the inconspicuous marks left by the central bud (vs. lacking), shorter pedicels, much larger diameter of the infructescences, and beaked fruits with spreading valves (vs. straight fruit valves apically rounded). Sterile plants of this taxon were first erroneously reported as *A. impressa* (Cházaro Basáñez & Valencia 2003). For differences from the closely related *A. garciaruii* see there.

**A. ×arizonica** Gentry & J. H. Weber *pro sp.* (Cact. Succ. J. (US) 42(5): 223–225, ill., 1970). **Type**: USA, Arizona (Weber s.n. [US, ASU, DES]). — **Lit**: Gentry (1977a: 40–41, with ill.); Gentry (1982: 254–257, with ill.); both as *A. arizonica*; Hodgson (1999a: 4, 18, with ill.); Reveal & Hodgson (2002); Parker (2018a: 20–21, with ill.). **Distr**: USA (Arizona); open rocky slopes in chaparral vegetation or juniper-dominated grasslands, 900–1800 m; flowers May to July. **I**: Pilbeam (2013: 33); Hochstätter (2015: IX: 20).

[1e × 2h] Identified as the diploid natural hybrid *A. toumeyana* ssp. *bella* × *A. chrysantha* by Reichenbacher (1985), Pinkava & Baker (1985) and others. The taxon is of conservation concern since only about 50–60 clones are known (Hodgson 1999a, Reveal & Hodgson 2002). Parker (2018a) knows of only two living plants in habitat and reports a natural hybrid with *A. toumeyana* ssp. *bella* (as var. *bella*). — For the in vitro propagation, see Powers & Backhaus (1989).

**A. arubensis** Hummelinck (Recueil Trav. Bot. Néerl. 33: 236–237, 248, figs. 14–15, tt. 3a, 4, 1936). **Type** [syn]: Aruba (Hummelinck 17a + b [U]). — **Lit**: Hummelinck (1938: 19, 27); Hummelinck (1993: 104–105, 108, 219, 223, with ill.); Thomson (2014: with ill.). **Distr**: Leeward Islands (Aruba: Fontein and vicinity); debris of coral rocks, calcareous terraces, 30–550 m; flowers in June. **I**: Pilbeam (2013: 34); Hochstätter (2015: VIII: 33).

[2u] Acaulescent, **Ros** 1.3–1.6 m Ø, suckering (?); **L** rather few, broadly lanceolate, slightly S-curved, flat, margins upcurved and infolded during drought, widest somewhat below or in the middle, usually slightly acuminate, usually guttered and lower face round, 60–80 × 13–14 cm, 4.25–6 × as long as broad; **marginal teeth** usually pointing downwards somewhat below the middle of the leaves, often upcurved farther up, slenderly acicular, usually rough at the base, 4–6 (–7) mm, 8–12 per 10 cm, on rather weakly to strongly developed green or hardening prominences; **terminal Sp** acicular, straight or very slightly upcurved at the tip, sometimes slightly flexuous, narrowly to broadly grooved basally or to the

middle, margin blunt or rather sharp, usually rough, covered with many minute tubercles, 27–32 × 2.5–4 mm, shortly decurrent, dorsally at most very slightly intruding into the leaf tissue; **Inf** 3.5–5 m, paniculate, narrowly oblong, peduncle with 6–13 **Bra** (4–) 6–12 (–14) cm long, part-**Inf** rather many, on slightly S-curved ± ascending **Br**, in the upper ½–⅔ of the **Inf**, forming few fruits but freely bulbiferous; **Ped** 4–7 mm; general **Fl** shape and **Ov** not described; **Tep** tube 7–8 mm, lobes 19–21 mm; **Fil** 30–35 mm, inserted 2–4 mm below the throat; **Anth** 14–19 mm; **Sty** 35–40 mm; **Fr** narrowly oblong, 33–40 × 12–15 mm, long-beaked, long-stipitate; **Se** 4.5–5 × 4–4.5 mm.

According to the protologue hardly different from *A. vicina* (as *A. vivipara*) in vegetative characters, but clearly differing in generative parts (small number of bracts, long tube with filaments inserted low down, form of capsules). The species was recently re-studied in habitat by Thomson (2014).

**A. asperrima** Jacobi (Hamburg. Gart.- & Blumenzeit. 20: 561, 1864). **Type** [neo]: USA, Texas (Gentry & Barclay 20012 [US, DES]). — **Lit**: Gentry (1975: with ill., as *A. scabra*); Gentry (1982: 296–303, with ill., as *A. scabra*); Ullrich (1992j: with ill.); Reveal & Hodgson (2002); Villarreal & al. (2005); González-Elizondo & al. (2009: 54–57, with ill.); Starr (2012: 50–55, with ill.). **Distr**: USA (Texas), Mexico (Chihuahua, Coahuila, Nuevo León, Durango, Zacatecas, San Luis Potosí, Querétaro).

The nomenclature of this taxon was discussed controversially. Gentry (1982: 296) used the name *A. scabra* Salm-Dyck (1859) for this taxon, but this is an illegitimate later homonym of *A. scabra* Ortega (1797), as shown by Ullrich (1992j). Ullrich consequently re-established the oldest synonym *A. asperrima* Jacobi (1864) as correct name for *A. scabra* sensu Gentry, and he was followed by later authors. The neotype cited above was designated by Ullrich (1992j: 253). *A. wislizeni* Engelman (1875) received alternative interpretations (see Villarreal & al. (2005)) as *A. parryi* (Ullrich 1992j), *A. parrasana* (Gentry 1975), or *A. ovatifolia* (Villarreal & al. 2003, Villarreal & al. 2005), but all these interpretations are flawed

since *A. wislizeni* was published as a legitimate replacement name for the illegitimate *A. scabra* Salm-Dyck and must thus be typified by the type of the latter (Villarreal & al. 2005). Gentry (1982: 296) designated one of his own collections (*Gentry & Engard* 23268) as neotype for *A. scabra* Salm-Dyck, which he equated with *A. asperrima*. Ullrich (1992j) seemingly rejected Gentry's neotypification as a misinterpretation of *A. scabra*, but did not propose a replacement type. Since Gentry's neotype is not in serious conflict with Salm-Dyck's protologue of *A. scabra*, there are no grounds for superseding Gentry's neotypification, and the type for *A. scabra* is also the type of *A. wislizeni*, which then also becomes a synonym of *A. asperrima* (Villarreal & al. 2005).

**A. asperrima** ssp. **asperrima** — **Lit:** Gentry (1982: 276, 296–299, with ill., as *A. scabra*); González-Elizondo & al. (2009: 54–56, with ill.); Starr (2012: 51–55, with ill.). **Distr:** USA (Texas), Mexico (SE Chihuahua, C & S Coahuila, C & S Nuevo León, NE & E Durango, N & C Zacatecas, Guanajuato); dry, sandy to gravelly, often calcareous places in desert scrub, 500–1500 (–1900) m; flowers April to December. **I:** Irish & Irish (2000: t. 36, as *A. scabra*); Heller (2006: 64); Richter (2011: 115, 117–118); Pilbeam (2013: 35); Hochstätter (2015: VII: 10).

**Incl.** *Agave scabra* Salm-Dyck (1859) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave wislizeni* Engelm (1875); **incl.** *Agave caecilians* A. Berger (1915).

[2a] Acaulescent, **Ros** frequently suckering with new rosettes appearing at some distance, rather open, 0.7–1 × 1.5–2 m; **L** 30–40, lanceolate, rigid, spreading to recurved and mostly reflexed, very broad at the base and constricted just above, long-acuminate, convex below, flat above but deeply guttering in the lower ½, scabrous, generally 60–110 × 12–16 cm, light green to glaucous-grey, without imprints from the central bud, margins sometimes horny along the upper ½; **marginal teeth** generally deflected below the middle of the leaves, larger teeth 8–15 mm, brown to pruinose-grey, from broadly rounded bases; **terminal Sp** subulate to acicular, very narrowly grooved above, base scabrous,

30–60 mm, dark brown to blackish, long decurrent on the involute leaf margin; **Inf** mostly 4–7 m, paniculate, peduncle with persistent triangular **Bra** 3–10 cm long, part-**Inf** 8–12 in the upper ⅓ of the inflorescence, small, compact, slightly ascending, >10 cm, with 14–18 flowers; **Fl** erect, 60–80 mm; **Tep** yellow, tube cylindrical, 13–18 × 14–16 mm, lobes erect, lanceolate-linear, involute, subequal, 18–26 × 4–6 mm, outer 2 mm longer, inner broadening at the base, with narrow, prominent keel, both cucullate; **St** long-exserted; **Fil** erect, slender, tapering, 50–65 mm, yellow, inserted just above mid-tube; **Anth** centric, 24–30 mm, yellow; **Ov** slender, 30–40 mm, greenish, neck constricted, 4–6 mm; **Sty** longer than the stamens after anthesis, broadly clavate towards the apex; **Sti** 3-lobate; **Fr** oblong, 40–50 × 17–20 mm, beaked, shortly stipitate; **Se** crescent-shaped, 6–7 × 5 mm, margin with wavy wing. — **Cytology:** 2n = 60, 87, 174–180, 148–186 (2×, 6×; Cave 1964, Simpson & al. 2011).

This is the most widespread and common *Agave* in the Chihuahuan Desert of N Mexico, with the exception of *A. lechuguilla*. In contrast to most other species, it inhabits the broad valleys and plains as well as the stony slopes of the mountains (Gentry 1982: 296). It is related to *A. americana* and distinguished by its more scabrous and shorter leaves, less branched inflorescences, a longer flower tube, and smaller tepal lobes (Gentry 1982: 296). Cave (1964) gave chromosome counts of n = 74–93, but according to Gentry (1982: 273), only the count n = 87 applies to ssp. *asperrima*. It shows introgressive hybridization with *A. americana* and *A. nickelsiae* (= *A. ×santilloensis*; see there) (Gentry 1982: 299).

**A. asperrima** ssp. **maderensis** (Gentry) B. Ullrich (*Sida* 15(2): 254, 1992). **Type:** Mexico, Coahuila (*Gentry & Engard* 23251 [DES, ARIZ, CAS, MEXU, US]). — **Lit:** Gentry (1982: 301–302, with ill., as *A. scabra* ssp.); Starr (2012: 55). **Distr:** Mexico (Coahuila); local endemic in (limestone) canyons of desert mountains in pine-oak forests or oak-chaparral vegetation, 1850–2000 m; flowers June to July. **I:** Hochstätter (2015: VII: 11).

≡ *Agave scabra* ssp. *maderensis* Gentry (1982) (*incorrect name*, Art. 11.4).

[2a] Differs from ssp. *asperrima*: Stems short, thick; **Ros** solitary; **L** triangularly linear-lanceolate, relatively smooth, 50–60 × 7–12 cm, green to yellow-green; **marginal teeth** slender, larger teeth 5–8 mm, mostly 20–30 mm apart; **Inf** with >11 large spreading part-**Inf**, each several times compound; **Fl** 65–70 mm; **Tep** tube 11–16 × 12–15 mm, lobes linear, 15–20 mm.

A local endemic of the Chihuahuan Desert mountains, well characterized by its (always?) solitary rosettes, short thick stems, and smooth green leaves (Gentry 1982).

**A. asperrima** ssp. **potosiensis** (Gentry) B. Ullrich (Sida 15(2): 254, 1992). **Type**: Mexico, San Luis Potosí (Gentry & al. 20162 [US, ARIZ, MEXU]). — **Lit**: Gentry (1982: 301–302, with ills., as *A. scabra* ssp.); Starr (2012: 50–51, 55, with ill.). **Distr**: Mexico (San Luis Potosí, Querétaro); rocky slopes and desert plains with limestone, in desert scrub or pine-oak forests, 1130–2070 m; flowers in July. **I**: Etter & Kristen (2007b: 177); Richter (2011: 120); Pilbeam (2013: 35).

≡ *Agave scabra* ssp. *potosiensis* Gentry (1982) (*incorrect name*, Art. 11.4).

[2a] Differs from ssp. *asperrima*: **Ros** more open, spreading, sparingly surculose; **L** broadly lanceolate, tip outcurving and sigmoid, asperous to nearly smooth, 65–110 × 14–20 cm, glaucous-grey to nearly white, frequently cross-zoned; **marginal teeth** sometimes on tuberculate elevations; **Inf** with 10–18 small part-**Inf**; **Tep** tube large, 15–22 mm; **Ov** slender, 32–50 mm.

Best distinguished by its more open and spreading graceful rosettes with broad and less rigid, lightly glaucous leaves, flowers with slender ovaries and a large tube, but often difficult to separate due to apparent introgression with *A. americana* ssp. *protoamericana* (Gentry 1982: 301–302). Zamudio & Galván Villanueva (2011: as *A. scabra*) provide a new record of “*A. scabra*” from Guanajuato which, due to geographical proximity, must represent ssp. *potosiensis*.

**A. asperrima** ssp. **zarcensis** (Gentry) B. Ullrich (Sida 15(2): 254, 1992). **Type**: Mexico, Durango (Gentry & Arguelles 22084 [US, ARIZ, ASU, MEXU, MICH]). — **Lit**: Gentry (1982: 302–303, with ills., as *A. scabra* ssp.); González-Elizondo & al. (2009: 56–57, with ills.); Starr (2012: 55). **Distr**: Mexico (Durango); sunny rocky slopes with limestone in transition between desert and grama grasslands, 1120–1675 m; flowers in June and July. **I**: Pilbeam (2013: 36); Hochstätter (2015: VII: 13).

≡ *Agave scabra* ssp. *zarcensis* Gentry (1982) (*incorrect name*, Art. 11.4).

[2a] Differs from ssp. *asperrima*: **Ros** surculose, forming large clumps; **L** linear-ovate, guttered, 55–60 × 15–20 cm, greyish-green; **marginal teeth** mostly reflexed, moderate, larger 5–7 mm, 10–20 mm apart; part-**Inf** 8–14, in the upper 1/3 of the **Inf**, on sigmoid branches; **Fl** 68–92 mm; **Tep** tube deeply furrowed, thickly 12-ridged within; **Ov** 3-angled and 6-grooved, 35–50 mm.

A highland ecotype within *A. asperrima*, distinguished best by its short broad leaves with moderate teeth, large flowers, 2-level insertion of filaments, and large woody fruits. The insertion of the filaments at 2 levels suggests an affinity with *A. havardiana* where this character sporadically occurs, as well as in ssp. *asperrima* — the character is thus not exclusive to Sect. *Ditepalae* (as Group), where it is so prominent (Gentry 1982: 302–303). González-Elizondo & al. (2009) show plants from Durango with introgression of *A. salmiana* and *A. ×gracilipes*.

**A. atrovirens** Karwinsky ex Salm-Dyck (Hort. Dyck., 7: 302, 1834). **Type** [neo]: Mexico, Oaxaca (Gentry 22377 [US, ARIZ, MEXU]). — **Distr**: S Mexico.

The neotype cited above was designated by Gentry (1982: 469).

**A. atrovirens** var. **atrovirens** — **Lit**: Gentry (1982: 468–476, with ills.); Ullrich (1990a: with ill.); Piña Luján (1994: with ill.); García-Mendoza (2011a: 17–21, with ills.). **Distr**: Mexico (C Guerrero, Oaxaca); strictly high-montane in



oak forests, 1850–3400 m; flowers October to March. **I**: Cact. Suc. Mex. 39(3): front cover, 1994; García-Mendoza (2002: 178); Heller (2006: 65); Richter (2011: 41–42); Greulich (2012c: 39); Pilbeam (2013: 37); Hochstätter (2015: VI: 5); Moore (2016: 238).

**Incl.** *Agave coccinea* Roez l ex K. Koch (1862); **incl.** *Agave schlehtendahl ii* Jacobi (1864); **incl.** *Agave coccinea* Roez l ex Jacobi (1865) (*nom. illeg.*, ICN Art. 53.1)  $\equiv$  *Agave americana* var. *coccinea* (Roez l ex Jacobi) A. Terracciano (1885); **incl.** *Agave ottonis* Jacobi (1866); **incl.** *Agave canartiana* Jacobi (1868); **incl.** *Agave canartiana* var. *laevior* Jacobi (1868); **incl.** *Agave deflexispina* Jacobi (1870); **incl.** *Agave gracilis* Jacobi (1870); **incl.** *Agave macroculmis* Todaro (1878); **incl.** *Agave coccinea* hort. ex A. Berger (1898) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave atrovirens* var. *cochlearis* Trelease (1914); **incl.** *Agave atrovirens* var. *marginata* Trelease (1914); **incl.** *Agave atrovirens* var. *sigmatophylla* A. Berger (1915).

[2o] Acaulescent, **Ros** openly spreading, large to very large, 1.5–2.5  $\times$  3–4 m, solitary or caespitose; **L** 40–70, erect to recurved, broadly lanceolate, thick at the base (to 25 cm), usually narrowed below the middle, convex below, openly concave above, mostly 150–200 (–220)  $\times$  20–40 cm, dark to blackish-green to light glaucous or glaucous-variegated, margins  $\pm$  straight or slightly wavy; **marginal teeth** regular, straight, antrorse, 4–8 (–12)  $\times$  10–13 (–17) mm (mid-leaf), dark brown, greyish-brown or reddish, with low broad bases, 10–20 (–40) mm apart, sometimes bases fused into a continuous band; **terminal Sp** straight, conical, strong, broad at the base, widely openly grooved above, (30–) 60–70 mm, decurrent for 10–20 cm, keel rounded below and markedly intruding into the leaf tip for 1.5–2.5 cm, dark brown; **Inf** 6–12 m, paniculate, peduncle with long triangular dark brown **Bra** 40–50 cm long, fertile part narrow, oblong, part-**Inf** congested in the upper  $\frac{1}{3}$ – $\frac{1}{2}$  of the **Inf**, globose, (18–) 35–60, 20–30 cm long, with >600 flowers, axis reddish; **Fl** thickly fleshy, (70–) 80–90 (–100) mm; **Ped** 10–20 mm; **Tep** red to purple in bud, at anthesis yellowish to yellowish-green within, tip reddish, tube deeply furrowed, thick-walled, 10–15  $\times$

10–20 mm, bulging at the insertion of the stamens, lobes triangular or oblong, erect, conduplicate-revolute, thickly fleshy, unequal, 30–40  $\times$  4–6 (–9) mm, incurved at the tips; **OTep** slightly larger; **ITep** with very thick keel and thin margins, red with paler margins; **Fil** large, flattened, 70–80 (–90) mm, purplish or red-spotted, inserted in the middle or at the mouth of the tube, yellowish or with purple dots; **Anth** excentric, straight to sinuous, (25–) 30–43 mm, yellow(ish) to bronze; **Ov** cylindrical, tapering at the base, 3- to 6-angled, 30–50  $\times$  (4–) 6–8 mm, neck thick, furrowed, 4–7 mm; **Sty** 80–110 mm, much longer than the stamens after anthesis; **Sti** clavate, 4–5 mm  $\varnothing$ ; **Fr** ovoid, ellipsoid or clavate, 40–50 (–65)  $\times$  20–30 mm, 5–12 mm stipitate, tapering from the apex; **Se** crescent-shaped, 7–9  $\times$  4–6 mm, shiny, with inconspicuous wing. — **Cytology**: 2n = 180 (Simpson & al. 2011).

A very large species with affinities to species of Sect. *Guatemalenses* (as Group *Hiemiflorae*) from Chiapas and Guatemala, which flower in winter, produce straight and strong peduncles, and with tightly arranged flowers in bracteolate globose purplish clusters in narrow panicles (Gentry 1982: 468–476). Karwinski's type locality "Monte Tanga" (see Piña Luján (1994)) was re-named as Monte Fiscal-Santos and is located W of Ciudad Oaxaca (David 2009), and this is supported by Karwinski's letters (Phillips 2013). Earlier authors (Baker, Berger, Trelease) confused the species with *A. salmiana* (Gentry 1982). Gentry's records from NE Puebla and C Veracruz apparently refer to cultivated plants of var. *mirabilis* (see there). Ullrich (1990a) reports on a new locality from Guerrero. The records from México state (Ávila-Akerberg & al. 2008: 617) (specimens *Castañeda Rojas* 27, MEXU 1047763 & 1047765) need verification. *A. macroculmis* is a synonym to be placed here (Ullrich 1990i), and was misinterpreted by Gentry (1982: 598) for plants later described as *A. gentryi* and *A. montana* (see there). Leaves frequently show necrotic spots caused by a herbivorous fly whose larvae develop inside the leaves of *A. atrovirens* and *A. salmiana* (Brunel & Rull 2010).



**A. atrovirens** var. **mirabilis** (Trelease) Gentry (Agaves Cont. North Amer., 473, ill. (p. 476), 1982). **Type:** Mexico, Veracruz (*Trelease* 7 p.p. [MO, DES]). — **Lit:** García-Mendoza (2011a: 20–21, with ills.). **Distr:** Mexico (NE & S Puebla, C Veracruz, N Oaxaca); cool montane habitats, in pine-oak forests and cultivated, 2150–2480 m. **I:** García-Mendoza (2002: 179); Richter (2011: 83); Spracklin (2014); Hochstätter (2015: VI: 6).

≡ *Agave mirabilis* Trellease (1920) ≡ *Agave atrovirens* ssp. *mirabilis* (Trellease) Hochstätter (2015).

[2o] Differs from var. *atrovirens*: **L** broadly lanceolate, consistently light grey-glaucous; **Fl** smaller, 60–80 mm, without large bracteoles; **Ov** 25–30 mm.

A light glaucous form cultivated for pulque and as fences about Las Vigas, Veracruz, without confirmed occurrence elsewhere according to Gentry (1982: 473). Photographs from the type locality were published on the web by Spracklin (2014). Gentry's records for var. *mirabilis* from NE Puebla and C Veracruz apparently belong here according to García-Mendoza (2011a), who also reports the taxon from Oaxaca.

**A. attenuata** Salm-Dyck (Hort. Dyck., 303, 1834). **Type:** [neo — icon]: Curtis's Bot. Mag. 88: t. 5333, 1862. — **Distr:** Mexico (Sinaloa, SW Durango, Nayarit, Jalisco, Colima, Michoacán, México, Guerrero, Oaxaca).

The neotype cited above was designated by Gentry (1982: 68).

**A. attenuata** ssp. **attenuata** — **Lit:** Gentry (1982: 66–68); Ullrich (1990h); Cházaro Basáñez & al. (1998); Vázquez-García & al. (2007b: 47, t. F); Ullrich (2007); all with ills. **Distr:** Mexico (Jalisco, Colima, Michoacán, México); rocky outcrops in pine forests, 1900–2500 m; flowers November to December. **I:** Curtis's Bot. Mag. 88: t. 5333, 1862, as *A. glaucescens*; Irish & Irish (2000: t. 5); Heller (2006: 21, 37, 41, 66, 67); Etter & Kristen (2012: 87); Pilbeam (2013: 38); Meer (2014: as *A. cernua*); Hochstätter (2015: VIII: 38); Moore (2016: 246). — Fig. 7.



**Fig. 7** *Agave attenuata* ssp. *attenuata* (Etter & Kristen 1569; Mexico; Michoacán, between Morelia and Ciudad Hidalgo, 2260 m). (Copyright: J. Etter & M. Kristen)

**Incl.** *Ghiesbreghtia mollis* Roehl (1861) (*incorrect name*, Art. 11.4); **incl.** *Agave glaucescens* Hooker (1862) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave attenuata* var. *compacta* Jacobi (1865); **incl.** *Agave attenuata* var. *subundulata* Jacobi (1866); **incl.** *Agave attenuata* var. *coarctata* Jacobi (1866) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave ghiesbreghtii* [?] *mollis* Hort. Belg. ex Jacobi (1866) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave attenuata* var. *elliptica* Jacobi (1868) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave spectabilis* Roehl ex Baker (1877) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave attenuata* var. *glauca* Carrière (1879) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave attenuata* var. *latifolia* Salm-Dyck ex A. Terracciano (1885); **incl.** *Agave attenuata* var. *brevifolia* Jacobi ex A. Terracciano (1885) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave attenuata* var. *paucibracteata* Trellease (1914); **incl.** *Agave cernua* A. Berger (1915); **incl.** *Agave compacta* Hort. Besauccèle ex

*A. Berger* (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave elliptica* Hort. Besaucèle *ex A. Berger* (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave spectabilis* Hort. Besaucèle *ex A. Berger* (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave virens* Hort. Besaucèle *ex A. Berger* (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave attenuata* ‘Nova’ Kimmach & Trager (1990) (*nom. inval.*, Art. ICNCP 17.9); **incl.** *Agave attenuata* ‘Boutin Blue’ C. C. Walker (2000).

[1b] Stems 1 to several, usually ascending-curved, 0.5–1.5 m, becoming naked in age; **L** relatively short-lived, ovate-acuminate, softly succulent, broadest in the middle, flat to concave, 50–70 × 12–16 cm, light glaucous-grey to pale yellowish-green, margins smooth, straight, without teeth, leaf tip finely tapered, soon fraying, soft; **Inf** 2–3.5 m, ‘spicate’, densely flowered, part-**Inf** shortly pedunculate ‘fascicles’ with 3–8 flowers in the axils of chartaceous **Bra**; **Fl** 35–50 mm; **Tep** greenish-yellow, tube shallowly funnel-shaped, 3–5 mm, lobes linear-oblong, thin, recurving, equal, 16–24 mm, inner frequently broader, with broad low keel, mucronate with white-floccose tips; **Fil** slender, flattened, tapered, 35–45 mm, whitish, inserted on the rim of the tube; **Anth** centric, 15–20 mm, greenish-yellow; **Ov** fusiform, 15–25 mm, green, neck constricted; **Fr** oblong, 20–30 × 10 mm or smaller, shortly beaked, stipitate; **Se** crescent-shaped to deltoid, 3–3.5 × 2–2.5 mm, marginal wing low. — **Cytology**: 2n = 45–62 (Lv & al. 2009).

The presence of a flower tube groups this species in Sect. *Inermes* (Group *Amolae*) and not in Sect. *Choritepalae*, where the otherwise similar *A. bracteosa* and *A. ellemeetiana* are placed. It is closely related to *A. gilbertii* (Gentry 1982: 70). For relationships, see also under ssp. *dentata*. Cházaro Basáñez & al. (1998) provide a new record for Colima.

*A. attenuata* ‘Boutin Blue’ (Walker 2000: 97–98), first invalidly named *A. attenuata* ‘Nova’, differs in its leaves with an extremely blue colouration and its erect inflorescence; it was collected in 1970 as *Kimmach & Boutin* 3019 (ARIZ, DES, HNT) in the Sierra de Manantlán (Jalisco). *A. attenuata* ‘Emery Stripy’ (Walker 2000) and

‘Myron’s Magic’ (Smith 2004) are variegated cultivars (Alsemgeest 2006), and ‘Blue Flame’ is a hybrid with *A. shawii* (Trager 2005, Mays 2005: 44, Starr 2014: 219). The latter and further cultivars are illustrated by Guillot Ortiz & Meer (2009b). ‘Blue Glow’ is a hybrid with *A. ocahui* (Starr 2012: 56–58, with ills.), and ‘Snow Glow’ (Starr 2014: 224, with ill.) is a variegated sport selected from it.

The taxon is reported as casually naturalized in Gran Canaria (Canary Islands) (Verloove 2013: 80) and in Portugal (Silva & al. 2015: 73), and introduced in Madeira and Libya (Euro+Med 2006+: accessed Jan. 2019).

**A. attenuata** ssp. **dentata** (Roezl) B. Ullrich (Haseltonia 12: 27, ills. (pp. 23–27), 2007). **Type** [neo]: Mexico, Guerrero (*Rzedowski & McVaugh* 289 [ENCB, MICH]). — **Lit**: Gentry (1982: 79–82, with ills.); McVaugh (1989); Cházaro Basáñez & al. (1998); Vázquez-García & al. (2007b: 47, t. V-W); González-Elizondo & al. (2009: 58–60, with ill.); all as *A. pedunculifera*. **Distr**: Mexico (Sinaloa, SW Durango, Nayarit, Jalisco, Michoacán, Guerrero, Oaxaca); mountain slopes in tropical deciduous or pine-oak forests, 300–2200 m; flowers November to February. **I**: Richter (2011: 10, 61, 111, as *A. pedunculifera*); Etter & Kristen (2012: 88); Pilbeam (2013: 166–167, as *A. pedunculifera*); Hochstätter (2015: VIII: 39).

≡ *Ghiesbreghtia dentata* Roezl (1861) (*incorrect name*, Art. 11.4); **incl.** *Agave pruinosa* Lemaire *ex Jacobi* (1865); **incl.** *Agave debaryana* Jacobi (1868); **incl.** *Agave kellockii* Jacobi (1868); **incl.** *Agave ghiesbreghtii* [?] *dentata* Hort. Belg. *ex Jacobi* (1868) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave attenuata* [?] *dentata* J. Verschaffelt (1876); **incl.** *Agave dentata* hort. *ex Baker* (1877) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave attenuata* var. *subdentata* Cels *ex Carrière* (1879); **incl.** *Agave attenuata* var. *serrulata* A. Terracciano (1885) ≡ *Agave cernua* var. *serrulata* (A. Terracciano) A. Berger (1915); **incl.** *Agave pedunculifera* Trelease (1920).

[1b] Differs from ssp. *attenuata*: Stems short; **L** mostly ovate-acuminate and 50–70 × 15–18 cm, or lanceolate and 80–90 × 11–15 cm,

pale green to glaucous-white, margins narrowly lined with brown or white, with closely set denticles 0.5–2 mm, otherwise smooth; **terminal Sp** acicular, weak,  $\pm 10$  mm; **Inf** erect or recurving (on cliffs), part-**Inf** with 2 or 4 flowers; **Ped** 20–30 mm; **Tep** lobes 12–22  $\times$  5–6 mm; **Fil** 30–35 mm; **Fr** 15–20 mm; **Se** 2.5  $\times$  2 mm.

Known since Trelease (1920) as *A. pedunculifera*. Gentry (1982) considered it closely related to *A. attenuata* based on leaf and flower characters, but distinguished by being nearly stemless throughout all observed populations. The subspecies exhibits considerable variability in leaf form and size and depth of the flower tube, but the different forms are linked by intermediates (Gentry 1982: 80). González-Elizondo & al. (2009) provide a new record from Durango. The recently described blue-leaved *A. manantlanicola* from Jalisco is closely related (see there). There has been some argument which name is the correct basionym for this taxon. Since *Ghiesbreghtia dentata* is merely incorrect, rather than invalid, its use as basionym is not precluded.

**A. aurea** Brandegee (Proc. Calif. Acad. Sci., ser. 2, 2: 207, 1889). **Type** [lecto]: Mexico, Baja California Sur (Brandegee s.n. [UC, CAS, MO]). — **Lit**: Trelease (1912b: 44, 49–51, tt. 32–37); Berger (1915: 168–170); Gentry (1978: 70–83, tt. 3–4); Gentry (1982: 309–322, with ills.); Webb & Starr (2015: 68–71, 97–98, with ills.). **Distr**: Mexico (C & S Baja California Sur).

Gentry (1978) and Gentry (1982) recognized 3 species (*A. aurea*, *A. capensis* and *A. promontorii*) within Sect. *Campaniflorae* (as Group), which, at the latitude of Todos Santos, become similar to each other, suggesting interfertility (Gentry 1982: 313). Based on detailed field studies, Webb & Starr (2015) recognized a single species only and reduced *A. promontorii* to subspecific and *A. capensis* to varietal status. Brandegee's protologue does not indicate a type, but according to Trelease (1912a: 50), the type is "Brandegee, Feb. 13, 1889". The designation of "Brandegee s.n." at UC by Gentry (1972: 78) represents a lectotypification.

**A. aurea** ssp. **aurea** — **Lit**: Trelease (1912b: 49–50, tt. 32–34); Berger (1915: 168–169); Gentry (1978: 71, 74, 77–81, t. 4); Gentry (1982: 311–315, with ills.); Turner & al. (1995: 43–44); all as *A. aurea*; Webb & Starr (2015: 68–70, 97–98, with ills.). **Distr**: Mexico (Baja California Sur: Sierra de la Giganta and Cape district); lava fields and granitic or volcanic slopes, mostly 300–1070 m; flowers September to April. **I**: Heller (2006: 20); Richter (2011: 74); Pilbeam (2013: 39); Hochstätter (2015: V: 4); all as *A. aurea*.

**Incl.** *Agave campaniflora* Trelease (1912).

[2e] Stems short; **Ros** rather open, 1–1.2  $\times$  1–2 m, solitary; **L** linear to long-lanceolate, widely arching, pliable, guttered, rounded below, thickly fleshy towards the base, 60–110  $\times$  7–12 cm, green to yellow-green, somewhat glaucous, margins straight to wavy; **marginal teeth** moderate, mostly 4–7 mm from low angular bases, regularly spaced, 10–20 mm apart, dark to light brown; **terminal Sp** subulate, 25–35 mm, dark brown or greyish-red, shortly decurrent or decurrent as dark horny margin through the uppermost 8–10 tooth bases; **Inf** 2.5–5 m, paniculate, peduncle with remote lanceolate **Bra**, reddish, fertile part broad, part-**Inf** broad, congested, 15–25, in the upper  $\frac{1}{2}$  of the inflorescence, red to purplish in bud and fruit; **Fil** campanulate, 43–70 mm; **Tep** red to purplish in bud, opening yellow to orange-yellow, tube evenly grooved from the lobe sinuses, 8–14  $\times$  14–18 mm, lobes lanceolate, acute, incurved, 16–19 mm, outer larger, with tufts of white papillae below the distinctly hooded tip, inner ones with a distinct long keel and yellow, the thin margin involute; **Fil** stout, 35–45 mm, those in front of the outer tepals inserted 5–10 mm above the tube base, slightly higher than those in front of the inner tepals; **Anth** 19–23 mm; **Ov** slender, angular-cylindrical, 25–35 mm, reddish, neck constricted, furrowed, 6–10 mm; **Sty** somewhat longer than the tepals; **Sti** capitate; **Fr** oblong, 35–45  $\times$  15–17 mm, reddish, drying light brown, rounded-apiculate, not stipitate; **Se** irregularly crescent-shaped, 7–8  $\times$  5–5.5 mm, dull.

The most widespread and common taxon in Sect. *Campaniflorae* (as Group), easily

recognized by its long, narrow, green leaves arching out to form an open, spreading rosette, its broad, rather diffuse, reddish inflorescences, and its bright yellow flowers from reddish buds and ovaries (Gentry 1982: 313, Webb & Starr 2015). N of Todos Santos, it intergrades with both ssp. *promontorii* and var. *capensis* in the colour and shape of the leaves (Gentry 1982: 313 (as *A. promontorii* and *A. capensis*), Webb & Starr 2015: 69), and lower elevation populations of ssp. *aurea* in the Sierra de la Giganta are very similar to ssp. *promontorii* (Webb & Starr 2015: 69).

**A. aurea** ssp. **promontorii** (Trelease) R. H. Webb & G. D. Starr (Haseltonia 20: 70, ill. (p. 71), 2015). **Type:** Mexico, Baja California (*Nelson & Goldman* 7437 [US]). — **Lit:** Trellease (1912b: 50–51, tt. 35–37); Berger (1915: 169–170); Gentry (1978: 71, 74, 80–83, t. 3); Gentry (1982: 319–321, with ill.); all as *A. promontorii*; Webb & Starr (2015: 70–71, 98, with ills.). **Distr:** Mexico (S Baja California Sur: Sierra La Laguna, Cape District); slopes and summits of granitic mountains, 720–1800 m; flowers January and April to May. **I:** Goldman (1916: t. 111B); Richter (2011: 74); Pilbeam (2013: 178); Hochstätter (2015: V: 6); all as *A. promontorii*.

≡ *Agave promontorii* Trellease (1912a).

[2e] Differs from ssp. *aurea*: **Ros** larger, 1–2 × 2–2.5 m; **L** larger, 100–150 × 11–17 cm, margins straight; **marginal teeth** curved, 5–10 mm apart, reddish-brown; **terminal Sp** longer, 30–50 mm, dark brown; **Inf** larger, 5–9 m, peduncle with deltoid **Bra**, fertile part with 25–30 part-**Inf**; **Fl** 60–75 mm, larger in nearly all parts.

This subspecies is larger and occurs at higher elevations than ssp. *aurea*. Since the 2 taxa intergrade, subspecies status (Webb & Starr 2015) is more appropriate than species status (Gentry 1978, Gentry 1982).

**A. aurea** var. **capensis** (Gentry) R. H. Webb & G. D. Starr (Haseltonia 20: 70, ill., 2015). **Type:** Mexico, Baja California Sur (*Gentry & Fox* 11247 [US, ARIZ, MEXU]). — **Lit:** Gentry (1978: 72–78); Gentry (1982: 310, 316–318); both with

ills. and as *A. capensis*; Webb & Starr (2015: 70–71, 98, with ills.). **Distr:** Mexico (Baja California Sur: Cape District); arid slopes, ± sea-level to >300 m. **I:** Heller (2006: 71); Richter (2011: 74); Pilbeam (2013: 49); Hochstätter (2015: V: 5); all as *A. capensis*.

≡ *Agave capensis* Gentry (1978).

[2e] Differs from ssp. *aurea*: **Ros** smaller, 0.6–0.8 × 0.8–1.2 m, caespitose by axillary budding, eventually in large clusters; **L** smaller, mostly 35–60 × 4–7 cm, grey-green with a light glaucous covering, margins wavy; **marginal teeth** reddish-brown to greyish, on short mamillate prominences; **terminal Sp** short, 15–30 mm, dark brown; **Inf** mostly 2.5–3.5 m, fertile part relatively narrow; **Fl** 50–65 mm; **Fil** with an apical gland at the point of anther attachment. — **Cytology:** 2n = 60 (Pinkava & Baker 1985: as *A. capensis*).

Differs from the other 2 taxa primarily in its prolifically offsetting growth leading to large clusters of rosettes (Webb & Starr 2015: 70). The varietal status is warranted because of its distribution, which overlaps with that of ssp. *aurea*.

**A. avellanidens** Trellease (Annual Rep. Missouri Bot. Gard. 22: 60, tt. 61–62, 1912). **Type:** Mexico, Baja California (*Brandeggee* 6 [UC]). — **Lit:** Berger (1915: 267); Gentry (1978: 61–64, with ills.); Gentry (1982: 361–363, with ills.); Heim (2014: 8–11, with ills.); Webb & Starr (2015: 71–73, 98, with ills.). **Distr:** Mexico (S Baja California: Sierra La Libertad); desert scrub, to 325 m; flowers April to May. **I:** Irish & Irish (2000: t. 6); Richter (2011: 104); Pilbeam (2013: 40); Hochstätter (2015: V: 24). — Fig. 8.

[2j] Stems to 0.5 m; **Ros** 0.6–1.2 × 1–1.5 m, solitary; **L** many, broadly linear-lanceolate to ovate, thickly fleshy, rigid, little or not narrowed at the base, shortly acuminate, smooth, 40–70 × 9–14 cm, yellow-green, green or blue-green, margins straight, frequently horny; **marginal teeth** straight or variously curved, variable in size and curvature, flattened, 5–15 mm, grey to brown, mostly 10–30 mm apart, rather regularly spaced, on small to large, broadened bases; **terminal Sp** conical, strong, broadly grooved above, 25–45 mm, brown to greyish, strongly decurrent as horny margin; **Inf** 4–6 m,



**Fig. 8** *Agave avellanidens* (cult.: USA; Arizona, Desert Botanical Garden Phoenix). (Copyright: J. Thiede)



paniculate, peduncle with small **Bra**, fertile part in the upper  $\frac{1}{2}$  of the inflorescence, conical, with 25–35 dense large globose part-**Inf**; **Fl** slender, 40–70 mm; **Tep** pale greenish-yellow, drying orange-yellow, tube flaring, ridged within and grooved on the outside from overlapping lobe sinuses, 4–6  $\times$  13–15 mm, lobes  $\pm$  equal, 16–24 mm; **Ov** fusiform, tapering to the base, 20–40 mm, pale yellow, neck sometimes constricted; **Sty** somewhat shorter than the filaments; **Sti** capitate; **Fr** broadly oblong, 35  $\times$  20 mm, not stipitate, scarcely beaked, dark brown; **Se** unknown. — **Cytology**:  $2n = 60$  (Bennett & Leitch 1995, Simpson & al. 2011).

According to Gentry (1982: 354, 394), *A. avellanidens*, *A. gigantensis* and *A. moranii* form a separate group within Sect. *Deserticolae* (as Group), differing from other members in non-surculose rosettes with broader and greener leaves. Webb & Starr (2015) formalized this group as Sect. *Conicae*, named after its characteristic conical inflorescences, and added the greyish-leaved *A. turneri* to it. Within Sect. *Conicae*, *A. avellanidens* is differentiated by its short green broadly linear-lanceolate leaves not or scarcely narrowed towards the base (Webb & Starr 2015). — *A. avellanidens* resembles *A. shawii* ssp. *goldmaniana* from Sect. *Umbelliflorae* (as Group) in habit, and they appear to hybridize near Rosarito where their ranges overlap (Gentry 1982, Webb & Starr 2015).

**A. azurea** R. H. Webb & G. D. Starr (Haseltonia 19: 90–92, ills., 2014). **Type**: Mexico, Baja California Sur (Webb & Starr 20130418-1 [HCIB]). — **Lit**: Webb & Starr (2015: 88–89, with ills.). **Distr**: Mexico (Baja California Sur: Picachos de Santa Clara); rocky colluvial hillslopes and alluvial fans, 295–360 m, in desert scrub; flowers in April, but appearing opportunistically.

[2k] Acaulescent, **Ros** 0.8–0.9  $\times$  1–1.5 m, solitary; **L** 13–32, obovate to oblanceolate, flat to slightly guttered, attenuate at the tip, slightly rough and waxy above, smooth to slightly rough below, 55–76  $\times$  14–22 cm, widest just above the middle, 10–17 cm broad at the narrowest point below the middle, glaucous blue-green, faintly to moderately banded, with light imprints from the central bud, margins straight to rarely repand; **marginal teeth** deflexed, 10–15 mm, orange-yellow, reddish-purple or brownish-red, aging to whitish-grey, 40–50 mm apart, sessile or on small prominences; **terminal Sp** 40–70 mm, decurrent to the first 1–2 pair(s) of teeth; **Inf** 2–4.5 m, paniculate, peduncle 0.7–3 m; primary **Bra** triangular, 14–17  $\times$  2–3 (at the base) cm, fertile part 1.3–1.5 m, **Bra** 7  $\times$  4 cm, without terminal **Sp**, with 6–9 part-**Inf** with 6–8 stalked ‘umbels’ with 8–14 flowers each; **Ped** 6–30 mm; **Fl** 79–85 mm; **Tep** yellow-orange, tube 9–22  $\times$  15–22 mm, lobes slightly unequal, outer 22–30  $\times$  9–13 mm, inner 21–29  $\times$  10–13 mm; **Fil** 43–65 mm, inserted on the rim of the tube or 14–15 mm above the base of the tube; **Anth** 16–28 mm; **Ov** 30–40 mm, neck 6–10 mm;

**Sty** 85–90 mm when fully exerted; **Fr** oblong, 35–60 × 16–19 mm, with transverse lineations on the locules, beaked for 1–5 mm; **Se** crescent-shaped to ovate, 5–7 × 4–5 mm, shiny black.

Plants from the Picachos de Santa Clara were included in, but recognized as different from, *A. vizcainoensis* by Gentry (1982: 407) and were also identified by him as *A. sebastiana* or *A. gigantensis* according to the protologue, but have now been named *A. azurea*. *A. azurea* differs from *A. vizcainoensis* in its mostly solitary habit, larger size of most characters, leaves with significantly different shape and margins, and smaller fruits. It also resembles *A. turneri* of Sect. *Conicae* in habit, but the latter has a different inflorescence. Webb & Starr (2015) placed *A. azurea* and *A. vizcainoensis* — both characterized by long tepal tubes — in a separate Sect. *Intermediae*, which is considered intermediate between Sect. *Deserticolae* and Sect. *Umbelliflorae* (see under *A. vizcainoensis*).

**A. bahamana** Trelease (Mem. Nation. Acad. Sci. 11: 40, tt. 84–86, 1913). **Type:** Bahamas (Britton & Millspaugh 2340 [MO, NY, F]). — **Lit:** Berger (1915: 203); Britton & Millspaugh (1920: 74–75); Gillis (1976); Correll & Correll (1982: 310). **Distr:** Bahamas (Andros, Berry Islands, Cat, Cave Cay, Eleuthera, Exuma, Grand Bahamas, San Salvador [Watling] Island); open rocky plains and ridges, open coppices and pinelands, and sandy beach dunes, in dry broad-leaf evergreen wood- or scrubland; flowers mostly January to May. **I:** Hochstätter (2015: VII: 79, 82).

**Incl.** *Agave sobolifera* Hitchcock (1893) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave rigida* Northrop (1902) (*nom. illeg.*, ICN Art. 53.1).

[2r] Acaulescent; **Ros** solitary; **L** rather narrowly lanceolate, fleshy, curved, concave, occasionally somewhat conduplicate, 200–300 × 15–20 cm, dull greyish to greyish-green, margins nearly straight; **marginal teeth** straight or the longer teeth appressed-recurved, triangular, scarcely lenticular at the base, 3–5 mm, usually 5–10 mm apart, reduced near base and tip of the leaf or rarely greatly reduced throughout or nearly lacking, sometimes on small green tubercles;

**terminal Sp** slightly recurved, stoutly conical, usually becoming involutely grooved below the middle, smooth, 10–15 × 4–5 mm, brownish becoming grey, dull, decurrent; **Inf** to ±10 m, paniculate, peduncle with deltoid non-overlapping **Bra**, fertile part ovoid, part-**Inf** on slightly ascending **Br**, ± in the upper 1/3 of the **Inf**; **Ped** ±10 mm; **Fl** 50–60 mm; **Tep** ±15 × 4 mm, golden-yellow, tube conical, ±7 mm, lobes 15 × 4 mm; **Fil** 30–35 mm, inserted almost in the tube throat; **Ov** oblong-fusiform, 30–35 mm; **Sti** ± as long as the filaments; **Fr** oblong, 40–50 × 20–25 mm, shortly stipitate and beaked; **Se** 8 × 6 mm.

The most widespread *Agave* species on the Bahamas. Its area covers all larger islands of the N Bahamas. — Britton & Millspaugh (1920) suggested that *A. acklinicola*, *A. cacozela*, *A. indagatorum* and *A. millspaughii* “may be but races of *A. bahamana*”. Gillis (1976) included these four species as well as *A. braceana* (i.e., all other members of Sect. *Bahamaneae*) in the synonymy of *A. bahamana*, but this concept was not followed by subsequent authors. The recent accounts by Álvarez de Zayas (1995), Acevedo-Rodríguez & Strong (2012), and Freid & al. (2014) recognize all six species as distinct, pending a detailed study of the group.

**A. ×bedinghausii** Rebut (Suppl. Cat. Cact., 3, 1893). **Type:** not typified. — **Lit:** Koch (1865: 112); Ladenburg (1893: 74). **Distr:** Cultivated only.

[1g × 3a] According to the protologue (not seen) reported as the artificial hybrid between *A. ghiesbreghtii* (of Subgen. *Littaea*) and *A. maculata* (of Subgen. *Manfreda*) (= ×*Mangave*). *A. ×bedinghausii* was first mentioned by Koch (1865: 112) as mere name in the catalogue of “van Sweet in Gent”, most probably an error for L. de Smet, Gent, Belgium. The plant was exhibited by the private nursery of M. Bedinghaus, Gent (Ladenburg 1893: 74). Trelease (1920: 123) listed an *A. bedinghausii* as a mere form in the synonymy of the strong-toothed *A. verschaaffeltii* (= *A. potatorum*), which thus must have been a different plant.

**A. ×beguinii** hort. ex A. Berger (Agaven, 61, 1915). **Type:** not typified. — **Lit:** Ullrich

(1993b: 27, 31–32, as *A. beguinii*). **Distr:** Cultivated only.

[1] This is a garden hybrid of unknown parentage that was probably raised in the “Jardin Botanique au Parc de la Tête d’Or” at Lyon (France) and named and distributed by P. Rébut at Chazey-d’Azerognes (France). It was given to La Mórtoia via M. le Chanoine Béguin (Brignoles, France) in 1899 and flowered there in 1905 (Berger 1912: 357, Berger 1915: 61). Apparently lost from cultivation.

**A. bicolor** (Solano & García-Mendoza) Thiede & Egli (Kakt. and. Sukk. 52(6): 166, 2001). **Type:** Mexico, Oaxaca (García-Mendoza & al. 2403 [MEXU, BRIT, FEZA, SMU]). — **Lit:** Solano Camacho & García-Mendoza (1998); García-Mendoza (2011a: 83–86); both as *Polianthes* and with ill. **Distr:** Mexico (NW Oaxaca); grasslands and in pine and pine-oak forests, 2300–2500 m, flowers July to August. **I:** Castro-Castro & al. (2015: 145); Hochstätter (2016: II: 6); Castro-Castro & al. (2016: 721); all as *Polianthes*.

≡ *Polianthes bicolor* Solano & García-Mendoza (1998).

[3b2] Herbaceous; corm cylindrical, 4–6 × 2–2.5 cm, bulb ovoid, (2–) 3–5 × (1–) 1.5–2.5 cm, covered with dry leaf bases; **R** contractile, thickened; basal **L** (3–) 4–6 (–12), lanceolate, semi-succulent, generally undulate, smooth to papillose, apex acute, (5–) 8–15 × (0.6–) 1–4 cm, shiny green, margins papillose, hyaline, usually repand; **Inf** erect, 24–40 (–54) cm, peduncle with lanceolate **Bra**, lower **Bra** 3–5 (–7.5) × 0.2–0.5 cm, upper **Bra** progressively smaller, fertile part with 3–5 (–9) flowering nodes; **Ped** 6–13 mm, reddish; **Fl** geminate, (20–) 23–29 mm, fragrant; **Tep** yellowish-green, tube funnel-shaped, abruptly widened at the base, basal part erect, abruptly curved outwards just above the ovary, horizontal or down-curved at anthesis, (1.6–) 2.4–3 (–5.5) mm Ø at the mouth; **Tep** lobes orbicular to transversally elliptic, apiculate, subequal, outer 2–3 (–4) × (1.7–) 2–3 (–4) mm, inner with cucullate apex and pilose tips; **Fil** filiform, inserted somewhat above mid-tube 11–18 (–19) mm above the ovary, free part 4 (–15) mm,

included, green; **Anth** oblong, 4–5 (–9) × 1–1.5 (–2.5) mm, yellowish-green; **Ov** cylindrical, ±10 × 3–4 mm; **Sty** (10–) 19–26 (–32) mm; **Sti** 3-lobate; **Fr** globose, 11–13 × 10–11 mm, with persistent perianth remains; **Se** semicircular, one face straight, 4.5 × 2.4 mm, black.

According to the protologue characterized by its semisucculent undulate leaves with repand margins, flowers with the tube abruptly widened above its base, green tepal lobes, and included stamens. The species belongs to Ser. *Bravoia* of Sect. *Polianthes* and is morphologically closest to *A. coetocapnia* and *A. graminifolia*. *A. bicolor*, *A. alboaustralis* and *A. oaxacana* represent the S-most species of Sect. *Polianthes* and its sole representatives in Oaxaca (key in Solano & Ríos-Gómez (2014)).

**A. ×blissii** (Worsley) Thiede & Egli (Kakt. and. Sukk. 50(5): 111, 1999). — **Lit:** Worsley (1911: with ill.); Howard (1977); both as *Polianthes*. **Distr:** Cultivated only. **I:** Howard (2001: 9).

≡ *Polianthes ×blissii* Worsley (1911).

[3b1 × 3b2] This is the garden hybrid *A. coetocapnia* (as *Bravoia geminiflora*) × *A. amica* (as *Polianthes tuberosa*) first raised in 1911, but still extant in cultivation (Howard 2001).

**A. boldinghiana** Trelease (Mem. Nation. Acad. Sci. 11: 21, tt. 11–13, 1913). **Type** [syn]: Curaçao (*Boldingh* A2 [MO [6 sheets]]). — **Lit:** Berger (1915: 225–226); Hummelinck (1936: 239–240, 248–249, tt. VI, VIIIc, figs. 19–20); Hummelinck (1938: 20–21); Hummelinck (1993: 107–109, 219, with ill.). **Distr:** Leeward Antilles (Aruba, Bonaire, Curaçao), NE Colombia (?); coral rocks and coral debris, 2–50 m; flowers in May. **I:** Heller (2006: 68); Pilbeam (2013: 42–43); Hochstätter (2015: VIII: 87).

[2u] Stems almost none; **Ros** ±2 m Ø, suckering; **L** rather many to rather few, narrowly oblanceolate, subacuminate, rather slightly S-curved, apex slightly curved upwards, openly concave, 90–125 × ±15 cm, green, passing into somewhat glaucous, margins rather straight; **marginal teeth** often irregularly upcurved above and recurved below, heavily triangular or from crescent-shaped

bases, mostly 4–5 (–7) mm, scarlet becoming chestnut-brown, mostly 10–15 mm apart, on rather well to strongly developed hardening or partly green prominences; **terminal Sp** acicular, (very) slightly upcurved at the tip, somewhat flexuous, grooved and usually involute towards the base, smooth, polished towards the tip, 15–30 × 2–4 mm, red-brown, shortly or not decurrent, dorsally rather slightly intruding into the leaf tissue; **Inf** ±5 m, paniculate, peduncle with rather distant, narrowly triangular, appressed **Bra**, fertile part narrowly oblong, part-**Inf** few, distant, on ascending **Br** in the upper ½ or less of the **Inf**, freely bulbiferous; **Ped** 4–7 mm; **Fl** 45–46 mm; **Tep** golden-yellow, tube conical, 5–7 mm, lobes 15–20 × 4 mm; **Fil** 34–35 mm, inserted 0–1 mm below the tube throat; **Anth** 18–21 mm; **Ov** broadly fusiform or oblong, 20–25 mm; **Sty** length unknown; **Fr** 33–36 mm, beaked, stipitate; **Se** unknown.

Always distinguishable from all other species in its geographical range, but less well defined compared with certain forms of *A. cocui* and *A. vicina* (as *A. vivipara*) from other regions (Hummelinck 1938). The species appears not to belong to the indigenous flora (Hummelinck 1993) and was designated as “cultivated” already by Boldingh (1914: 17). Records from coastal NE Colombia (Bernal & al. 2015: 794) need verification against *A. cocui*. Trelease’s “type” at MO consists of 6 specimens that represent syntypes (Smith & Figueiredo 2014e: 229).

**A. bovicornuta** Gentry (Publ. Carnegie Inst. Washington 527: 92, 1942). **Type** [syn]: Mexico, Sonora (Gentry 3672 [CAS [2 sheets], ARIZ [2 sheets]]). — **Lit**: Gentry (1982: 328–332); González-Elizondo & al. (2009: 61–64); Starr (2012: 22, 59–63); all with ills. **Distr**: Mexico (S Sonora, SW Chihuahua, S Durango, N Sinaloa); rocky open slopes in oak woodlands and pine-oak forests, 930–1850 m; flowers December to May. **I**: Irish & Irish (2000: t. 7); Heller (2006: 69); Richter (2011: 73, 108); Pilbeam (2013: 44–45); Greulich (2014a: 56); Hochstätter (2015: IV: 19); Moore (2016: 270). – Figs. 9 and 10.

≡ *Agave maximiliana* var. *bovicornuta* (Gentry) González-Elizondo & al. (2009) (*nom. inval.*, ICN Art. 36.1b).

[2d] Acaulescent, **Ros** 0.6–1 × 1.5–2 m but often smaller, solitary; **L** lanceolate to spatulate, much narrowed towards the base, widest at or above the middle, smooth, 45–80 × 10–17 cm, yellowish-green to light or deep green, younger **L** frequently shining glaucous, with conspicuous imprints from the central bud, margins crenate; **marginal teeth** dimorphic, larger teeth mostly 8–12 mm, flexuous and slender above a broad base, mostly 20–40 mm apart, on prominent prominences, smaller teeth mostly 2–5 mm, 1 to several between the larger teeth, all chestnut-brown or dark brown to greyish-brown with age; **terminal Sp** strong, 30–50 mm; **Inf** 2.5–7 m, paniculate, peduncle short, with triangular-

**Fig. 9** *Agave bovicornuta* (Etter & Kristen 561: Mexico; Sonora, near San Bernardo, Río Mayo, 1700 m). (Copyright: J. Etter & M. Kristen)





**Fig. 10** *Agave bovicornuta* (Cultivated material without known wild origin). (Copyright: U. Eggli)



acuminate reflexed **Bra** 20–30 cm long, fertile part narrow, part-**Inf** short, compact, 20–30 in the upper  $\frac{1}{2}$  of the inflorescence; **Ped** 5–10 mm; **Fl** 55–65 mm; **Tep** greenish-yellow, tube 6–9  $\times$  12–14 mm, lobes linear-lanceolate, ascending-spreading, conduplicate, involute, sinuses broadly overlapping, 15–21  $\times$  4–7 mm, **ITep** broader and 2-costate within, yellow; **Fil** 30–45 mm, yellow, inserted (3–) 4–5 mm above the tube base; **Anth** 18–24 mm, yellow; **Ov** 26–29 mm, pale green, neck constricted, 4–6 mm; **Sty** hardly longer than the tepals; **Sti** capitate, 3-lobate; **Fr** oblong, 40–50  $\times$  15–20 mm, stipitate, valves thin; **Se** finely punctate, 15  $\times$  7 mm, curved side with a flange or wing, hilar notch shallow.

Gentry's protologue does not indicate a holotype so that all specimens represent syntypes. The designation of "Holotype DS" (Gentry 1982: 329) is a lectotypification which is ineffective under ICN Art. 8.1, since the 2 sheets at DS (now at CAS) are not cross-labelled (ICN Art. 8.3).

Distinguished within Sect. *Crenatae* by light to yellowish-green leaves with narrow bases, relatively small flowers, and the low insertion of the filaments in the middle of the tube. *A. bovicornuta* is common and widespread in the N Sierra Madre Occidental, but with usually local populations with a limited number of individuals. Its nearest relative appear to be the populations of *A. maximiliana* from Durango and Nayarit, but these have more glaucous, pale-coloured rosettes with more pronouncedly heteromorphic teeth and a mostly shorter terminal spine (Gentry 1982). González-Elizondo & al. (2009)

provide a new record from Durango and provisionally suggest to treat the species as variety of *A. maximiliana*. Etter & Kristen (2003a: 9) mention and depict a putative natural hybrid with *A. angustifolia* (as *A. vivipara*). The flowers, washed to remove the bitterness, are eaten cooked or in the form of tortillas, and the "hearts" are baked for preparing a strong alcoholic beverage "suguí" (Bye & al. 1975: 94). — 'Reggae Time' is a cultivar with bluish-green leaves, and 'Holstein' and 'Heifer's Cream' are variegated cultivars (Starr 2012).

**A. braceana** Trelease (Mem. Nation. Acad. Sci. 11: 40, t. 83, 1913). **Type:** Bahamas (*Brace* 1982 [MO, F, NY]). — **Lit:** Berger (1915: 203); Britton & Millspaugh (1920: 74); Correll & Correll (1982: 310–311, with ill.); Freid & al. (2014: 217). **Distr:** Bahamas (Abaco, Andros, Great Bahama); rocky or sandy soils in open pine-lands or coastal coppices; flowers mostly October to February. **I:** Hochstätter (2015: VII: 83).

**Incl.** *Agave mexicana* Dolley & al. (1889) (*nom. illeg.*, ICN Art. 53.1).

[2r] Acaulescent; **Ros** solitary; **L** broadly oblanceolate, fleshy, curved, nearly flat, 65–70  $\times$  19–20 cm,  $\pm$  3  $\times$  as long as broad, grey, margins between the teeth straight or concave when the teeth are raised on low green prominences; **marginal teeth** straight or the lower teeth gently recurved, triangular, 2–3 mm, scarcely lenticular at the base, usually 5–10 mm apart; **terminal Sp** conical, straight or gently curved, flat or roundly grooved to about the middle or becoming

involute, smooth, 10–15 × 3 mm, brownish becoming grey, dull, slightly decurrent; **Inf** 4–7 m, paniculate, not known to be bulbiferous; **Ped** ±10 mm; **Fl** 40–45 mm; **Tep** golden-yellow, tube conical, ±7 mm, lobes 15–17 × 3–4 mm; **Fil** 35 mm, inserted almost at the tube throat; **Ov** oblong-fusiform, 20 mm; **Sty** longer than the filaments; **Sti** capitate; **Fr** broadly oblong, 20–35 × 20 mm, beaked, shortly stipitate; **Se** 8 × 6 mm.

The flowers are visited at day by birds (hummingbirds, warblers (*Dendroica* spp.) and others). Wintering warblers show temporal territorial aggression against conspecifics and hummingbirds (Emlen 1973). Documented from the islands Abaco and Great Bahama in the protologue; Freid & al. (2014: 217) add Andros. — See also the note under *A. bahamana*.

**A. bracteosa** S. Watson *ex* Engelm (Gard. Chron., ser. nov. 18: 776, ills., 1882). **Type**: [lecto — icono]: l.c. figs. 138–139. — **Lit**: Gentry



**Fig. 11** *Agave bracteosa* (Etter & Kristen 696: Mexico; Coahuila, between Saltillo and Monterrey, 1370 m). (Copyright: J. Etter & M. Kristen)

(1982: 90–93); Ullrich (1990b); García-Mendoza (2003); Starr (2012: 64–68); all with ills. **Distr**: Mexico (SE Coahuila, W-C Nuevo León); scattered on limestone cliffs and rocky slopes of the N Sierra Madre Oriental, 900–1750 m; flowers May to July. **I**: Curtis’s Bot. Mag. 140: t. 8581, 1914; Irish & Irish (2000: t. 8); Heller (2006: 70, 154); Richter (2011: 62, 116); Pilbeam (2013: 46–47); Hochstätter (2015: VII: 35). — Fig. 11.

[l.c.] **Ros** open, small to medium-sized, forming caespitose mounds by above-ground axillary budding; **L** relatively few, ±30, long-lanceolate, arching and recurving, with weak fibres, widest near the base, convex in the basal 1/3, flat above, asperous, (40–) 50–70 × 3–5 cm, yellow-green, margins minutely serrulate, without teeth; **terminal Sp** absent, leaf tip drying early, friable, wind-scuffed, yellowish; **Inf** ascending to erect, 1.2–1.7 m, ‘spicate’, peduncle with erect triangular-acuminate **Bra**, fertile part densely flowered in the upper 1/2 of the inflorescence; **Fl** geminate, 22–26 mm; **Tep** white to pale yellow, tube virtually none, reduced to a short receptacle, lobes ovate, spreading, hyaline, distinct, 11 mm, the outer overlapping the inner, lanceolate, acute, the inner broadly ovate, obtuse, all floccose at the tips; **Fil** long-exserted, 50–60 mm, white, inserted on the receptacle, persisting, elongating after anthesis; **Anth** sagittate, 7–8 mm, yellow; **Ov** fusiform, 12–14 mm, virtually without neck; **Sty** eventually exceeding the stamens; **Fr** ovoid-oblong, obtuse, 18–20 × 8–10 mm, stipitate; **Se** deltoid to semicircular, 3–3.5 × 2–2.3 mm.

Very distinctive on account of its unarmed curling leaves and white flowers, so that is has never been confused with other species (Gentry 1982). Its distinctiveness prompted Ullrich (1990b) to place it within a reconsidered monotypic Group *Serrulatae* Baker. Gentry (1982) reports the inflorescences to emerge laterally from upper leaf axils so one and the same rosette may flower repeatedly, but this was dismissed as erroneous by Zona (2018). — The neotypification by Gentry (1982: 91) was superseded with a lectotype by Ullrich (1990b) as given above. ‘Monterrey Frost’ (Starr 2012: 68, with ill.), ‘Stingray’ (Starr 2014: 221, with ill.), and ‘Medio-Picta Alba’ (Greulich

2017c: 161, with ill.) are variegated cultivars. A plant cultivated outdoors on a protected site in Switzerland withstood temperatures of  $-12\text{ }^{\circ}\text{C}$  to  $-18\text{ }^{\circ}\text{C}$  (Bolliger 2014).

**A. brevipedata** Trelease (Repert. Spec. Nov. Regni Veg. 23: 362, 1927). **Type:** Hispaniola, Haiti (*Ekman* 1604 [US [2 sheets], B, G, GH, ILL, S]). — **Distr:** Hispaniola (Haiti: Massif de La Selle, top of Morne Cabaio), 2350 m; flowers in August.

[2p] Acaulescent; **Ros** solitary; **L** broadly lanceolate,  $\geq 100$  cm, green, rather dull; **marginal teeth** broadly triangular, variously curved, with lenticular bases, 5–10 mm but apical and basal teeth smaller, glossy chestnut-brown, 10–15 mm apart, teeth at mid-leaf clasping the green marginal prominences below them, intervening margin straight; **terminal Sp** smooth, curved, subterete, involutely narrowly grooved,  $20\text{--}25 \times 6$  mm, rather glossy chestnut-brown, decurrent for some 10 cm and connecting to the small upper teeth; **Inf** paniculate, part-**Inf** with densely clustered flowers at their tips, not known to be bulbiferous; **Ped**  $\pm 5$  mm; **Fl**  $\pm 35$  mm; **Tep** colour unknown, drying dark, tube 5 mm, lobes 10 mm; **Fil** 25 mm, inserted towards the tube throat; **Ov** thick, oblong, 20 mm; **Fr** and **Se** unknown.

Described on the base of the dried type material only. According to Álvarez de Zayas (1995) possibly conspecific with *A. antillarum* (see there). See also the note for *A. brevispina*.

**A. brevispina** Trelease (Repert. Spec. Nov. Regni Veg. 23: 363, 1927). **Type:** Hispaniola, Haiti (*Ekman* 5371 [US [2 sheets], B, GH, ILL, S]). — **Distr:** Hispaniola (Haiti: Croix-des-Bouquets, Plaine Cul de Sac); limestone, 150 m; flowers in December.

[2p] Acaulescent; **Ros** solitary; **L** broadly lanceolate,  $\geq 100 \times 10$  cm, dark green, rather dull; **marginal teeth** straight or some of the lower teeth recurved, rather narrowly triangular, with lenticular base, 1–3 mm, 5–15 mm apart, intervening margin almost straight; **terminal Sp** straight, somewhat flattened, involutely narrowly grooved, slightly granular,  $10 \times 3$  mm, rather dull hazel-

brown, tip darker, decurrent for  $2 \times$  its length; **Inf** 4 m, ‘paniculate’, part-**Inf** rather slender, recurving, shortly few-flowered at the tips and flowers densely clustered, not known to be bulbiferous; **Ped** slender, 10–15 mm; **Fl**  $\pm 40$  mm; **Tep** yellow, tube 5 mm, lobes  $12 \times 5$  mm; **Fil** 25 mm, inserted almost at the tube throat; **Ov** oblong-fusiform, 25 mm; **Fr** and **Se** unknown. — **Cytology:**  $2n = 60$  (Granick 1944: identity doubtful).

Described on the base of the dried type material only. The sample studied cytologically by Granick (1944) is of unknown origin. Trelease left this species and *A. brevipedata* unplaced, which was followed in the first edition of this handbook. According to Álvarez de Zayas (1995), both are possibly conspecific with *A. antillarum* (see there) and belong to Sect. *Antillanae*.

**A. brittoniana** Trelease (Mem. Nation. Acad. Sci. 11: 44–45, tt. 98–99, 1913). **Type:** Cuba, Santa Clara (*Britton & al.* 4776 [MO [3 sheets, cross-labelled later], NY [4 sheets], MEXU]). — **Lit:** Berger (1915: 273–274); Álvarez de Zayas (1996: 121–125, with ills.). **Distr:** C Cuba.

A polymorphic species, which occurs abundantly and prolifically at anthropogenic sites. It differs from *A. acicularis* esp. in its broadly lanceolate leaves with decurrent terminal spine, and from *A. grisea* in its shorter leaves. Álvarez de Zayas (1995: 41) and Álvarez de Zayas (1996), and the first edition of this handbook recognize 2 heterotypic subspecies, while Acevedo-Rodríguez & Strong (2012: 85) and Govaerts (2014+) place both in the synonymy of the species.

**A. brittoniana** ssp. **brachypus** (Trelease) A. Álvarez (Fontqueria 44: 121, 1996). **Type:** Cuba (*Britton & al.* 6183 [MO, NY [2 sheets]]). — **Lit:** Trelease (1913: 45, t. 99: 1, as var.); Álvarez de Zayas (1996: 121–125, with ills.). **Distr:** C Cuba (Alturas de Santa Clara); on skeletal soils and serpentine rocks in xeromorphic shrublands and derived secondary formations.

≡ *Agave brittoniana* var. *brachypus* Trelease (1913).

[2q] Differs from ssp. *brittoniana*: **L** tip canalicate, normally with small denticles at the

inner margin; **Inf** somewhat laxer; **Fl** smaller; **Fr** more cylindrical.

The shorter pedicels given as diagnostic in the protologue are not a constant feature (Álvarez de Zayas 1996). — The basionym could be regarded as a provisional and hence invalid (ICN Art. 36.1b) name, but Trelease's illustration and the adjacent caption leaves no doubt that he fully accepted the taxon. The lectotypification proposed by Álvarez de Zayas (1996: 121) is unnecessary and moreover erroneous, since an element not originally included by Trelease is selected.

**A. brittoniana** ssp. **brittoniana** — **Lit:** Trelease (1913: 44–45, tt. 98–99); Berger (1915: 273–274); Álvarez de Zayas (1996: 121–124, with ills.). **Distr:** C Cuba; on limestone, shale and slate, in evergreen forests and montane rain forests, primarily abundant in secondary formations and heavily disturbed sites, 100 to >1000 m; flowers January to March. **I:** Richter (2011: 92, 137); Hochstätter (2015: VII: 90); both as *A. brittoniana*.

[2q] Acaulescent, **Ros** solitary; **L** broadly lanceolate, abruptly acute towards the tip, (70–) 80–100 (–110) × (13–) 15–20 (–24) cm, green, sometimes somewhat greyish, slightly glossy, margins often concave between the teeth; **marginal teeth** variously curved, 4–6 (–8) × 3–6 (–7) mm at mid-leaf, (6–) 8–10 (–15) mm apart, slender-tipped from lenticular or voluminous bases, bases sometimes on retrorse green prominences in the lower 1/3 of the lamina; **terminal Sp** unguiculately curved, subconical or involutely much thickened in the basal parts, openly grooved to the middle or involute, smooth, somewhat polished, (10–) 15–20 (–25) × 4–6 mm, brown, dotted with white, ± decurrent; **Inf** (4–) 5–8 m, paniculate, peduncle very short or nearly none, part-**Inf** ascending, (11–) 15–30 cm, not bulbiferous; **Ped** slender, 5–10 mm; **Fl** 25–35 (–45) mm; **Tep** yellow, tube conical, sometimes very open, 3–6 × 5–8 (–10) mm, lobes 9–14 (–16) × 3–5 mm, dorsally greenish; **Fil** 18–25 mm, inserted nearly in the tube throat; **Anth** 9–15 mm; **Ov** fusiform, 15–20 (–25) mm; **Sty** longer than the filaments; **Sti** capitate; **Fr** oblong, sometimes nearly cylindrical, 23–40 (–45) × 11–15 (–17)

mm, dark chestnut-brown, tip slightly beaked, basally strongly stipitate; **Se** semicircular to subtriangular, 5–6 × 3–4 mm.

Occurs at least sometimes in regions with a predominance of ophiolitic soils (López Almira 2013).

**A. brittoniana** ssp. **sancti-spirituensis** A. Álvarez (Fontqueria 44: 125, ill. (p. 122), 1996). **Type:** Cuba, Sancti Spiritus (*Jiménez & al.* 69532 [HAJB]). — **Distr:** C Cuba (Montañas de Sancti Spiritus); on calcareous and shale rocks in montane rain forests and derived secondary formations; flowers in February.

[2q] Differs from ssp. *brittoniana*: **L** much shorter, more broadly oblong and less lanceolate; **Fl** 36–46 mm, with longer tepals and anthers.

**A. brunnea** S. Watson (Proc. Amer. Acad. Arts 26: 156, 1891). **Type:** Mexico, Coahuila (“Tamaulipas”) (*Pringle* 2218 [GH, US [photo]]). — **Lit:** Rose (1903c: 19); Berger (1915: 31–32); Verhoek-Williams (1975: 187–191); Piña Luján (1985: 28–29, 59–61, with ills.); García-Mendoza (2003: with ill.); Castillejos-Cruz (2009: [109]–[114], with ills.); all as *Manfreda* except Berger. **Distr:** Mexico (SE Chihuahua, N, NW, W & C Coahuila, N, NE & E Durango); dry hills or desert plains, volcanic or alluvial alkaline soils (sandy or gravelly clay), in desert scrub, grasslands, and low pine forests, 1000–1700 m; flowers late June to July. **I:** Hochstätter (2016: I: 15, as *Manfreda*).

≡ *Manfreda brunnea* (S. Watson) Rose (1903) ≡ *Polianthes brunnea* (S. Watson) Shinnars (1966).

[3a1] Herbaceous, robust; corm (1–) 2–5.5 × 0.9–2.5 cm, reproducing vegetatively by buds below the leaf bases; bulb cylindrical to ovoid, 3–7.5 × 1.5–4 (at the base) cm, completely covered with membranous dry leaf bases fraying into fine fibres at the tip, (4.5–) 5.5–9.5 cm; **R** fleshy and fibrous, contractile, with filiform ramifications; **L** evergreen, succulent, 4–8, linear-lanceolate to broadly lanceolate, erect to semi-erect, recurved to undulate, channelled above, tip acute, with a long point, smooth, 10–33 × 1.2–2.9 (–4) cm, light green to glaucous, intensely mottled with



purple to red above, both faces verrucose, margins with scattered, broad, hooked, cartilaginous teeth, usually large, deltoid or truncate-bipartite,  $\pm 2.5$  mm, 3–11 mm apart, with narrow pale hyaline band on the leaf margin between the teeth; **Inf** 0.7–1.3 m, ‘spicate’, green with purplish tinge, peduncle with lanceolate, narrowly attenuate **Bra** shorter than the internodes, fertile part (5–) 14–25 (–29) cm, dense, with 9–30 solitary flowers; **Fl**  $\pm 30$ –60 (–75) mm, sessile, ascending to appressed to the axis; **Tep** membranous to semisucculent, tube narrowly funnel-shaped, straight, gradually constricted above the ovary, 30–45  $\times$  5–6 mm, outer face yellowish-green, inner face brown, lobes oblong to narrowly oblong, spreading to revolute, tip obtuse, cucullate, with a tuft of short hairs, 8–18  $\times$  4–6 mm, greenish-red to brown with purple tinge; **St** much exerted; **Fl** 45–65 (–70) mm, exceeding the tube for 40–60 mm, inserted at  $\frac{3}{4}$  near the mouth of the tube, greenish-red to cherry-red; **Anth** 11–17 mm, reddish to yellowish-green; **Ov** cylindrical to long-ellipsoid, 10–20 (–23)  $\times$  4–6 mm; **Sty** (50–) 70–100 mm, exerted for 35–53 (–65) mm; **Sti** clavate, 3-lobate, deeply furrowed, yellowish-green with small purple dots; **Fr** ellipsoid to subcylindrical, 18–30 (–36)  $\times$  12–16 mm, without scar; **Se** deltoid, plano-concave, 4–5  $\times$  3–4 mm, shiny, somewhat rough.

Easily distinguished from the other species in Ser. *Brunneae* of Sect. *Polianthes* by its long narrow tepal tube with exerted stamens and styles and by the coarse teeth on the leaf margins (Verhoek-Williams 1975: 190). The corm is used as soap and shampoo, and the leaves, corm and bulb were formerly used as antidote against snakebites (Castillejos-Cruz 2009). “One of the most attractive manfredas” which “definitely requires a dry winter—early spring rest” (Hannon 2002: 251).

**A. bulbulifera** (Castillejos & E. Solano) Thiede (Haseltonia 17: 94, 2012). **Type:** Mexico, Guerrero (Castillejos & al. 1807 [MEXU, CHAPA, FEZA, IEB, MICH, NY, US]). — **Lit:** Castillejos-Cruz & Solano (2008); Castillejos-Cruz (2009: [115]–[120]); both with ill. as *Manfreda*. **Distr:** Mexico (Guerrero); slightly

inclined, somewhat rocky slopes rich in organic material, in pine-oak forests, 1200–1260 m; flowers June to July; only known from the type locality. **I:** Hochstätter (2016: I: 16, as *Manfreda*).

$\equiv$  *Manfreda bulbulifera* Castillejos & E. Solano (2008).

[3a3] Herbaceous; corm compressed, 0.5–0.7 cm, forming bulbils 0.5–1.5 cm long at its distal part, bulb ovoid, 3–5  $\times$  2.5–3 cm, covered with dry leaf bases 4.5–6 cm long, membranous below and fibrous above; **R** fleshy, fibrous, contractile; **L** drought-deciduous?, 2–4, prostrate or semi-erect, linear to lanceolate, attenuate, channelled, glabrous, tip acute, 12–25  $\times$  0.3–0.6 cm, green-yellowish to dark green, surface often slightly rough, margins hyaline, narrow, entire, partly microscopically papillose; **Inf** erect, 0.7–0.8 (–0.86) m, ‘spicate’, peduncle 0.63–0.74 m, with 5–7 **Bra** similar to the leaves, fertile part 7–8.5 (–12) cm, with 7–10 solitary, laxly arranged flowers; **Ped** 1–3 mm; **Fl** 25–32 mm; **Tep** green-yellowish to green-whitish, tube minute, 0.5–1  $\times$  2–3 mm, lobes linear, erect or revolute, 25–30 (–35)  $\times$  15–30 mm, apex thickened, cucullate, with a bundle of whitish hairs; **St** 50–60 mm, reddish; **Ov** obclavate, 12  $\times$  2.3 mm, green-yellowish; **Sty** 50–68 mm; **Sti** 3-lobate, green-yellowish; **Fr** subglobose, triquetrous, 10–12  $\times$  11–12 mm, apex without scar; **Se** 3–4  $\times$  3 mm, black, dull.

Belonging to Ser. *Guttatae* of Sect. *Manfreda* and most similar to *A. guttata*, *A. littoralis* and *A. pratensis* according to the protologue (as *Manfreda*). It differs from these in its compressed corms forming bulblets at their distal portion, its very short tepal tube, filiform tepal lobes, stamens and style by far exceeding the perianth in length, and an obclavate ovary.

**A. bulliana** (Baker) Thiede & Eggli (Kakt. and. Sukk. 50(5): 112, 1999). **Type:** Mexico (*Karwinsky* s.n. [not preserved]). — **Lit:** Rose (1903b: as *Prochnyanthes*); McVaugh (1989: 260–263, as *P. mexicana*); Castro-Castro & al. (2010: as *P. mexicana*); Thiede (2012a); all with ill. **Distr:** Mexico (Durango, Zacatecas, Nayarit, Aguascalientes, Jalisco, Guanajuato, Querétaro, Michoacán); dry rocky slopes or roadcuts, in

**Fig. 12** *Agave bulliana*  
(Etter & Kristen 1353:  
Mexico; Aguascalientes, ±  
20 km SE of Aguascalientes,  
2270 m). (Copyright: J. Etter  
& M. Kristen)



**Fig. 13** *Agave bulliana*  
(Etter & Kristen 2735:  
Mexico; Jalisco, ± 20 km  
SE of Concepción Buenos  
Aires, 1860 m). (Copyright:  
J. Etter & M. Kristen)



pine-oak grasslands, or in shaded moist ravines, 1150–3100 m; flowers late June to early September. **I:** Curtis's Bot. Mag. 121: t. 7427, 1895, as *Prochnyanthes*; Howard (2001: 13, as *P. mexicana*); Hannon (2002: as *P. mexicana*); Etter & Kristen (2012: 85); Hochstätter (2016: II: 31–32, as *P. mexicana*); Castro-Castro (2017: 139, as *P. mexicana*). – Figs. 12 and 13.

≡ *Bravoa bulliana* Baker (1884) ≡ *Prochnyanthes bulliana* (Baker) Baker (1895); **incl.** *Polianthes mexicana* Zuccarini (1837) ≡ *Prochnyanthes mexicana* (Zuccarini) Rose (1903); **incl.** *Prochnyanthes viridescens* S. Watson (1887).

[3b2] Herbaceous, large (for Subgen. *Manfreda*), usually single; corm cylindrical, 1–3 × 1.5–2.5 cm, bulb oblong, covered with fibrous

dried leaf bases 7–10 (–12.5) cm long; **R** fusiform, semifleshy with a wiry core, contractile; **L** few, deciduous, (1–) 2–3 (–7), the larger in a basal **Ros**, upwards diminishing up to the small **Bra**, chartaceous, thin, fibrous, erect or occasionally curved backwards from about the middle, often twisted, with a distinct midrib, shallowly channelled over the midrib, lamina flat, broadly undulate, or revolute, linear-lanceolate to oblanceolate, narrowed towards the base, (8–) 20–47 (–65) × (0.7–) 1.3–5.2 (–8) cm, light or dark green, dull, often speckled with magenta towards the base, spotted or not, veins slightly prominent on both surfaces, papillate, margins very narrow, hyaline, papillate to erose-papillate or papillate-denticulate, tip a soft **Sp**; **Inf** (0.6–) 0.9–2 (–2.8)

m and more, 'spicate', fertile part elongate, (9–) 17.5–47 (–83.5) cm, with (2–) 4–22 (–25) flowering nodes with geminate flowers; **Ped** (0.2–) 25–40 (–90) mm; **Fl** functionally pendent by an abrupt curve in the tepal tube; **Tep** white tinged with grey-green or dull green and red, white or creamy within, tube curved near the middle or at  $\frac{1}{3}$  from the ovary, narrow below, 5–17.5  $\times$  3–8 mm, abruptly widened above the bend, upper part (11–) 15–27  $\times$  5–20 mm, lobes flaring, broadly deltoid, (3–) 4–9 (–15)  $\times$  3–12 mm, tips pubescent; **Fil** 8–20 mm, inserted near the base of the bend of the tube; **Anth** linear, 3–15 mm; **Ov** ellipsoid, 4–8 (–12) mm; **Sty** filiform, 12–32 mm, finally equalling the tube or longer, white; **Sti** 0.7–4 mm, 3-lobate; **Fr** globose to oblong, 8–25  $\times$  10–17 mm; **Se** deltoid to semi-circular, 3.5–6  $\times$  2.5–3, black.

For some time recognized as monotypic genus *Prochnyanthes*, separated from *Polianthes* on account of the downward-curved perianth tube widening above the bend. The detailed morphometric studies of Castro-Castro & al. (2010) confirmed that *Prochnyanthes* consists of a single species only with a considerable variability in floral and other features. When treating *Prochnyanthes mexicana* as *Agave*, a change of name was necessary to avoid homonymy with the earlier *A. mexicana* Lamarck 1783. Therefore, the second-oldest epithet (*Prochnyanthes bulliana*) had to be chosen (Thiede & Egli 1999).

In the first edition of this handbook, the former genera *Prochnyanthes* and *Polianthes* were placed as distinct informal groups within Subgen. *Manfreda*, but the recently described *Agave (Polianthes) oaxacana* is morphologically intermediate, and *Prochnyanthes* was also included in *Polianthes* by García-Mendoza & Solano (2007: 115–116).

The history, introduction, horticulture, biology and taxonomy of *A. bulliana* was summarized by Thiede (2012a). Guillot Ortiz & Meer (2006b) erroneously stated that they introduced the species for the first time into European horticulture, but it was in fact cultivated much earlier at Munich in 1837 and at Kew in 1884 (Thiede 2012b). The ethnobotany and uses of the species are dealt with by Verhoek-Williams (1978b).

**A.  $\times$  bundrantii** (T. M. Howard) Thiede & Egli (Kakt. and. Sukk. 50(5): 111, 1999). **Type:** not typified. — **Lit:** Howard (1978: with ill.). **Distr:** Cultivated only. **I:** Hochstätter (2016: II: 27).

$\equiv$  *Polianthes  $\times$  bundrantii* T. M. Howard (1978).

[3b1  $\times$  3b2] This is the garden hybrid *A. amica* (as *Polianthes tuberosa*)  $\times$  *A. howardii* (as *Polianthes howardii*), still extant in cultivation. Solano Camacho (2002: 55, as *Polianthes*) erroneously lists the hybrid (as "*P. brundrantii*") in the synonymy of *P. howardii*. 'Chirp', 'Opal Eyes' and 'Mexican Firecracker' are commercially offered cultivars (Guillot Ortiz & al. 2006, Hochstätter 2016: II: 27, both with ill.).

**A. cacozela** Trelease (Mem. Nation. Acad. Sci. 11: 41, tt. 89–91, 1913). **Type:** Bahamas, New Providence (*Cunningham* s.n. [not located]). — **Lit:** Berger (1915: 204); Britton & Millspaugh (1920: 75); Correll & Correll (1982: 312). **Distr:** Bahamas (New Providence); rocky margins of salt marshes; flowers mostly January to March. **I:** Hochstätter (2015: VII: 83).

[2r] Acaulescent; **Ros** solitary; **L** lanceolate, fleshy, curved, deeply guttered, typically roughish, 150–200  $\times$  20 cm, yellowish-green, somewhat overcast with grey; **marginal teeth** nearly straight or the larger teeth appressed-recurved, narrowly triangular, rarely lenticular at the base, 2–5 mm (middle of the lamina), usually 10–15 mm apart, intervening margin straight or somewhat concave; **terminal Sp** triquetrously conical, straight or the tip slightly curved, openly grooved below the middle, smooth, 15–20  $\times$  3–5 mm, brownish becoming grey, dull, decurrent; **Inf** 6–7 m, paniculate, peduncle with broadly triangular non-imbricate **Bra**, fertile part dense, ovoid, part-**Inf** on horizontal or slightly ascending **Br**, in the upper  $\frac{1}{3}$  of the inflorescence, reportedly sometimes bulbiferous; **Ped**  $\pm$  10 mm; **Fl** 50–60 mm; **Tep** golden-yellow, tube rather open,  $\pm$  7 mm, lobes  $\pm$  20  $\times$  4–5 mm; **Fil** 40–45 mm, inserted nearly in the tube throat; **Ov** oblong-fusiform, 35–40 mm; **Sty** longer than the filaments; **Fr** narrowly oblong, 35–45  $\times$  15 mm, beaked, shortly conical-stipitate; **Se** 6–7  $\times$  4 mm.



According to the protologue, the leaves of seedlings of the type collection were decidedly papillate-roughened on both faces. See also the note under *A. bahamana*.

**A. cajalbanensis** A. Álvarez (Revista Jard. Bot. Nac. Univ. Habana 1(2–3): 33–39, ill., 1981). **Type:** Cuba, Pinar del Río (*Bisse & Álvarez* 32466 [HAJB [4 sheets]]). — **Lit:** Álvarez de Zayas (1985: 9, 13); Urquiola Cruz & al. (2010: 35, with ill.); González-Oliva & al. (2014: 11). **Distr:** W Cuba (Pinar del Río: Sierra de Cajálbana); denuded slopes of ultrabasic rocks, in pine forests and xeromorphic thorn scrubs; 100–400 m. **I:** Pilbeam (2013: 48); Hochstätter (2015: VII: 68).

[2p] Stems short; **Ros** solitary, semiglobose, to 1.2 m Ø; **L** many, oblanceolate in the lower  $\frac{2}{3}$ , straight, fleshy, coriaceous, only slightly concave, 50–100 × 8–10 cm, grey-green, somewhat dull, margins with asymmetrical slightly recurved prominences, these 3 × 4–5 mm, intervening margin nearly straight; **marginal teeth** basally slightly recurving, 2–4 mm, dark chestnut-brown to nearly black, 10–20 mm apart; **terminal Sp** conical, straight, basally flattened, 10–15 mm, dark chestnut-brown, not lustrous, not decurrent; **Inf** 3–6 m, paniculate, part-**Inf** 3-parted, broad, slightly incurved, 30–40 cm; **Ped** 18–25 (–35) mm; **Fl** 40–45 mm; **Tep** orange or yellow, tube open, 5–6 mm, lobes with broad margins, 12–15 mm, inner membranous, outer dorsally sulcate; **Fil** 15–20 mm, filiform, inserted near the base of the tube; **Anth** 10–12 mm; **Ov** fusiform, trigonous, basally constricted, 15–20 × 5–7 mm; **Fr** oblong, apically acute or apiculate, 20–25 × 15 mm; **Se** unknown.

Easily identifiable by its somewhat lobed leaf margins, the recurved marginal teeth, its orange (or yellow) flowers and small fruits. It is closest to *A. grisea*, but the leaves and inflorescences are only  $\frac{1}{2}$  as large according to the protologue. It differs from *A. legrelliana* (another species with broad panicles and orange flowers from W Cuba) by its greyish leaves < 1 m long (Álvarez de Zayas 1985: 9). Known only from the Sierra de Cajálbana where it occurs on ophiolitic soils (López Almira 2013), and categorized as “Vulnerable” by

Berazaín & al. (2005). Pollinated by the bat *Mono-phyllus redmani* (González-Oliva & al. 2014: 11).

**A. calodonta** A. Berger (Hort. Mortol. 364, 1912). **Type** [neo]: Ex cult. La Mortola (*Berger* s.n. [US 1023798]). — **Lit:** Berger (1898: 603, with ill., as *A. scolymus*); Berger (1915: 195–196, with ill.); Gentry (1982: 332–335, ill.). **Distr:** Only known from cultivation.

**Incl.** *Agave scolymus* A. Berger (1898) (*nom. illeg.*, ICN Art. 53.1).

[2d] Acaulescent; **Ros** semiglobose, 1.5–1.6 m Ø, solitary, with thick conical central bud; **L** many, spatulate, ± erect, older **L** many, spreading, the oldest prostrate, fleshy, narrowed towards the base (7.5–8 cm), upwards markedly thin, shortly acuminate, basally convex on both faces, upper face shallowly guttered, somewhat keeled on the back under the apex,  $\geq 80 \times 20$ –21 (upper  $\frac{1}{3}$ ) cm, light green, with light grey bloom, both faces with imprints of the central bud, margins sinuous in the middle of the lamina; **marginal teeth** irregular, 10–13 mm, 25–35 mm apart, with broad horny bases and deltoid antrorsely or retrorsely hooked tips, on broad fleshy prominences, intervening margins with much smaller intermittent teeth, teeth in the lower  $\frac{1}{2}$  of the leaf much smaller, straight or reflexed, all teeth light brown; **terminal Sp** broadly deeply grooved above, keeled on the back and with a deltoid protrusion, 30–40 mm, decurrent to the upper 3–4 teeth; **Inf** tall, paniculate, peduncle strong, at the base with numerous, deltoid, reflexed **Bra**, the lowest leaf-like but with pale broad horny margins with small teeth and a strong terminal spine, fertile part long pyramidal; **Ped** to 10 mm; **Fl** 85 mm excl. filaments (dried); **Tep** yellow, tube broadly funnel-shaped, ± 10 mm, lobes linear, acute, 35–40 mm, yellow-green, green at the tip, the inner with a broad keel; **Fil** 60 mm, inserted above mid-tube; **Anth** 28–32 mm; **Ov** narrow, 35–40 mm, both ends strongly constricted; **Sti** thick, blunt, 3-lobed; **Fr** and **Se** unknown.

Berger (1898) showed a photograph of the rosette of the only plant known up to now, first misidentified as *A. scolymus* Karwinsky. This plant flowered in La Mortola in 1897 and died without producing seeds or offsets. It was later

described as *A. calodonta* by Berger (1912) which is considered closest to *A. crenata* (Berger 1915). The neotype designated by Gentry (1982: 335) (as “type”) consists of bracts and flowers and was prepared by Berger (s.n., erroneously given as “Berger 603” in the database of US, referring to the page number of the prologue of *A. scolymus* that was added to the sheet) from the original plant; a second specimen (Berger s.n., US 1023799) consists of flowers only. The identity of the plant illustrated under this name by Hochstätter (2015: IV: 20) is doubtful.

**A. cantala** Roxburgh ex Salm-Dyck (Index Pl. Succ. Hort. Dyck, 1, 1822). **Type:** not typified. — **Lit:** Gentry (1982: 568–571, with ills.). **Distr:** Known from cultivation only.

≡ *Furcraea cantala* (Roxburgh) Voigt (1845); **incl.** *Agave cantula* Roxburgh (1832) (*nom. inval.*, ICN Art. 61.1).

**A. cantala** var. **acuispina** (Trelease) Gentry (Agaves Cont. North Amer., 569, ill. (p. 555), 1982). **Type:** El Salvador, San Miguel Dept. (Calderón 2084 [US [2 syntype sheets]]). — **Lit:** Lott & García-Mendoza (1994: & online version). **Distr:** Known from cultivation only (S Mexico, Honduras, El Salvador).

≡ *Agave acuispina* Trellease (1925) ≡ *Agave cantala* ssp. *acuispina* (Trellease) Hochstätter (2015).

[2g] Differs from var. *cantala*: **L** sturdier, shorter, mature leaves 120–170 × 6–9 cm, margins straight to repand; terminal **Sp** 3–5 mm broad at the base, longer, >15 mm; **Inf** with 20–35 part-**Inf**; **Fl** shorter, 45–63 mm; **Ov** shorter, 25–30 mm, neck short; **Tep** green, lobes subequal, 15–21 mm, light greenish-yellow.

Gentry (1982: 569) identified a cultivar from El Salvador as Trellease’s *A. acuispina* and placed it here.

**A. cantala** var. **cantala** — **Lit:** Berger (1915: 236–237); Trellease (1920: 119); Gentry (1982: 568–570, with ills.); McVaugh (1989: 146). **Distr:** Cultivated worldwide, esp. in SE Asia; not known from the wild. **I:** Todaro (1876–92: t. 15, as *A. candelabrum*); Morris (1889: as *A.*

*candelabrum*); Richter (2011: 77); Hochstätter (2015: VII: 34).

**Incl.** *Agave bulbifera* Salm-Dyck (1834); **incl.** *Agave laxa* Karwinsky ex Otto (1842) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave rumphii* Hasskarl (1843); **incl.** *Agave vivipara* Dalzell & A. Gibson (1861) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave candelabrum* Todaro (1878).

[2g] Stems 30–60 cm; **Ros** tall, slender, laxly leafy, 2–2.5 m Ø, surculose; **L** linear, long-acuminate, thin, frequently reflexing, guttered, roundly keeled below towards the base, rough below, smooth above, 150–200 × 7–9 cm, light or dark green, margins straight; **marginal teeth** antrorsely curved, larger teeth 3–4 mm, brown, mostly 20–30 mm apart, reduced or lacking towards the leaf tip; **terminal Sp** very small, 5–15 mm; **Inf** 6–8 m, paniculate, peduncle slender, with narrow chartaceous **Bra** soon becoming reflexed, part-**Inf** ascending to recurved, lax, ±20, on slender stalks, in the upper ½ of the inflorescence, freely bulbiferous; **Fl** slender, 70–85 mm; **Tep** greenish tinged purple or reddish, tube cylindrical-funnelform, grooved, 14–17 × 15 mm, lobes subequal, linear-spatulate, rapidly involute-conduplicate, 25–28 mm, apex rounded-cucullate, inner with narrow keel; **Fil** stout, abruptly outcurving from the tube wall, 50–55 mm, inserted 11–14 mm above the tube bottom; **Anth** excentric, slender, slightly curved, slatey purple; **Ov** fusiform, tapering below to a basal rim, roundly 6-ribbed, 32–42 mm, shortly constricted above but virtually neckless; **Sty** stout, shorter than the filaments; **Sti** capitate; **Fr** and **Se** unknown. — **Cytology:** 2n = 77–97 (3×) (Lv & al. 2009, Simpson & al. 2011).

Recognizable by the thin, long, narrow, weak leaves which are frequently reflexed above the middle, and by small teeth and large purplish-green flowers in broad, diffuse, slender-peduncled panicles which are only rarely produced (Gentry 1982). Roxburg published it from India whereto it was most certainly brought from North America by European traders. It has apparently been cultivated since long for fibre in SE Asia from the Philippines to India and is still hardly known in the Americas, where it remained unrecognized for long (Gentry 1982). Gentry (1982) collected

offsets from a plant at Villa Guerrero, Jalisco, very much looking like *A. cantala* and said to be spontaneous there. No plants from W-C Mexico were known to McVaugh (1989), and Hernández-Vera & al. (2007a) could not find *A. cantala* near Villa Guerrero.

The triploid chromosome number explains the sterility of the species. According to Trelease (1920) it is related to *A. tequilana* (which originated from *A. angustifolia*) and according to Valenzuela-Zapata & Nabhan (2003) it is merely a domesticated taxon obtained from *A. angustifolia*, for both of which triploid cultivars are known.

**A. ×cavanillesii** D. Guillot & P. Van der Meer (Flora Montiber. 28: 73–74, ill., 2004). **Type:** Spain, Valencia (Guillot s.n. [VAL]). — **Lit:** Guillot Ortiz & al. (2008: 81, with ill.). **Distr:** Cultivated only. **I:** Hochstätter (2015: VII: 101).

[2g × 2g] A spontaneous hybrid *A. decipiens* × *A. fourcroydes* found among its naturalized parental species in Spain.

**A. caymanensis** Proctor (Fl. Cayman Islands, ed. 2, 183, fig. 71, t. 7, 2012). **Type:** Cayman Islands (Proctor 52171 [IJ]). — **Lit:** Proctor (1984: 241–242); Hummelinck (1984: 208–212, 226–228); both with ills., as *A. sobolifera*. **Distr:** Cayman Islands (Grand Cayman, Little Cayman, Cayman Brac); dominant in dry rocky situations, semi-deciduous forests and deciduous shrublands with *Bursera* and *Pilosocereus*. **I:** Burton (2005: 168, 170, 174); Hochstätter (2015: VII: 69, 78).

[2p] Acaulescent when young, at maturity commonly with woody stems to 1 m clothed by dead leaves; **Ros** solitary; **L** ±30, elliptic-oblancoate to (narrowly) lanceolate, fleshy, massive, somewhat S-shaped, guttered, sometimes folded, narrowed at the base, acuminate at the apex, to 125–150 × 20–25 cm (above the middle), ± 5 × as long as broad, medium to dark green; **marginal teeth** curved or reflexed-triangular (rarely straight), 1–7 mm, glossy dark brown, 5–15 mm apart, usually 6–9 per 10 cm at mid-leaf, often from green prominences of the margin 1.5–3 mm high, very small below the terminal spine, intervening margin concave; **terminal Sp** slenderly conical to subulate, lower ½ usually clearly grooved between the

converging leaf margins, 17–23 × 2.5–4 (at the base) mm, decurrent only in outer leaves; **Inf** to 6 m or more, paniculate, peduncle ±3.5 m, with ±30 **Bra**, fertile part densely paniculate towards the apex, ±2 m, 2.5 × as long as broad, with up to ±15 part-**Inf**, longest 40 cm, main one 24 cm, freely bulbiferous; **Ped** 5–10 mm; **Fl** 41–51 mm; **Tep** bright yellow, tube 3–5.5 mm, lobes expanded at the base, narrowing to an elongate apex, 12–20 mm; **Fil** 30–41 mm, inserted 0.5–2.5 mm below the mouth of the tube; **Ov** narrowly fusiform, 25–40 × 7–8 mm; **Sty** 30–35 mm, almost as long as the filaments; **Sti** expanded; **Fr** ovoid, ±28 × 17 mm, stipitate for ±6 mm, very shortly apiculate; **Se** crescent-shaped, ±6–7 × 4–4.5 mm.

Plants now placed here were included in the Jamaican *A. sobolifera* by earlier authors such as Adams (1972), Proctor (1984) and Hummelinck (1984). *A. caymanensis* differs, according to the protologue, by forming woody stems at maturity, broader leaves in relation to their length, and by flowers with a much longer ovary (30–40 mm vs. 15–25 mm), shorter tepal lobes, and a longer, exerted style. Fruits and seeds were not described in the protologue, and data is here added from the published figure. Hummelinck (1984) carried out a detailed field study of *Agave* in the Cayman Islands. His detailed descriptions and many photographs supplement the short protologue and leave the purported differences less clear: The ovary is given as 25–32 mm (vs. 25–35 mm in Jamaican *A. sobolifera*), the lobes as 13–20 mm (vs. 20–25 mm), and the style as 30–35 mm (vs. 39–55 mm). Thus, the distinction of *A. caymanensis* is in need of re-study against more ample Jamaican material of *A. sobolifera*. Burton (2005) published 3 habitat photographs and used the name *A. caymanensis* 7 years before it was formally published. The Vitelline Warbler (*Setophaga vitellina*) feeds on nectar from the flowers (Bradley & Rey-Millet 2013: 236).

**A. cerulata** Trelease (Annual Rep. Missouri Bot. Gard. 22: 55, 1912). **Type:** Mexico, Baja California (Nelson & Goldman 7180 [US]). — **Lit:** Berger (1915: 262, 264); Gentry (1978: 35–48, with ill.); Gentry (1982: 363–375, with

ills.); Turner & al. (1995: 44–45, with ills.); Navarro-Quezada & al. (2003); Starr (2012: 69–73, with ills.); Webb & Starr (2015: 77–81, with ills.). **Distr:** Mexico (Baja California, Baja California Sur).

Molecular population studies including 5 samples of all 4 subspecies of *A. cerulata* showed a clade that also includes one sample of *A. deserti*, and which is nested within further clades with *A. deserti* and *A. subsimplex*, thus questioning the separation of these species (Navarro-Quezada & al. 2003). — The leaf shape of *A. cerulata* changes geographically with climate, and the leaf size decreases with increasing aridity (Burgess 1986).

**A. cerulata** ssp. **cerulata** — **Lit:** Trelease (1912b: 45, 55, tt. 45–47); Berger (1915: 264); Gentry (1978: 35–43, with ills.); Gentry (1982: 363–369, with ills.); Turner & al. (1995: 44–45); Starr (2012: 69–73, with ills.); Webb & Starr (2015: 77–78, with ill.). **Distr:** Mexico (C & S Baja California, N-most Baja California Sur); on hills and rocky mountain sides, in desert scrub with frequent fog and sea breezes, 25–640 m; flowers April to June. **I:** Irish & Irish (2000: t. 10); Heller (2006: 72); Richter (2011: 102); Pilbeam (2013: 51); Hochstätter (2015: V: 1, 14).

[2i] **Ros** 0.2–0.5 × 0.4–0.75 m, abundantly surculose or rarely solitary; **L** few, narrowly lanceolate to triangular-lanceolate, long-acuminate, mostly 25–50 × 4–7 cm and 5–12× as long as broad, yellow to light green, sometimes cross-zoned, rarely light glaucous-grey, margins nearly straight to shallowly repand; **marginal teeth** weakly attached, 1–4 mm, greyish-brown, bordered with a brown ring at the base, irregularly spaced, on low tubercles, sometimes lacking through much of the leaf length; **terminal Sp** acicular, 30–60 mm, light to dark grey, decurrent only to the uppermost teeth or less; **Inf** 2–3.5 m, paniculate, peduncle with small scarious triangular **Bra**, fertile part slender, narrow, part-**Inf** small, mostly 6–12, all white waxy-glaucous at bud stage; **Fl** mostly 45–60 mm; **Tep** in bud white waxy-glaucous, at anthesis pale yellow, tube broadly funnel-shaped or discoid, with thick **Nec** and bulges opposite the filament insertions, 3–5 × 11–14 mm, lobes

ascending to spreading, elliptic, equal, 16–22 mm, the inner wide with low broad keel and broadly overlapped at the base by the outer lobes; **Fl** usually incurved at anthesis, variable in length, 30–40 mm, inserted at the base of the lobes on the rim of the nectary; **Anth** centric to excentric, 15–20 mm; **Ov** fusiform, narrowly tapering towards the base, 22–32 mm; **Sty** shorter than the filaments; **Sti** capitate; **Fr** narrowly oblong, 30–50 × 12–13 mm, waxy light grey, bluntly apiculate, narrowly stipitate; **Se** crescent-shaped, hilar notch open or obscure, marginal wings pronounced on both sides around the curvature, 5 × 3 mm, sooty black.

Mostly characterized by slender, yellow, long-acuminate, lanceolate leaves with a brown ring at the weakly attached, moderate to small teeth, small narrow panicles with a conspicuous waxy bloom on peduncle, pedicels and fruits, and light-yellow, spreading tepal lobes. *A. cerulata* may be confused with the closely related *A. deserti*, but the latter is more robust, has grey-green (rather than yellow-green) leaves 4–7× longer than broad (vs. 5–12× longer than broad) and generally without the distinctive brown rings at the base of the teeth, and the capsules are generally broader and without waxy white bloom (Gentry 1982) (see *A. deserti* for further notes). Breslin (2015) provides a new record from Isla Cedros.

**A. cerulata** ssp. **dentiens** (Trelease) Gentry (Occas. Pap. Calif. Acad. Sci. 130: 43, 1978). **Type:** Mexico, Baja California (*Rose* 16819 [MO, NY, US]). — **Lit:** Trelease (1912b: 45, 51, tt. 38–40, as *A. dentiens*); Berger (1915: 264, as *A. dentiens*); Gentry (1978: 43–44, tt. 2–3); Gentry (1982: 369–371, with ills.); Turner & al. (1995: 45, with ill.); Wilder & al. (2008: 135–136, ill. p. 140); Guillot Ortiz & Meer (2008b: 24, ill. p. 30); Starr (2012: 70, 73); Webb & Starr (2015: 77–80, with ill.). **Distr:** Mexico (Baja California: Isla San Esteban); hillsides and arroyos; budding in April. **I:** Heller (2006: 73); Pilbeam (2013: 52); Hochstätter (2015: V: 15);

≡ *Agave dentiens* Trelease (1912).

[2i] Differs from ssp. *cerulata*: **Ros** 0.5–0.7 × 0.8–1.5 m; **L** long-acuminate, 40–55 (–70) cm,



**Fig. 14** *Agave cerulata* ssp. *subcerulata* (Etter & Kristen 383: Mexico; Baja California Sur, Vizcaino Desert, 170 m). (Copyright: J. Etter & M. Kristen)



light glaucous-grey, margins straight; **marginal teeth** friable, 1–2 mm, or nearly toothless; **terminal Sp** acicular, 30–50 mm, brown to grey; **Inf** broad, part-**Inf** 8–18 in the upper ½ of the inflorescence, on 30–40 cm long **Br**.

An isolated island population closely related to typical *A. cerulata*. With its broad inflorescences, it could bridge the gap between Sect. *Deserticolae* and Sect. *Conicae* (Webb & Starr 2015: 80). — Naturalized at one locality in Spain (Guillot Ortiz & Meer 2008b).

**A. cerulata** ssp. *subcerulata* Gentry (Occas. Pap. Calif. Acad. Sci. 130: 44–48, ills. (pp. 46–47, 49), 1978). **Type:** Mexico, Baja California Sur (Gentry 10330 [US, ARIZ, MEXU]). — **Lit:** Trelease (1912b: 45, 51, 55, tt. 30–40, 45–47); Gentry (1978: 44–48, with ills.); Gentry (1982: 371–374, with ills.); Turner & al. (1995: 45); Starr (2012: 70); Webb & Starr (2015: 81, with ills.). **Distr:** Mexico (S-most Baja California, N Baja California Sur); volcanic or gypsum slopes in desert scrub; flowers April to May. **I:** Heller (2006: 72); Richter (2011: 80, 141); Pilbeam (2013: 54); Hochstätter (2015: V: 17). — Fig. 14.

[2i] Differs from ssp. *cerulata*: **Ros** 0.15–0.3 × 0.3–0.5 m; **L** short-acuminate, 15–30 × 2.5–7 cm, mostly 3–6× as long as broad, mostly light grey to bluish-glaucous over green, margins conspicuously crenate with prominent tubercles; **marginal teeth** well developed, weakly attached, larger,

3–8 mm in the middle of the lamina; **terminal Sp** subulate, usually sinuous, 20–40 mm.

The S-most element in the *A. cerulata* complex, resembling *A. subsimplex* from the opposite Sonoran coast in habit (Gentry 1982). It might represent a genetic connection to the more southern *A. sobria* (Webb & Starr 2015).

**A. cerulata** var. *nelsonii* (Trelease) R. H. Webb & G. D. Starr (Haseltonia 20: 80, ill., 2015). **Type:** Mexico, Baja California (*Nelson & Goldman* 7111 [MO]). — **Lit:** Trelease (1912b: 45, 61, tt. 65–67, as *A. nelsonii*); Gentry (1978: 44–46, with ills.); Gentry (1982: 371–373, with ills.); Turner & al. (1995: 45, with ill.); Starr (2012: 70–71, ill.); the last 4 as ssp. *nelsonii*; Webb & Starr (2015: 78–81, with ill.). **Distr:** Mexico (C Baja California); igneous highlands in desert scrub or chapparal vegetation, 140–1120 m; flowers June to September. **I:** Goldman (1916: t. 111D, as *A. nelsonii*); Heller (2006: 73); Richter (2011: 102, 103); Pilbeam (2013: 53); Hochstätter (2015: V: 16). — Fig. 15.

≡ *Agave nelsonii* Trelease (1912) ≡ *Agave cerulata* ssp. *nelsonii* (Trelease) Gentry (1978); **incl.** *Agave shawii* E. C. Nelson (1911) (*nom. illeg.*, ICN Art. 53.1).

[2i] Differs from ssp. *cerulata*: **Ros** 0.5–0.75 m Ø; **L** short-acuminate, 20–35 × 6–8 cm, mostly 3–6× as long as broad, mostly light grey to bluish-glaucous over green, margins either repand and with small prominences, or nearly straight;

**Fig. 15** *Agave cerulata* var. *nelsonii* (cult.: USA; Arizona, Arizona-Sonora Desert Museum Tucson). (Copyright: J. Thiede)



**marginal teeth** firmly attached, larger, 3–9 mm, frequently on small tubercles; **terminal Sp** strongly subulate, 20–40 mm; **Inf** with 15–20 part-**Inf**.

The N-most element in the *A. cerulata* complex. Recognized at subspecies rank by Gentry, but reduced to varietal status by Webb & Starr (2015) since its distribution shows substantial geographical overlap with ssp. *cerulata* at its S end. Webb & Starr speculate that the taxon might represent a stabilized hybrid between *A. cerulata* and *A. shawii* ssp. *goldmaniana*. Hochstätter (2015: V: 16) depicts a natural hybrid with the latter.

**A. chamelensis** (E. J. Lott & Verhoek-Williams) Thiede & Eggli (Kakt. and. Sukk. 50 (5): 110, 1999). **Type:** Mexico, Jalisco (Lott & Wendt 1663 [MICH, BH, CAS, MEXU]). — **Lit:** Lott & Verhoek-Williams (1991); Castillejos-Cruz (2009: [121]–[126]); both with ills., both as *Manfreda*. **Distr:** Mexico (Jalisco, Oaxaca); uncommon along arroyos in tropical (semi-) deciduous and oak forests, 25–75 (–1170) m; flowers December to February. **I:** Hochstätter (2016: I: 17); Castro-Castro & al. (2017: 62); both as *Manfreda*.

≡ *Manfreda chamelensis* E. J. Lott & Verhoek-Williams (1991).

[3a2] Herbaceous; corm 3–15 × 2–3 cm, reproducing vegetatively by buds from the corm, bulb shortly cylindrical, 2–3.5 × 1.5–3 cm,

covered with membranous dry leaf bases 2.5–3.5 cm long and not separating into fibres; **R** fleshy and fibrous, with filiform ramifications, contractile; **L** drought-deciduous, 9–12, linear-lanceolate, spreading, brittle, herbaceous to somewhat fleshy, narrowly channelled, nearly conduplicate near the narrow base, tip acute, veins papillate on both faces, 37–77 (–91) × (1–) 1.6–4.8 (–6.5) cm, margins with a narrow yellowish cartilaginous band, minutely denticulate, teeth regular; **Inf** 0.75–1.2 (–2) m, ‘spicate’, fertile part 10–20 cm, with 10–25 (–35) sessile flowers; **Fl** nearly erect at anthesis; **Tep** green, tube funnel-shaped, 6–13 × 4–5 mm, lobes oblong, reflexed to tightly revolute, tip obtuse, with a tuft of short hairs, 8–11 × 4–5 mm; **Fil** erect, filiform, 21–32 mm, inserted in the middle of the tube, greenish-yellow with many purple dots; **Ov** oblong to ovoid, not constricted, not protruding into the tepal tube, 5–10 mm; **Sty** 25–35 mm, exserted; **Sti** clavate, trigonous; **Fr** globose, 12–16 × 10–15 mm; **Se** deltoid, plane-concave, 5–6 × 4–5 mm, shiny.

This species appears to be closest to *A. scabra* and *A. jaliscana*. It differs from both by shorter floral bracts, filaments curved near the tip at bud opening, and by the absence of coarse fibrous remains of old leaves, from the first-named by its shorter floral tube and globose beakless capsules, and from the last-named by its wider leaves and shorter styles and filaments (Lott & Verhoek-

Williams 1991, as *Manfreda*). The tropical lowland habitat is untypical and apparently not known for other species of Subgen. *Manfreda* except *A. littoralis*, *A. petskinil* and *A. paniculata*.

**A. chazaroi** A. Vázquez & O. Valencia (in Vázquez-García & al. (eds.), *Agaves Occid. Méx.*, 48–49, ills. (tt. CC-DD, pp. lxx-lxxiii), 2007). **Type**: Mexico, Jalisco (*Cházaro Basáñez & al.* 8161 [IBUG]). — **Distr**: Mexico (N Jalisco); basaltic cliffs in tropical deciduous forests, 900–1200 m; flowers January to February. **I**: Richter (2011: 56); Etter & Kristen (2012: 91–92); Pilbeam (2013: 55); Hochstätter (2015: IX: 26).

[1b] Acaulescent; **Ros** 1.45 × 0.8 m, solitary, not surculose; **L** up to 20, rigid, convex below, concave to flat above, to 80 × to 20 (mid-leaf) cm, yellowish-green, margins entire and horny dark brown all along; **marginal teeth** none; **terminal Sp** thin, large, canaliculate, 30–50 mm, dark brown; **Inf** erect, to 2.5 m, ‘spicate’, peduncle with filiform **Bra**, these 20–30 × 0.5 mm; **Ped** 10–15 mm; **Fl** 20–30 mm, geminate, densely arranged in the upper ½ of the inflorescence, funnel-shaped; **Tep** ivory-white, tube, lobes, **Fil** and **Anth** not described; **Ov** cylindrical, 10 mm incl. neck, cream-white; **Fr** oblong, 20 mm, glaucous when unripe, turning green (?) when ripe; **Se** unknown.

Based on the inadequately short protologue appearing close to *A. pelona* from Sonora, which differs esp. by the dark reddish flowers. It differs from other species of Sect. *Heteracanthae* (as Group *Marginatae*) in having few and broad leaves, and is better placed in Sect. *Inermes* (as Group *Amolae*) (Cuevas Guzmán & al. 2012). Here, it appears to be closest to *A. gilbertii* from which it differs by its stemless habit, and broader leaves without paler median stripe and with a much longer terminal spine. The tube length is not given in the protologue, but it appears to be very short (cf. t. CC-3), in contrast to 11–12 mm in *A. gilbertii* and 8–9 mm in *A. pelona*.

**A. chiapensis** Jacobi (Hamburg. Gart.- & Blumenzeit. 22: 213, 1866). **Type** [neo]:

Mexico, Chiapas (*Gentry* 12178 [US, ARIZ, MEXU, MICH]). — **Lit**: Jacobi (1871: 80–82); Berger (1915: 44–46, with ill.); Gentry (1982: 224–226, with ills.); Lott & García-Mendoza (1994: online version with ills.); García-Mendoza (2003: with ill.); García-Mendoza (2011a: 22–24). **Distr**: Mexico (N Oaxaca, Chiapas), Guatemala; limestone cliffs in the Montañas del Oriente, in humid oak, pine, pine-oak or pine-juniper forests or desert scrub-oak forest ecotones, 1400–3000 m; flowers March to April. **I**: Irish & Irish (2000: t. 11); Hils (2001); García-Mendoza (2002: 179); Heller (2006: 74); Lochner (2010); Richter (2011: 114); Pilbeam (2013: 56); Hochstätter (2015: IX: 4).

**Incl.** *Agave chiapensis* var. *major* hort. ex A. Berger (1915); **incl.** *Agave teopiscana* Matuda (1974).

[1f] Stems short or none; **Ros** openly spreading, robust, 0.5–0.8 × 1.3–1.5 m, mostly caespitose, rarely solitary; **L** 25–36, ovate, rarely lanceolate, soft, ascending, narrowed near the base, shortly acuminate, rounded below, flat to slightly hollowed above and upcurving, smooth, (20–) 30–50 (–65) × 7–17 cm, light shiny grey-green or grey-green to glaucous, lower face with imprints from the central bud, margins slightly repand to crenate, sometimes reddish or glaucous; **marginal teeth** deltoid, straight or upcurved, (1–) 2–4 × 2–4 mm, closely spaced and (1–) 4–5 (–10) mm apart, blackish or dark brown to greying, sometimes reddish; **terminal Sp** subulate, straight to sinuous, strong, rigid, ± openly grooved above, rounded to broadly keeled below, (15–) 25–40 × 3–4 mm, blackish or reddish, decurrent for (20–) 25–30 (–40) cm; **Inf** 2–3.5 m, ‘spicate’, peduncle long, green, closely bracteate with **Bra** to 13–22 × 2.5–4 cm, greenish-red or purple, fertile part dense, in the terminal ½–⅓; **Ped** 1–2 mm; **Fl** geminate, trigonous, fleshy, funnel-shaped, (40–) 60–70 (–85) mm, obscured in large tufts of broad-based bracts, the longer bracts equaling the flowers, reddish; **Tep** yellowish, whitish or green, sometimes tinged reddish or purple, tube funnel-shaped, thick-walled, 3-angled, grooved, 8–12 × 9–10 mm, lobes oblong or



linear-elongate, divaricate to recurved, fleshy, thick, unequal, 25–32 × 4–8 mm, the outer slightly longer, the inner with a prominent keel and involute, all cucullate and glandular at the tip, copiously papillate on and below the hood; **Fil** very broad at the base, (45–) 65–80 mm, reddish to dark purple-brown, inserted at the tube mouth; **Anth** (15–) 20–25 (–30) mm, yellow; **Ov** cylindrical to trigonous, truncate at base and apex, grooved to the base, (10–) 20–25 (–30) × 3–4 mm, neck 4 mm, sulcate; **Sty** very robust, 85–90 (–110) mm, dark purple-brown, thickened below the stigma; **Sti** weakly 3-lobed; **Fr** oblong to obovoid, rounded-truncate at the base, shortly apiculate at the apex, 30–40 × 10–15 mm, thin-walled; **Se** hemispherical, with regular complete marginal wing, 4–5 × 3–4 mm, black.

Gentry (1982: 226) designated the neotype cited above. The species is characterized by forming large caespitose clones and its ovate leaves with small teeth to 4 mm long, its dense inflorescences with large greenish-red or purple bracts, and its yellowish, whitish or green flowers with reddish to purple filaments (García-Mendoza 2011a). It appears to be closely related to *A. warelliana*, which differs in its brown (Gentry in error “red”) leaf margins with denticles 1–3 mm apart (Gentry 1982: 226). García-Mendoza (2011a) provides a new record from Oaxaca.

**A. chrysantha** Peebles (Proc. Biol. Soc. Wash. 48(4): 139, 1935). **Type:** USA, Arizona (Peebles & Harrison 5543 [US]). — **Lit:** Gentry (1982: 426–431, with ills.); Ullrich (1992i); Turner & al. (1995: 45–47); Hodgson (1999a: 4–5); Reveal & Hodgson (2002); Klopper & al. (2010: 56, 57, 59, with ills.); Parker (2017: 256, 258, with ills.). **Distr:** USA (C & S-C Arizona); very common on sandy to gravelly places on granitic or volcanic soils in desert scrub, grasslands, pinyon-juniper and oak woodlands, 700–2100 m; flowers June to July (to August). **I:** Irish & Irish (2000: t. 12); Heller (2006: 65); Richter (2011: 127); Pilbeam (2013: 57); Hochstätter (2015: IV: 6).

≡ *Agave palmeri* var. *chrysantha* (Peebles) Little ex L. D. Benson (1943) ≡ *Agave palmeri* ssp. *chrysantha* (Peebles) B. Ullrich (1992).

[2h] Acaulescent, **Ros** rather open to somewhat dense, 0.5–1.2 × 0.8–1 m, usually solitary, infrequently caespitose; **L** linear-lanceolate to lanceolate, spreading to ascending, straight, rigid, usually only a little narrowed below the middle, deeply guttered, 40–75 (–82) × (4–) 8–10 (–11) cm, pale to glaucous-green or yellowish-green to green, not cross-zoned, margins repand to wavy; larger **marginal teeth** straight or flexed, 4–10 mm, (8–) 10–30 (–40) mm apart, smaller towards the leaf base, intermittent teeth lacking or 1–3 (–5), mostly in the distal ⅓ of the leaves; **terminal Sp** slender, acicular, openly grooved above, 25–45 mm, reddish-brown or brown to grey, decurrent for 5–15 cm to the upper teeth; **Inf** 4–7 m, narrowly to broadly paniculate, open, peduncle with persistent triangular **Bra** 1–5 cm long, fertile **Inf** part narrowly to broadly paniculate, open, part-**Inf** slightly ascending, small, congested, (6–) 8–18 in the upper ¼–⅓ of the inflorescence, >10 cm, 12- to 21-flowered; **Fl** erect, 35–65 (–67) mm; **Tep** golden-yellow, rarely red-tipped, tube campanulate, 6–18 × (7–) 10–21 (–26) mm, lobes erect, persistent and often leathery during and after anthesis, strongly unequal, (6–) 9–15 (–18) mm; **St** long-exserted; **Fil** erect, (32–) 35–50 mm, pale yellow, inserted at 2 levels ± at mid-tube; **Anth** 7–20 mm, yellow; **Ov** slender, (14–) 22–30 (–33) mm, neck slightly constricted, (0.5–) 4–6 (–8) mm; **Sty** slightly longer than the tepals; **Sti** capitate; **Fr** narrowly oblong to obovoid, 35–50 mm, sessile or short-stipitate, apex shortly beaked; **Se** 6–7 mm. — **Cytology:** 2n = 60 (Pinkava & Baker 1985).

The closest relative is clearly the largely allopatric *A. palmeri* with often broader leaves with shorter and less distant teeth, and a very similar flower structure, but the latter differs consistently in its clear yellow flowers with tepal lobes conspicuously red to brownish at the tips, its more congested ‘umbels’, and its shorter panicles (Gentry 1982, Klopper & al. 2010). Benson (1943) and Ullrich (1992i) both suggest infraspecific ranks under *A. palmeri*, with which it shows introgression where they meet (Gentry 1982: 429, 446). *A. chrysantha* hybridizes with *A. delamateri*, *A. mckelveyana*, *A. murpheyi*, *A. palmeri*, *A. parryi* var. *couesii*, *A. schottii*, and *A. toumeyana* (Hodgson 1999a, Reveal & Hodgson 2002, Parker 2017).



**Fig. 16** *Agave chrysoglossa* (Etter & Kristen 548: Mexico; Sonora, Nacapule Canyon, 280 m). (Copyright: J. Etter & M. Kristen)

*A. chrysantha* appears to have developed minor shifts in several floral characters that enhance diurnal pollination; bats were not recorded as important pollinators (Slauson 2000).

**A. chrysoglossa** I. M. Johnston (Proc. Calif. Acad. Sci., ser. 4, 12: 998–999, 1924). **Type:** Mexico, Sonora (*Johnston* 3123 [CAS, ARIZ, GH, US]). — **Lit:** Gentry (1982: 71–75); Ullrich (1994a); Turner & al. (1995); Wilder & al. (2008); Felger & al. (2011); all with ill. **Distr:** Mexico (C & S Sonora: coastal and San Pedro Nolasco & Tiburón islands); slopes or often bare rocks in hot coastal and lowland regions, in desert and thorn scrub, 300–760 m; flowers mid-March to mid-May. **I:** Etter & Kristen (2001: 172–173); Richter (2011: 60); Pilbeam (2013: 58–59); Hochstätter (2015: VIII: 20). — Fig. 16.

[1b] Stems short; **Ros** openly spreading, 1–1.3 × 2–2.4 m, mostly solitary, sometimes suckering

profusely; **L** few, linear-lanceolate, straight or slightly curved, deflexed at maturity, convex below, flat above, smooth, 70–120 × 4–7 cm, widened at the base, light green, margins fragile, 1 mm wide, brown; **marginal teeth** none; **terminal Sp** acicular, with a short fine groove at the base above, 20–40 mm, brown, aging greyish; **Inf** mostly 2–4 m, ‘spicate’, peduncle with dry chartaceous **Bra**, lower **Bra** longer than the flowers, fertile part densely flowered, in the upper ¾ of the inflorescence; **Ped** bifurcate, 10–15 mm; **Fl** geminate, 35–45 mm; **Tep** yellow, tube shallow, 4–4.5 × 9 mm, lobes ovate, flat, outcurving at anthesis, clasping the filaments after anthesis, thin, ± equal, outer 14–16 × 6 mm, keeled, the inner wider (8 mm) and unkeeled; **Fil** 40–45 mm, inserted on the rim of the tube at the base of the lobes; **Anth** 14–18 mm; **Ov** slender, scarcely grooved, 16–20 mm incl. a 3–5 mm long neck; **Fr** mostly oblong, 20 × 10 mm, shortly apiculate, parallel-veined and slightly cross-ridged; **Se** crescent-shaped, with 1 to several wrinkles on the faces, marginal wing low, firm, the hilar notch sharply angled, mostly 4–4.3 × 2.5–2.8 mm.

Closely related to *A. vilmoriniana*, but distinguished by straight narrow flat leaves (vs. deeply guttered and arching in *A. vilmoriniana*) and without bulbils in the inflorescence. Gentry (1982) considers the inland populations at Río Yaqui as showing introgression from *A. vilmoriniana*; Turner & al. (1995) map these as *A. chrysoglossa*. The Sierra Seri populations of *A. chrysoglossa* appear to bridge a morphological gap to *A. pelona* (Turner & al. 1995). Specimens by R. Felger cited by Gentry (1982: 87) seem closer to *A. pelona* and are placed there by Turner & al. (1995). See also under *A. ocahui*. For the habitats on the Gulf Islands, see Wilder & al. (2008) and Felger & al. (2011). The seed production is estimated as 500,000–750,000 seeds per plant. The flowers are visited by numerous insects, hummingbirds, and other birds (Gentry 1982).

**A. cocui** Trelease (Mem. Nation. Acad. Sci. 11: 19, tt. 5–7, 1913). **Type:** Venezuela (*Zuloaga* s.n. [MO [syn, 4 sheets]]). — **Lit:** Berger (1915: 224–225); Hummelinck (1936: 244–247, 249, tt. VII, VIIIa); Hummelinck (1938: 21–23, tt. Ib,

IVb); Figueredo (2010: with ill.). **Distr:** Venezuela (incl. Isla Margarita), Colombia; mainly coastal, but also extending into inter-Andean valleys, 400–1000 m; flowers January to May. **I:** Hoyos F. (1985: fig. 83); Mostul (2005: 70); Figueredo (2010); Richter (2011: 96); Pilbeam (2013: 60); Hochstätter (2015: VII: 36).

**Incl.** *Agave americana* Humboldt (1808) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave cocui* var. *cucutensis* Hummelinck (1936); **incl.** *Agave cocui* var. *laguayrensis* Hummelinck (1936).

[2u] Acaulescent or sometimes subcaulescent; **Ros** to 2.5 m Ø, suckering; **L** rather many, lanceolate to elliptic, sometimes sub-oblong, rarely oblanceolate, guttered, often slightly S-curved, tip often slightly upcurved, sharply acute or subacuminate, (80–) 100–120 (–140) × 20–30 cm, (3.5–) 4–5 (–6) × as long as broad, glaucous, soon green and glossy; **marginal teeth** mostly upcurved above and recurved below, acuminately triangular or from crescent-shaped bases on green or later hardening prominences, (2–) 2.5–6 (7) mm, reddish chestnut-brown, (6–) 10–14 (–22) per 10 cm, intervening margin concave; **terminal Sp** conical or rarely acicular, sometimes triquetrous, rather often distinctly laterally flattened, very rarely flexuous, often recurved near the tip, shallowly grooved below the middle and involute below, smooth, sometimes rough, (10–) 12–22 (–30) × (2–) 3–5 (–6) mm, red-brown, slightly or not decurrent, dorsally very slightly immersed into the leaf tissue; **Inf** (5–) 6–8 (–10) m, paniculate, peduncle with 15–25 **Bra**, **Bra** serrate towards the tips, narrowly triangular, at length recurved, fertile part in the upper ½ of the inflorescence, narrowly oblong, part-**Inf** on nearly horizontal branches, freely bulbiferous; **Ped** (3–) 4–8 (–12) mm; **Fl** (40–) 45–55 (–65) mm; **Tep** yellow, tube openly conical, (3–) 4–6 (–7) mm, lobes (18–) 20–24 (–25) × 5–7 mm; **Fil** (30–) 35–45 (–55) mm, inserted 1 mm above to 0–1 (–1.5) mm below the throat; **Anth** (15–) 18–23 (–25) mm; **Ov** 25–40 × 7–8 mm; **Sty** (38–) 44–50 (–55) mm; **Fr** oblong, (35–) 40–50 × 20–25 mm, usually very slightly beaked, shortly stipitate; **Se** 7–9 × 5–6 mm. — **Cytology:** 2n = 60 (Mata-Sucre & al. 2017).

The type at MO consists of 4 sheets which are not cross-labelled and thus represent syntypes

(Smith & Figueiredo 2014e: 231). Not always clearly separated from *A. vicina* (Hummelinck 1938: as *A. vivipara*). Hummelinck's concept of *A. cocui* included plants from Curaçao and neighbouring islands here separated as *A. vivipara* (see there). The species is not restricted to coastal regions and extends into inter-Andean valleys as far as Táchira (Venezuela) and Santander (Colombia; Hummelinck (1938: 21)).

*A. cocui* is an important crop in Venezuela, used from wild plants in traditional production systems esp. for liquor, soap, fibres, and preserves (Salazar & al. 2009, Figueredo 2010). Flowering starts mainly with the onset of the dry period in January or later and is highly synchronized among the populations (Figueredo & Nassar 2011). Molecular populational studies showed that *A. cocui* has one of the lowest estimates of genetic diversity as yet reported, which is esp. low in its centre of economic use, suggesting that human impact represents a significant threat to its gene pool (Figueredo & Nassar 2011), but 3 populations could be separated with AFLP data (Yépez & al. 2008). For the in vitro propagation, see Salazar & al. (2009). See also under *A. boldinghiana*.

**A. coetocapnia** (M. Roemer) Govaerts & Thiede (Willdenowia 43(2): 331, 2013). **Type:** Mexico (*Deppe* s.n. [†; [lecto — icono]: Link & Otto, Icon. Pl. Rar., t. 18, 1828, as '*Zetocapnia*'). — **Lit:** McVaugh (1989: 248–252); Solano & García-Mendoza (2013: with ills.); both as *Polianthes geminiflora*. **Distr:** N and C Mexico.

≡ *Bravoa coetocapnia* M. Roemer (1847); **incl.** *Bravoa geminiflora* Lexarza (1824) ≡ *Polianthes geminiflora* (Lexarza) Rose (1903); **incl.** *Coetocapnia geminiflora* Link & Otto (1828); **incl.** *Robynsia geminiflora* Drapiez (1841); **incl.** *Bravoa graminiflora* Hemsley (1884) (*nom. inval.*, Art. 61.1); **incl.** *Polianthes americana* Sessé & Moçino (1888); **incl.** *Polianthes tubulata* Sessé & Moçino (1894); **incl.** *Agave duplicata* Thiede & Eggl (1999) (*nom. illeg.*, ICN Art. 52.1).

This is the most widespread and well-known species of Sect. *Polianthes*. It is rather variable in the size of the plant, leaves, bracts, inflorescences, and the number of flowering nodes (McVaugh 1989, Solano & García-Mendoza 2013).

When transferring *Polianthes geminiflora* to *Agave*, Thiede & Eggli (1999) published the new name *A. duplicata* due to the earlier *A. geminiflora* (Tagliabue) Ker Gawler (1817), but were unaware of the prioritable epithet available as *Bravoa coetocapnia* (Govaerts & Thiede 2013). Solano & García-Mendoza (2013) provided a taxonomic treatment (as *Polianthes geminiflora*) and neotypification. The hybrid of this species with *A. bulliana* is known as *A. ×kewensis* (see there).

**A. coetocapnia** ssp. **clivicola** (McVaugh) Govaerts & Thiede (Willdenowia 43(2): 332, 2013). **Type:** Mexico, Jalisco (*Wilbur & Wilbur* 2133 [MICH, IEB]). — **Lit:** McVaugh (1989: 250); Solano & García-Mendoza (2013); Castro-Castro & al. (2015: with ill.); all as *Polianthes geminiflora* var. **Distr:** Mexico (NW, SW, C & S Jalisco, W Michoacán); mostly on steep shaded slopes, barrancas, gullies, in oak, pine, and pine-oak forests, grasslands, or ecotones with tropical subdeciduous forests, (900–) 1200–2560 m; flowers June to September (to October). **I:** Guillot Ortiz & al. (2006: 67); Castro-Castro & al. (2015); Hochstätter (2016: II: 12); Castro-Castro & al. (2016: 721); all as *Polianthes geminiflora* var./ssp.

≡ *Polianthes geminiflora* var. *clivicola* McVaugh (1989) ≡ *Agave duplicata* ssp. *clivicola* (McVaugh) Thiede & Eggli (1999) (*incorrect name*, ICN Art. 11.4) ≡ *Polianthes geminiflora* ssp. *clivicola* (McVaugh) Hochstätter (2016).

[3b2] Differs from ssp. *coetocapnia*: **L** margins usually very narrowly revolute, with very thin pale scarious or hyaline edge, smooth and entire, rarely obscurely roughened.

This is the W element within *A. coetocapnia*, differing in leaf margin characters.

**A. coetocapnia** ssp. **coetocapnia** — **Lit:** McVaugh (1989: 248–252); Solano & García-Mendoza (2013: with ills.); Guillot Ortiz & Meer (2016a: 72–74); all as *Polianthes geminiflora*. **Distr:** Mexico (Durango, Nayarit, Jalisco, Guanajuato, Querétaro, Hidalgo, Michoacán, México, Tlaxcala, Distrito Federal, Morelos, Guerrero, Puebla); mainly on rocky slopes in oak, pine or cloud forests, mainly in the Trans-Mexican



**Fig. 17** *Agave coetocapnia* ssp. *coetocapnia* (Etter & Kristen 2835: Mexico; Jalisco, ± 20 km S of San Cristóbal de la Barranca, 1470 m). (Copyright: J. Etter & M. Kristen)

Volcanic Belt, 900–2800 m; flowers June to August (to November). **I:** Guillot Ortiz & al. (2006: 67, as *P. geminiflora*); García-Mendoza & Esparza Alvarado (2010: 62–63, as *P. geminiflora*); Etter & Kristen (2012: 85, as *A. duplicata*); Castro-Castro & al. (2015: 145, as *P. geminiflora* var.); Hochstätter (2016: II: 11, as *P. geminiflora* var.); Castro-Castro & al. (2016: 721, as *P. geminiflora* var.). – Fig. 17.

≡ *Agave duplicata* ssp. *duplicata*.

[3b2] Herbaceous; corm cylindrical, 1.5–2.7 × 1–2 cm, bulb ovoid, 1.8–4 × 1.3–3 cm, covered with dry leaf bases; **R** contractile, fleshy and fibrous; **L** 2–6 (–8), linear-lanceolate to broadly attenuate towards the acute tip, (8–) 12–35 (–50) × 0.1–2.5 (–3.7) cm, glaucous, plain green or spotted with small or large and confluent green or dark brown spots, lower face slightly papillose on the veins, margins entire, denticulate, papillose to erose; **Inf** 35–100 (–154) cm, ‘racemose’,



peduncle with linear to lanceolate **Bra** 4.5–31 × 0.1–2.3 (–2.8) cm, fertile part lax, denser towards the tip, 10–40 (–60) cm; **Ped** strongly ascending, (3–) 10–18 mm; **Fl** geminate, but often only 1 developing, pendent, unscented; **Tep** red, orange or coral-red, tube slender and terete at the base, broadened above, 14–21 × 1–3 (–5) (at the tip) mm, throat straight or slightly oblique, lobes erect, ovate, (sub-)orbicular to transversally elliptic, subequal, 2–3 (–5) × 1–2.5 mm, cucullate, apex obtuse to rounded, with a tuft of short white hairs; **St** included; **Fil** filiform, (5–) 10–21 (–24) mm, white, inserted 2–5 mm above the tip of the ovary; **Anth** linear, 3–6 mm, yellow; **Ov** erect, ellipsoid; **Sty** filiform, 10–25 mm, sometimes as long as the tepal tube, white; **Sti** 3-lobate; **Fr** shortly oblong or almost globose, 7–17 × 5–12 mm; **Se** semicircular, flat, 2–4 (–5) × 2–3 mm, black, shiny or dull.

Zamudio & Galván Villanueva (2011: 87) provide a new record for Guanajuato. The flowers attract hummingbirds and insects (Etter & Kristen 2012).

**A. coetocapnia** ssp. **pueblensis** (E. Solano & García-Mendoza) Govaerts & Thiede (Willdenowia 43(2): 332, 2013). **Type:** Mexico, Puebla (Solano & al. 849 [MEXU, CHAPA, ENCB, FEZA, HUAP, HUMO, IEB, US]). — **Lit:** Solano & García-Mendoza (2013: as *Polianthes geminiflora* var.). **Distr:** Mexico (W & SW Puebla); open spots on calcareous soils, in oak and juniper forests, desert scrub, grasslands and corn fields, 2160–2220 m; flowers July to August. **I:** Hochstätter (2016: II: 13, as *P. geminiflora* ssp.).

≡ *Polianthes geminiflora* var. *pueblensis* E. Solano & García-Mendoza (2007) ≡ *Agave duplicata* ssp. *pueblensis* (E. Solano & García-Mendoza) Thiede (2012) (*incorrect name*, ICN Art. 11.4) ≡ *Polianthes geminiflora* ssp. *pueblensis* (E. Solano & García-Mendoza) Hochstätter (2016).

[3b2] Differs from ssp. *coetocapnia*: **L** very narrow, 1–2 mm broad, papillose on the lower face, margins regularly denticulate.

This is the SE element within *A. coetocapnia*, differing in its leaf margin and very narrow leaves.

**A. colimana** Gentry (Cact. Succ. J. (US) 40: 212–213, ills., 1968). **Type:** Mexico, Colima (Gentry 18325 [US, ARIZ, DES, MEXU]). — **Lit:** Gentry (1982: 102–107, with ills.); McVaugh (1989); Ullrich (1991a: with ills.); Vázquez-García & al. (2007b: 49–50, t. G). **Distr:** Mexico (W, SW & S Jalisco, Colima, Michoacán); primarily coastal on rocky sites, or more inland in tropical deciduous forests, 0–1000 m; flowers November to March. **I:** Etter & Kristen (2012: 95); Pilbeam (2013: 61).

**Incl.** *Agave ortgiesiana* Roez (1871) (*nom. inval.*, ICN Art. 36.1b?); **incl.** *Agave schidigera* var. *ortgiesiana* Baker (1877) ≡ *Agave ortgiesiana* (Baker) Trelease (1914) (*nom. illeg.*, ICN Art. 53.1) ≡ *Agave angustissima* var. *ortgiesiana* (Baker) Trelease (1920); **incl.** *Agave maritima* Rose ex Hort. Kew (1897) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave ortgiesiana* var. *brevifolia* Hort. Besauccèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[1d] Shortly caulescent; **Ros** 0.4–0.6 × 1–1.2 m, solitary; **L** many, linear, straight, slightly narrowed above the base, widest near the middle, thin and flat above, smooth, 40–70 × 1–2.5 cm, green, with light green mid-stripe, margins narrow, brown, filiferous with fine, long, brown threads; **marginal teeth** none; **terminal Sp** weak, short, broadly rounded below, flattened or somewhat hollowed above, 5–8 mm, greyish-brown to dark brown, decurrent into the leaf margin; **Inf** 2–3 m, ‘spicate’, peduncle with linear-acicular dark brown or purplish **Bra**, lower **Bra** longer than the flowers, the upper somewhat shorter, fertile part of the inflorescence slender, from ±1 m above the base, part-**Inf** not crowded; **Ped** 10–15 mm; **Fl** geminate, 40–50 mm; **Tep** pale yellow or lavender, tube slightly 6-furrowed, narrow, 9–17 × 5–9 mm, lobes recurved at anthesis, subequal, 14–19 × 4–6 mm, outer 1 mm longer, thin, obtuse, with thickened papillate tip; **Fil** 30–40 mm, pale reddish, inserted 8–11 mm above the tube base and 1–2 mm below the lobe sinuses; **Anth** 17–21 mm, yellow; **Ov** round, 14–20 mm, greenish-yellow, neck 4–7 mm, slightly constricted; **Sti** contiguous with the style and not clavate, roundly trigonous, with papillae decurrent on the angles below the tip; **Fr** oblong,

20–25 mm, conspicuously constricted at the base, beaked, stipe stout, to 10 mm; **Se** small, hemispherical, rugulose, 2–3 × 3.5–4 mm.

Typical plants are distinctive with their elongate leaves and deep narrow flower tube, but sometimes approach *A. schidigera* in flower tube length and *A. multiflifera* in leaf characters and are then hard to distinguish without complete material (Gentry 1982). There has been a long dispute about the correct name for this species: McVaugh (1989: 135) regards the earlier name *A. ortgiesiana* Roezl (1871) as invalid since it was published in an excerpt of a letter only. Ullrich (1991a), in contrast, accepts *A. ortgiesiana* Roezl as validly published and thus as the correct name for the taxon. Govaerts (WCSP, April 2014) does not cite the Roezl name, but instead accepts *A. ortgiesiana* (Baker) Trelease (1914). Here, the established name *A. colimana* is retained for the time being, pending a formal proposal to conserve it over the earlier *A. ortgiesiana* (Baker) Trelease.

Tschapka & al. (2008) observed a highly specialized nectar-feeding bat on this species, *Ceiba pentandra*, *Pachycereus pecten-aboriginum* and *Pseudobombax ellipticum*; another species of migratory nectar-feeding bat was traced by Stoner & al. (2003).

**A. collina** Greenman (Contr. Gray Herb. 11: 296, 1897). **Type:** Mexico, Morelos (*Pringle* 6349 [MO, AC, BR, CAS, CM, ENCB, F, G, GH, GOET, JE, K, MEXU, MICH, MIN, MSC, NDG, NY, P, PH, S, US, VT]). — **Lit:** Berger (1915: 253); Trelease (1920: 116); Gentry (1982: 586). **Distr:** Mexico (Morelos, Guerrero); ±1500 m; flowers in June.

[2g] Acaulescent, unknown whether **Ros** solitary or offsetting; **L** 30–40, linear-attenuate, gradually narrowing towards the apex, convex below, concave above, 60–80 × 5–8 cm (in the middle, narrowing to 2 cm just above the base), bluish-green, somewhat green-banded below, margins narrowly cartilaginous; **marginal teeth** straight or upcurved, 3–5 mm, reddish-brown, on broad lenticular bases, 8–25 mm apart, intervening margin straight or very slightly emarginate, with a fine, brown or yellowish, horny line; **terminal Sp** conical, broadly and somewhat crookedly

canaliculate, 20–30 × 3–5 mm, reddish- or purplish-brown, somewhat decurrent; **Inf** 3–4 m, paniculate, fertile part 60–80 cm, lower part **Inf** ±30 cm; **Fl** ±60 mm (90 mm incl. the exerted stamens); **Tep** greenish-yellow, tube funnel-shaped, 15–16 mm, lobes linear-oblong, obtuse, thickened at the apex, 19–20 mm; **Fil** flattened, glabrous, ±50 mm; **Anth** 25–30 mm; **Ov** 25 mm, neck constricted; **Sty** slightly shorter or ± as long as the filaments; **Sti** capitate; **Fr** 45–50 × 25–30 mm, shortly beaked; **Se** crescent-shaped to obliquely triangular, 8–10 × 6–8 mm.

Listed by Gentry (1982: 586) under “incertae sedis”, but accepted as species by Espejo Serna & López Ferrari (1993), Govaerts (2014+), and Portal Datos Abiertos UNAM (2018+: accessed Jan. 2019). According to the protologue it is probably identical with *A. serrulata* (as “serratula”), a synonym of *A. angustifolia*. The measurements of the protologue fall well within the range of the variable *A. angustifolia*, and *A. collina* may belong to that complex as suggested by Gentry (1982: 586). Gentry deviates in part from the protologue, and describes the species as “a stout, short-stemmed plant with nearly white glaucous to pale green leaves with nearly black teeth and spine” and as “frequent in middle elevations from Morelos to Guerrero”. Fernández Nava & al. (1998: 2) list the species for the Balsas basin (Guerrero).

**A. colorata** Gentry (Publ. Carnegie Inst. Washington 527: 93–94, t. 14: fig. 2, 1942). **Type:** Mexico, Sonora (*Gentry* 3050 [CAS, ARIZ]). — **Lit:** Gentry (1972: 117–119, ills.); Gentry (1982: 431–433, ills.); Ullrich (1993f: with ills.); Turner & al. (1995: 48–49); Starr (2012: 78–83, 320–321, ills.). **Distr:** Mexico (S Sonora, N Sinaloa); foothills or coastal regions, open rocky sites in thorn or pine-oak forests, on volcanic or white limestone rocks, 60–200 m; flowers March to June. **I:** Irish & Irish (2000: t. 13); Heller (2006: 76); Klopper & al. (2010); Richter (2011: 131); Pilbeam (2013: 62–63); Hochstätter (2015: IV: 7); Moore (2016: 271). – Fig. 18.

[2h] Stems short; **Ros** compact, 0.45–0.9 × 0.45–1.2 m, tapered at the base or hemispherical, solitary or sparingly suckering; **L** few, ovate, shortly acuminate to lanceolate, thick, firm,



**Fig. 18** *Agave colorata*  
(Etter & Kristen 562:  
Mexico; Sonora, near  
Aquihuiquichi, 200 m).  
(Copyright: J. Etter &  
M. Kristen)



convex below towards the base, flat to concave above, asperous, 25–60 (–100) × 12–18 cm, light grey, glaucous, frequently cross-zoned and red-tinted, margins prominently crenate or with prominences; **marginal teeth** straight or flexuous, mostly 5–10 mm (in the middle of the lamina), brown to greyish, 15–30 mm apart, smaller below; **terminal Sp** subulate, straight or flexuous, narrowly grooved above in the lower ½, mostly 30–50 mm, brown to grey; **Inf** 2–3 m, paniculate, lower **Bra** leaf-like, the others soon drying, appressed at the base, reflexed above, 10–15 cm, reddish, fertile part of the inflorescence narrow, **part-Inf** densely flowered, 15–20 in the upper ⅓–½ of the inflorescence; **Fl** 53–73 mm; **Tep** yellow, reddish in bud, apex usually remaining reddish, tube cylindrical, thick-walled, narrowly grooved, 15–20 × 12–14 mm, lobes linear, strictly erect, thickly fleshy, unequal, outer larger, overlapping, 12–16 × 5–7 mm, inner shorter, thickly keeled; **Fil** stout, flattened, tapered, 45–65 mm, inserted at 2 levels at mid-tube, yellow or pink; **Anth** 21–26 mm; **Ov** 25–40 mm, pale green, neck short, not constricted; **Sty** thick, sometimes pink, exceeding the stamens after anthesis; **Sti** capitate; **Fr** oblong to clavate, 45–55 × 15–17 mm, thickly and shortly stipitate or sessile; **Se** tear-shaped, 6 × 5 mm, hilar notch frequently obscure, marginal wing narrow. — **Cytology**: 2n = 60 (Simpson & al. 2011).

The closest relative, both morphologically and geographically, is *A. shrevei*, from which

*A. colorata* differs in its broader cross-zoned leaves with deeply crenate to repand margins, more densely flowered panicles with closely set ‘umbels’, and its shorter, wider tepal tube and thicker ovary. The species is uncommon in nature. Its compact size and bright glaucous leaves with pinkish cross zones make it an attractive ornamental (Gentry 1982). Plants from near Guaymas and San Carlos Bay (Sonora) have longer and narrower leaves with smaller marginal teeth (Gentry 1982: 432–433, Starr 2012); these were first misplaced in *A. fortiflora* (Gentry 1972: 125). Bats and possibly also hummingbirds are the assumed pollinators (Gentry 1982). Flowers pollinated by the likely main pollinator, the bat *Leptonycteris yerbabuena*, show much higher fruit set, higher numbers of viable seeds, and a higher germination rate compared to fruits and seeds obtained from self-pollination (Borbón-Palomares & al. 2018).

**A. confertiflora** Thiede & Egli (Kakt. and Sukk. 50(5): 111, 1999). **Type**: Mexico, Chihuahua (*Hartman* 536 [US, MEXU, UC]). — **Lit**: Rose (1899: 155, t. 18, as *Pseudobravoa densiflora*); García-Mendoza (2003); Solano & Feria (2007); Feria-Arroyo & al. (2010: with ill.); all as *Polianthes densiflora*. **Distr**: Mexico (SW Chihuahua); open sites on calcareous soils, in pine or pine-oak forests, 2190–2500 m. **I**: Hochstätter (2016: II: 9).

≡ *Bravoia densiflora* B. L. Robinson & Fernald (1895) ≡ *Pseudobravoia densiflora* (B. L. Robinson & Fernald) Rose (1899) ≡ *Polianthes densiflora* (B. L. Robinson & Fernald) Shinnors (1966).

[3b1] Herbaceous, small, 7–15 cm; corm cylindrical, to  $\pm 1 \times 1$  cm, bulb oblong, to  $\pm 1 \times 1.5$  cm, covered with dry leaf bases; **R** many, contractile, thickened; **L** 4–10, linear, attenuate, apex acute, 7.5–11  $\times$  0.2–0.3 cm, green, margins entire, or partly papillose; **Inf** ‘spicate’, short; peduncle with **Bra** 2.5–5 cm, with broad scarious and attenuate tips; fertile part dense, with (2–) 4–6 floral nodes, 7.5–13 cm; **Ped** none; **Fl** solitary, slenderly tubular, spreading, curved, 43–55 mm; **Te**p pulverulent-tomentose on the outer face, dull yellow, tube narrow, scarcely widened, 21–44  $\times$  3–4 mm, throat oblique, lobes erect, ovate, obtuse, equal, 2.5–4 mm, tip with a tuft of short white hairs; **St** included; **Fil** filiform, inserted in the tube; **Anth** linear, 5–10  $\times$  1–2 mm, yellow to green-yellowish, at anthesis surrounding the throat; **Ov** cylindrical; **Sty** filiform, as long as the tube, included at anthesis; **Sti** 3-lobate; **Fr** globose, 8–12  $\times$  7–10 mm; **Se** deltoid or semicircular, flat, 3–4  $\times$  2.4–3.3 mm, shiny or dull.

A hardly known but seemingly very distinct species. Long known from the type collection only, but Solano & Feria (2007: 1888) mention 13 records from 5 localities. The geographical distribution, niche modelling and extinction risk of the species are dealt with by Solano & Feria (2007) and Feria-Arroyo & al. (2010). The type locality is incorrectly cited as “Varogachic” in the protologue, but is Norogachi, a Tarahumara community in the town of Guachochi (database note for GH 00030302!), and the type is “Hartman, 5 July, 1892 (no. 536)” (US, MEXU, UC) and not Hartman 546, 6 July 1892 (GH, K, MEXU), partly labelled as “Type”. — When *Polianthes densiflora* is transferred to *Agave*, a new name is necessary to avoid homonymy with *A. densiflora* Hooker.

**A. congesta** Gentry (Agaves Cont. North Amer., 476–479, ills., 1982). **Type:** Mexico, Chiapas (Gentry 23651 [US [2 sheets], ARIZ, DES, MEXU, MICH]). — **Lit:** Lott & García-Mendoza

(1994: online version with ills.); García-Mendoza (2003: with ill.). **Distr:** Mexico (Chiapas); widely scattered in pine-oak forests and pine woodlands in the Montañas del Oriente, on calcareous rocks, (930–) 2100–2500 m; flowers December to February. **I:** García-Mendoza (2002: 187); Richter (2011: 114); Pilbeam (2013: 64); Hochstätter (2015: VI: 6).

[2o] Stems short; **Ros** compact, 0.5–1  $\times$  1–2 m, solitary; **L** many, lanceolate to lanceolate-spatulate, at first curved-ascending, then horizontally spreading, thick, narrowed at the base, (shortly) acuminate, flat, (40–) 50–120  $\times$  10–22 cm, green to yellow-green, sometimes faintly glaucous or pruinose, margins straight in the lower  $\frac{1}{2}$ , repand to crenate in the upper  $\frac{1}{2}$ ; **marginal teeth** straight to variously curved, moderate to rather large, dark to greyish-brown, usually remote, 20–50 mm apart, mostly on variously shaped prominences, 5–10 mm, base broad and low; **terminal Sp** stout, base very broad, widely flatly grooved above, 30–70 mm, grey to chestnut-brown, sharply decurrent to the upper teeth; **Inf** 6–8 m, paniculate (“racemose” in the protologue), peduncle with prominent **Bra**, fertile part straight, slender, with 40–50 part-**Inf** as congested rounded clusters, subsessile or on short lateral branches 2–10 cm long, in the upper  $\frac{1}{2}$  or more of the inflorescence; **Ped** closely subtended by small purplish bracts, 3–10 (–20) mm; **Fl** (45–) 55–70 mm; **Te**p orange to reddish or purplish in bud, yellow at anthesis, softly fleshy, tube deeply funnel-shaped to tubular, thick-walled, grooved, knobby, 10–13 mm, lobes linear-lanceolate to narrowly triangular, involute, thickly rounded-cucullate, unequal, 17–30 mm, the outer larger, dark-coloured apically, the inner shorter, with a thick prominent keel; **Fil** slender, 40–60 mm, purplish, inserted at 2 levels near the throat of the tube; **Anth** centric, irregularly curved to sinuous, 20–30 mm, bronze-coloured; **Ov** angular-fusiform, (25–) 30–40 mm, neck short; **Sty** stout, lengthening after anthesis, somewhat longer than the filaments; **Sti** capitate; **Fr** oblong, 50  $\times$  20 mm; **Se** unknown.

The species name alludes to the congested flowers in the dense globose ‘umbels’. It is further distinguished by the dimorphic dark-coloured

tepals and the filaments inserted at 2 levels. The closely related *A. hiemiflora* has the same but less pronounced characteristics, and is distinguished by smaller rosettes with fewer leaves, and paler tepals (Gentry 1982: 479). Gentry's "holotype" at US consists of 2 sheets which appear to have been cross-labelled later.

**A. convallis** Trelease (Contr. US Nation. Herb. 23: 138, 1920). **Type** [lecto]: Mexico, Oaxaca (Trelease 4 [MO [1128755 + 1256267]]). — **Lit**: García-Mendoza (2010); García-Mendoza (2011a: 23–26); León Vázquez & al. (2013). **Dist**: Mexico (S Puebla, NW & C Oaxaca); desert scrub and pine forests, in soils of volcanic origin, 1610–2640 m; flowers August to January.

**Incl.** *Agave dissimulans* Trelease (1920).

[lg] Acaulescent; **Ros** dense, 1–1.2 × 1.5–2 m, solitary or rarely caespitose; **L** (40–) 50–80, broadly lanceolate to lanceolate, erect, stiff, succulent, leathery, fibrous, thick and flat at the base, flat to slightly guttered towards the apex, (50–) 70–100 × 10–16 (in the middle) cm, dark green, yellow-green or purple, sometimes with a weak yellowish mid-stripe, margins straight, horny, continuous, white; **marginal teeth** broadly triangular, sometimes bifid, present towards the base, absent in the uppermost 5–15 (–35) cm, straight to variously curved, 9–15 (–20) × (4–) 7–10 mm, (10–) 25–45 (–70) mm apart, grey-white or brown, sometimes with a lenticular broadening beneath each tooth, sometimes with small intermittent teeth; **terminal Sp** conical, deeply channelled above, 30–55 × 5–8 mm, greyish-white, decurrent on the lower face for 4–15 mm; **Inf** 3–6 (–8) m, 'spicate', peduncle green, with linear chartaceous deciduous **Bra** 11–15 cm long, fertile part in the upper ½–⅓; **Ped** 3–4 (–10) mm; **Fl** geminate, campanulate, (34–) 38–43 mm; **Tep** yellowish-green outside, dark reddish inside, tube 4–6 × 4–6 (–10) mm, lobes oblong, 17–20 × 4–6 (–10) mm, inner ones keeled, outer ones larger; **Fil** (30–) 35–40 mm, red, inserted in the mouth of the tube; **Anth** 15–20 mm, reddish; **Ov** cylindrical, 16–20 × 4–6 mm, neck 2–4 mm, constricted; **Sty** 40–50 mm, yellowish; **Fr** obovoid, 24–25 × 12–16 mm; **Se** 5–6.5 × 3–4 mm, with inconspicuous wing, black.

Previously placed in the synonymy of *A. kerchovei* (Gentry 1982: 149), but recently re-established as a species of its own (García-Mendoza 2010, García-Mendoza 2011a, Govaerts 2014+). The species differs from *A. kerchovei* in its larger number of shorter, relatively broader, broadly lanceolate to lanceolate leaves per rosette, the lack of teeth in the uppermost 5–15 (–35) cm of the margins, its more closely placed teeth, its oblong tepals, and its obovoid capsules and larger seeds. Furthermore, *A. convallis* occurs at higher altitudes mainly on igneous soils (García-Mendoza 2011a). This author also provides a new record for Puebla. Smith & al. (2018b) designated the lectotype cited above.

**A. cundinamarcensis** A. Berger (Agaven, 222, 1915). **Type**: Colombia, Cundinamarca (*Wercklé* s.n. [not indicated]). — **Lit**: Bernal & al. (2015: 794). **Dist**: Colombia (Cundinamarca: Río Cuja valley S of Bogotá); ±1250 m. **I**: Hochstätter (2015: VII: 59).

[2v] **Ros** solitary, not suckering; **L** very thick above the base but only 15 cm broad, straightly spreading, then curved upwards and rapidly becoming broader, above the middle 45 cm broad and then again curved outwards, but the last 15 cm again curved upwards, 200 × 45 cm, lead-grey on yellowish-green base colour; **marginal teeth** flat and broad, nearly blunt, very short, hardly pungent; **terminal Sp** rather short; **Inf** paniculate, sparingly bulbiferous, not further described; **Fl**, **Fr** and **Se** not described.

Possibly first mentioned by Wercklé (1907: 122) as *Agave* "vom westlichen Cundinamarca", and still insufficiently known. Plants studied by J. Etter and M. Kristen in March 2019 near the type locality of *A. cundinamarcensis* largely match the protologue and appear to represent the true species. This and the second species from Colombia, *A. wallisii*, were both placed in his Reihe *Columbianae* by Berger (1915: 222), which he regarded as possibly closest to the *Caribaeae*. Neither of these 2 species appears close to the geographically adjacent Colombian-Venezuelan *A. cocui* from Sect. *Viviparae*. Xhonneux (2004), Greulich (2012b), and Hochstätter (2015: VII: 59) show plants placed here from habitats

**Fig. 19** *Agave cupreata*  
(Martinez & Eggli 188b:  
Mexico; Guerrero, between  
Mazatlán and  
Chilpancingo, 1350 m).  
(Copyright: U. Eggli)



W and N of Bogotá and variegated plants with broad yellow margins cultivated at Bogotá and in Europe, which differ clearly from the protologue in having smaller, less curved, green leaves much less broadened in the middle. The variegated plants were given the cultivar name ‘Condor’. According to P. van der Meer (pers. comm. Nov. 2018/Feb. 2019), these plants, including the variegated ones, are misnamed and belong to an undescribed species provisionally named “*A. bogotensis*”.

The variegated plant may be the same as the medium-sized plant with dark green leaves with broad yellow margins cultivated at Bogotá reported earlier by Wercklé (Berger 1915: 222). Wercklé (in Berger 1915) and P. van der Meer (pers. comm. Feb. 2019) both report further undescribed species from Colombia.

**A. cupreata** Trelease & A. Berger (Agaven, 197, 1915). **Type** [lecto]: Mexico, Michoacán/Guerrero (*Langlassé* 867 [B, GH, K, MEXU, MPU, P, US]). — **Lit:** Gentry (1982: 335–337, ill.). **Distr:** Mexico (E Michoacán, Guerrero); mountain slopes, dry hills and rocky ledges, in tropical dry and oak forests and grasslands, 1220–2100 m; flowers November to March. **I:** García-Mendoza (2002: 183); Smith (2002: 225); Heller (2006: 77); Etter & Kristen (2007b: 178); Richter (2011: 48, 73); Pilbeam (2013: 65); Greulich (2014a: 56). – Fig. 19.

[2d] Caulescent, **Ros** openly spreading, 0.8–1.6 m Ø, solitary; **L** broadly lanceolate or ovate, thickly fleshy, strongly narrowed at the base, flat to slightly concave above, 40–80 × 18–20 cm, bright shiny green, with conspicuous patterns from the central bud, margins deeply crenate-mamillate; **marginal teeth** straight to curved, strongly flattened, dimorphic, larger teeth 10–15 mm on distinct prominences, 30–60 mm apart, with smaller intermittent teeth of varying sizes, copper-coloured to grey; **terminal Sp** slender, sinuous, openly grooved above, 30–50 mm, light brown to greyish, with a sharp border decurrent to the upper teeth; **Inf** 4–7 m, paniculate, fertile part rather broad, part-**Inf** lax diffuse ‘umbels’, 14–25 in the upper ½ of the inflorescence, branches with dark small bracts; **Fl** 55–60 mm; **Tep** brown-red in bud, at anthesis orange-yellow, tube broadly funnel-shaped, 6–7 × 14–15 mm, lobes erect, linear-lanceolate, acute, subequal, outer 20–21 mm, apex rust-coloured, broader and thicker than the inner, inner with narrow keel and thin involute margins; **Fil** thickened towards the base, 35–40 mm, inserted at mid-tube; **Anth** excentric, curved, 23–24 mm, yellow; **Ov** fusiform, knobby, grooved, thick-walled, 30–35 mm, olive-green, neck constricted, doubly 3-grooved; **Sty** hardly longer than the tepals; **Sti** capitate; **Fr** and **Se** unknown. — **Cytology:** 2n = 60, 120, 150, 180 (Palomino & al. 2012, Gomez-Rodriguez & al. 2013).



A beautiful plant from the Río Balsas basin, distinguished by the broad, shiny green leaves with tall marginal prominences and conspicuous patterns from the central bud, and brightly copper-coloured marginal teeth (Gentry 1982: 335). Material of the type collection is present in several herbaria, and Gentry (1982: 352) lists the specimen at B as “holotype”, which is interpreted as unintentional lectotypification. See also under *A. potatorum*.

A morphological characterization of populations in Guerrero is provided by Avendaño-Arrazate & al. (2015), and a study of wild populations in Michoacán by Martínez Castro & al. (2015). *A. cupreata* regenerates successfully by seed in different habitats, but the population density is reduced by cattle trampling and grazing on seedlings and floral stalks (Martin & al. 2011). Martínez-Palacios & al. (2011) studied the genetic diversity and its implications for conservation. The continued extraction of reproductive individuals from wild populations does not produce a decline in genetic diversity in 5 studied populations (Aguirre-Dugua & Eguiarte 2013). The species (vernacular name “Agave papalote”) is locally semi-domesticated with only sexual reproduction, and used for mescal production (Illsley & al. 2007). Molecular populational data do not clearly separate *A. cupreata* from *A. potatorum*, and both are seen to represent one species only with two lineages: One in lower areas of the Balsas basin (*A. cupreata*), and another one in the highest forests and open areas (*A. potatorum*) (Eguiarte & al. 2013: 495–496).

**A. dasyliroides** Jacobi & C. D. Bouché (Hamburg. Gart.- & Blumenzeit. 21: 344, 1865). **Type** [neo]: Cult. BG Berlin (*Anonymous* s.n. [B]). — **Lit**: Baker (1877b: 556–557, with ill.); Berger (1915: 83–85); Standley & Steyermark (1952: 110–111); Gentry (1982: 237–240, with ill.); García-Mendoza (2003: with ill.); Thiede (2014a); Thiede (2017a). **Distr**: Mexico (Morelos, México); igneous rock cliffs on mountain slopes, in mixed pine and hardwood forests, 1500–2200 m; flowers in December. **I**: Curtis’s Bot. Mag. 94: t. 5716, 1868; Kemble (2002); Heller (2006: 78); Richter (2011:

36, 58); Pilbeam (2013: 66–67); Hochstätter (2015: VIII: 6).

**Incl.** *Agave dealbata* E. Morren ex K. Koch (1862); **incl.** *Agave dealbata* Lemaire ex Jacobi (1865) (*nom. illeg.*, ICN Art. 53.1)  $\equiv$  *Agave dasyliroides* var. *dealbata* (Lemaire ex Jacobi) A. Terracciano (1885); **incl.** *Agave dealbata* var. *nana* K. Koch (1869) (*nom. inval.*, ICN Art. 35.1); **incl.** *Agave dealbata* [?] *angustifolia* Hort. (1871) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave dealbata* [?] *compacta* Hort. (1871) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave dealbata* [?] *compacta angustifolia* Hort. (1871) (*nom. inval.*, ICN Art. 24.2, 38.1a); **incl.** *Agave intrepida* Greenman (1899).

[1a] **Ros** symmetrical, 0.3–0.5  $\times$  0.6–1 m, generally solitary; **L** 70–100, linear-lanceolate, straightly spreading, pliable, relatively thin, scarcely succulent, flat above, mostly 40–60  $\times$  2–3 cm, glaucous-green, smoothly striate below and above, margins 1 mm wide, pale yellowish-white, minutely serrulate; **marginal teeth** none; **terminal Sp** acicular, rounded below, flat near the base above, 5–15 mm, reddish-brown; **Inf** 1.5–2 m, ‘spicate’, arching, peduncle greenish to pale reddish, with conspicuous greenish to pale reddish persistent **Bra** 10–15 cm long, fertile part in the upper  $\frac{1}{3}$ – $\frac{1}{2}$  of the inflorescence, **part-Inf** with 1–4 flowers; **Fl** 26–35 mm, persistent after anthesis; **Tep** pale green to greenish-yellow, tube funnel-shaped, 8–12  $\times$  8–12 mm, shallowly grooved below the lobe sinuses, lobes spreading, ovate to oblong, mucronate, equal, 9–11  $\times$  6–7 mm, sometimes with dark midstripe, the outer flat, the inner with a broad keel and convergent ribs within; **Fil** 35–50 mm, whitish-green to pink, inserted at mid-tube; **Anth** centrally affixed, 12–15 mm, yellow to brownish, persistent; **Ov** linear-tapered, 3-angulate, truncate at the base, 9–12 mm, neckless intruding the tepal tube; **Sty** whitish, sometimes pale reddish apically; **Fr** ovoid,  $\pm 20 \times 10$  mm, without beak, pale grey to brown; **Se** 4  $\times$  3 mm.

The name *A. dealbata* is commonly ascribed to Jacobi (who used it in the same publication where *A. dasyliroides* was described 1865), but it was in fact first used by K. Koch in 1862. Because of priority, it would displace the universally used

name *A. dasylirioides*, and a conservation proposal is envisaged to avoid this (Thiede 2014a). *A. dealbata* var. *nana* is a long-forgotten name for a small-growing form.

The species is best known from Morelos esp. around Cuernavaca, but was recently also collected in the State of México (García-Mendoza 2003, Thiede 2014a). Gentry (1982: 249) cited one collection from San Luis Potosí (*Rzedowski* 7128a), but this most probably belongs to *A. graciellae* (Galván & Zamudio 2013). Plants in habitat near Yosondua in Oaxaca depicted as “*A. dasylirioides*” by Ullrich (1990f) and Polka (2006) and a cultivated flowering plant depicted by Brand (2012) belong to the close relative *A. kavandivi* (see there for differences). See also the comment for *A. petrophila*.

The type of *A. dasylirioides* was erroneously said to have been collected in Guatemala. Gentry (1982: 241) assumed this species to hold a very basal position in the genus based on its ‘primitive’ (plesiomorphic) features (leaves serrulate and scarcely succulent, inflorescences relatively simple, ovary incompletely inferior, tepals all equal, lobes nearly of equal length), and this assumption is principally confirmed by molecular data insofar as Sect. *Juncineae* (as Group *Striatae*) represents the sister group to the remainder of the genus (Bogler & Simpson 1996, Bogler & al. 2006, Gil-Vega & al. 2007; see also introduction to the genus).

**A. datylio** Simon ex F. A. C. Weber (Bull. Mus. Hist. Nat. (Paris) 8: 224, 1902). **Type** [neo]: Mexico, Baja California (*Gentry & Arguelles* 11200 [US, ARIZ, MEXU, MICH]). — **Lit**: Trelease (1912b: 45, 61–62, tt. 68–71, also as *A. vexans*); Berger (1915: 259–260, also as *A. vexans*); Gentry (1978: 97–99, also as var. *vexans*); Gentry (1982: 571–572, also as var. *vexans*); Turner & al. (1995: 49–50, also as var. *vexans*); Webb & Starr (2015: 90–91); all with ill. except Berger. **Distr**: Mexico (C & S Baja California Sur); sandy plains and rocky granitic slopes to 730 m; flowers September to December. **I**: Goldman (1916: t. 111C, as *A. vexans*); Richter (2011); Pilbeam (2013: 68–69); Hochstätter (2015: VII: 37–38, also as ssp. *vexans*).

**Incl.** *Agave vexans* Trelease (1912) ≡ *Agave datylio* var. *vexans* (Trelease) I. M. Johnston (1924) ≡ *Agave datylio* ssp. *vexans* (Trelease) Hochstätter (2015).

[2g] Acaulescent; **Ros** 0.3–1 × 0.6–1.5 m, suckering freely, rhizomes frequently elongate; **L** radiately spreading, lanceolate-linear, nearly straight, rather rigid, rounded below, guttered above, 20–80 × 3–4 cm, green to yellow-green or glaucous-green, young somewhat glaucous, margins nearly straight; **marginal teeth** deltoid, mostly recurved, triangular, flattened, rather blunt, mostly 2–5 mm, dark brown, 15–60 mm apart, more closely spaced below, often on broad or lenticular bases; **terminal Sp** conical to subulate, scarcely or flatly grooved above, 20–40 × 3–6 mm, dark brown to greyish, shortly decurrent; **Inf** 1.2–5 m, paniculate, part-**Inf** small ‘umbels’, 8–15 in the upper ½ of the inflorescence; **Ped** < 5 mm; **Fl** 40–55 mm; **Top** greenish-yellow, tube funnel-shaped, 5–15 × 3–4 mm, lobes erect to ascending, 12–20 × 3–4 mm; **Fil** 25–45 mm, inserted 4–6 mm above the tube base; **Anth** 15–30 mm, yellow; **Ov** fusiform or flask-shaped, 20–30 mm, glaucous; **Sty** shorter than the filaments; **Sti** capitate; **Fr** (broadly) oblong to pear-shaped, 35–45 × 15–20 mm, shortly stipitate, conspicuously beaked; **Se** 6–7 × 5–6 mm. — **Cytology**: 2n = 87, 90, 174 (3×, 6×; Cave (1964), Simpson & al. (2011: as *A. vexans*)).

Widely scattered in the Cape region of Baja California Sur. This is the only species of Sect. *Rigidae* (as Group) in Baja California, and is without close relatives (Gentry 1982). It belongs to the “sword-leaved group” within Sect. *Rigidae* whose geographically nearest member is *A. aktites* from the opposite Sonoran-Sinaloa coast. *A. aktites* differs clearly by narrower bluish leaves with sharply cuspid teeth, and larger flowers with a deep bulging tube (Gentry 1982). Var. *vexans* was differentiated by Gentry (1978) and Berger (1915) by its smaller rosettes and leaves, but Webb & Starr (2015) consider the size differences as resulting from edaphic conditions and refer it to the synonymy. The triploid chromosome number of the former var. *vexans* suggests that parts of it may have arisen as hybrid between a di- and a tetraploid parent.



**A. debilis** A. Berger (Agaven, 33, 1915). **Type** [lecto]: Mexico, Oaxaca (*Pringle* 4745 [US, BM, BR, CM, ENCB, G, GH, JE, LE, M, MEXU, MSC, NDG, P, S, VT]). — **Lit:** Rose (1903c: 19); Verhoek-Williams (1975: 248–254); Piña Luján (1985: 86–89); McVaugh (1989: 233); Castillejos-Cruz (2009: [238]–[247], with ill.); García-Mendoza (2011a: 79–79, 81); all as *Manfreda pringlei*. **Distr:** Mexico (Nayarit, Jalisco, Hidalgo, Michoacán, México, D.F., Tlaxcala, Morelos, Guerrero, Puebla, Veracruz, Oaxaca); moist forests or pine-oak ericaceous woods, in cloud, pine-oak, pine, oak, thorn and tropical deciduous forests, desert scrub and grasslands, (1000–) 1500–3000 m; flowers mid-July to November. **I:** Hochstätter (2016: I: 37, as *Manfreda pringlei*).

≡ *Manfreda pringlei* Rose (1903) ≡ *Polianthes debilis* (A. Berger) Shinnery (1966); **incl.** *Manfreda angustifolia* Rose in sched. (s.a.) (*nom. inval.*, ICN Art. 29.1).

[3a3] Herbaceous, of moderate size (for Subgen. *Manfreda*), reproducing vegetatively by stoloniferous horizontal rhizomes with plantlets at the tips; corm 3–5 × (1–) 1.5–2.5 cm, bulb cylindrical to ovoid, 3.5–7.5 × 1.8–3.2 (–6) cm, covered with membranous dry leaf bases fraying into fine fibres at the tip, (4–) 6–11 cm long; **R** half-fleshy, fibrous, vertical; **L** drought-deciduous, (2–) 4–10, erect-spreading, linear to linear-lanceolate, narrowed towards the base, somewhat succulent, slightly channelled, occasionally gently undulate, tip acute to acuminate, with medium-sized point, smooth, (12–) 24–45 (–80) × (0.5–) 1–2.7 cm, dark brown to shining green, sometimes with purple dots, at times red-speckled on the lower face near the base, without prominent veins, margins narrow, hyaline, sometimes streaked with purplish-red, papillate to erose-denticulate, usually rough to the touch; **Inf** 97–200 cm, ‘spicate’, peduncle greenish with purple tinge, peduncular **Bra** 6–12, similar to the leaves, fertile part (10–) 25–33 cm; **Fl** (5–) 10–25, sessile, diffuse to ascending, tubular, congested, nearly erect, 30–40 mm, slightly curved at the junction of ovary and tepal tube; **Tep** tube cylindrical, slightly widened towards the throat, tip cucullate, with a tuft of short hairs, 9–21 × (3–) 5–6 (in the middle) mm, lobes oblong, revolute,

8–16 × 2–4 (–7) mm, green-yellowish to reddish with purple tinge; **Fil** 26–45 (–54) mm, exceeding the tube for 22–42 (–50) mm, inserted slightly unequally in the middle of the tube, greenish-yellow to greenish-red; **Anth** 11–14 mm, reddish to yellowish-green; **Ov** cylindrical, (8–) 9–11 (–12) × 3–5 mm, not constricted, apex prolonged into the tepal tube for 1 mm; **Sty** 40–60 mm, exerted for 30–48 mm; **Sti** clavate, trigonous, shallowly furrowed, yellowish-green with small purple dots; **Fr** ellipsoid to subcylindrical, 15–20 × 12–17 mm; **Se** deltoid, plane-concave, with narrow margin, 3–4 × 4–5 mm.

This species shares many floral and fruit characters with *A. guttata*, but is nevertheless easily distinguished by its longer, narrower and more pliable and herbaceous leaves and its distribution. It may represent the moist-forest counterpart of the more xeromorphic *A. guttata* (Verhoek-Williams 1975: 252–253, as *Manfreda*). *A. debilis* is morphologically also similar to the recently published *A. verhoekiae* (for differences see there).

**A. decipiens** Baker (Bull. Misc. Inform. Kew 1892: 183, 1892). **Type** [lecto]: USA, Florida (*Dodge* s.n. [K, BUS, CICY?, US]). — **Lit:** Berger (1915: 242–243, with ill.); Gentry (1982: 573–574, with ill.); Zona (2002: with ill.); Reveal & Hodgson (2002); Franck (2012: 6–7, with ill.); Rubal Lobo & al. (2013: with ill.). **Distr:** USA (S Florida); coastal sands, sandy soil in hammocks, at sea-level; flowers November/December to March. **I:** Curtis’s Bot. Mag. 122: t. 7477, 1896, as *A. laxifolia*; Heller (2006: 79, 80); Richter (2011: 128); Pilbeam (2013: 70); Hochstätter (2015: VII: 39); Moore (2016: 263).

**Incl.** *Agave laxifolia* Baker (1896); **incl.** *Agave spiralis* Brandegees ex A. Berger (1912).

[2g] Arborescent, trunk 1–3 (–4) m, very broad through bulging leaf bases, frequently suckering; **Ros** extending down for some distance from the stem tip, 1–1.5 × 1.5–2 m, not caespitose; **L** 36–72, linear-lanceolate, rigidly spreading to recurving, fleshy, narrowed at the thickened base, long-acuminate, convex below towards the base, concave above towards the apex, (24–) 70–100 (–200) × (1.3–) 7–10 cm, bright green or yellowish-green, without imprints from the central

bud, margins slightly wavy, repand; **marginal teeth** 2–3.6 mm at mid-leaf, curved upwards or downwards, dark brown, 10–20 mm apart, on low prominences, the slender tips upcurving, often with some smaller intermittent teeth, intervening margins not continuously horny; **terminal Sp** conical, without groove, 10–29 mm, brown or brownish-black, decurrent or not; **Inf** 3–5 m, paniculate, peduncle with caducous **Bra**; part-**Inf** ascending, 8–18 in the upper ½ of the inflorescence, with ±15–23 flowers, to 45 cm, often bulbiferous; **Ped** 5–11 mm; **Fl** erect, 60–80 mm, foetid-scented; **Tep** greenish-yellow, tube funnel-shaped, 6–13 × 4–6 mm, lobes incurved, tips cucullate, with a tuft of short white hairs, subequal, 17–26 mm, greenish-yellow, outer linear, drying reflexed on the tube; **St** long-exserted; **Fil** erect, terete, 27–47 mm, yellow, inserted at 2 levels at or slightly above mid-tube; **Anth** 13–25 mm, yellow; **Ov** large and thick, 22–43 mm, neckless; **Fr** ellipsoid to oblong, 35–50 mm, apex beaked, shortly stipitate; **Se** unknown. — **Cytology**: 2n = 120, 150, 160, 180, 190 (Banerjee & Sharma 1989, Reveal & Hodgson 2002, Simpson & al. 2011).

Geographically isolated from the remainder of the genus (except *A. neglecta*). The taxon is most probably of cultivated origin. It was reported to occur at old Indian village sites in 1933 and may well represent an old pre-Columbian food or fibre plant, comparable to *A. delamateri*. The different chromosome numbers suggest a prolonged human propagation and probable hybrid origin (Reveal & Hodgson 2002). *A. decipiens* is possibly derived from *A. angustifolia*, from which it mainly differs in its obvious stem 1.5 m long or more (Gentry 1982, Zona 2002), but individuals of the latter with distinct stems are found on the Yucatán peninsula (Cruz-Ramos & al. 1985, Zona 2002). Plants from the Yucatán peninsula placed here belong to *A. angustifolia* (Gentry 1982, Zona 2002: as *A. vivipara*), Further differences from *A. angustifolia* are the longer ovaries and shorter anthers of *A. decipiens* (Zona 2002). Gentry's "lectotypification" (1982: 573) represents a neotypification and is superfluous, since the type material is extant (Zona 2002). Franck (2012) designated a lectotype at K from the 3 extant specimens of the type collection. Rubal Lobo &

al. (2013) and López-Pujol & al. (2015b): report the species as naturalized in Prov. Cádiz, Spain. The report of the species as naturalized in S Africa (Smith & Steyn 1999) actually refers to *A. angustifolia* (Smith & al. 2008: as *A. vivipara*). Introduced ants exploit the nectar of plants cultivated in Florida (Koptur & Truong 1998).

**A. delamateri** W. C. Hodgson & Slauson (Hazeltonia 3: 130–140, ill., 1995). **Type**: USA, Arizona (Hodgson 5478 [DES, ASU]). — **Lit**: Hodgson (1999a: 5, 14, 19, with ill.); Reveal & Hodgson (2002); Parker & al. (2007); Parker (2018a: 22, 24, with ill.). **Distr**: USA (C Arizona); gravelly places in desert scrub, rarely in chaparral or pinyon-juniper woodlands, 725–1555 m; flowers late June through July. **I**: Pilbeam (2013: 71).

**Incl.** *Agave repanda* Trelease ex Gentry (1982) (*nom. inval.*, ICN Art. 36.1c).

[2h] Acaulescent; **Ros** 0.9–1 × 0.9–1 m, solitary to caespitose, freely suckering; **L** lanceolate or oblanceolate, rigid, erect or erect-ascending, broadest near or just below the middle, acuminate, guttered, apex conspicuously incurved, mostly 50–63 (–74) × 7.5–9 cm, bluish-grey-glaucous with purple-maroon tinge and green cross-banding, margins straight or repand; **marginal teeth** variable, usually reflexed, becoming porrect near the leaf base, 3.5–5 mm, 10–30 mm apart, intermittent teeth 1–1.5 mm, (3–) 6–12 mm apart, mostly along the distal ⅓ of the leaf; **terminal Sp** slender, 28–35 (–49) mm, brownish-grey, decurrent for ⅙–⅓ of the leaf length; **Inf** 4.5–6 m, broadly paniculate, open, peduncle with persistent triangular **Bra** 1–5.5 cm long, part-**Inf** widely spaced, horizontal, 12–17 in the upper ⅓–½ of the inflorescence, >10 cm, with 14–20 flowers each; **Fl** erect, long-lived, 47–67 (–70) mm; **Tep** pale cream tinged light green, tube campanulate, 11–16 × 11–16 mm, lobes spreading, unequal, 9–18 mm, apex tinged with maroon, persistent and often leathery during and after anthesis; **St** long-exserted; **Fil** erect, 30–53 mm, yellow, apex tinged with maroon, inserted at a single level ± at mid-tube; **Anth** 11–20 mm, yellow; **Ov** 21–29 mm, neck slightly constricted, 1–3.5 mm; **Sty** cream-coloured, maroon-flecked, becoming more

maroon towards the stigma; **Sti** capitate, 3-lobed, cream-coloured tinged with maroon; **Fr** aborting, never fully developed; **Se** inexistent.

According to the protologue already collected around 1920 by S. D. McKelvey and recognized as distinct by Trelease, who in 1929 used the unpublished name *A. repanda*. It is most closely related to the allopatric *A. fortiflora* and *A. palmeri*, but distinguished esp. by its numerous rhizomatous offsets, easily cut leaves, and 1- (instead of 2-) seriate filaments. *A. delamateri* was first known only from about 90 sites, always in association with Mogollon or Salado settlement features, and probably represents a cultivar derived from *A. palmeri* or a closely related taxon by pre-Columbian people. Later field studies yielded more than 200 sites so that *A. delamateri* is the most common one among the pre-Columbian cultivars from Arizona (Parker 2018a). It hybridizes with *A. chrysantha* (Hodgson 1999a, Reveal & Hodgson 2002). Parker & al. (2007) found a low level of genetic diversity, relating to its continued vegetative propagation from few clones only (see also under *A. murpheyi*). *A. phillipsiana*, another pre-Columbian cultivar species in Arizona, differs in having longer leaves and flowers, a longer tepal tube, and longer tepal lobes (Klopper & al. 2010: 63). For further pre-Columbian cultivar species in Arizona, see also under *A. verdensis*.

**A. deserti** Engelm (Trans. Acad. Sci. St. Louis 3: 310–311, 370, 1875). **Type**: not established. — **Lit**: Trelease (1912b: 45, 52–53, tt. 41–42); Berger (1915: 262–263); Gentry (1978: 15–25, t. 1, with ills.); Gentry (1982: 376–385, with ills.); Turner & al. (1995: 50–54, with ills.); Hodgson (1999a: 5–6); Reveal & Hodgson (2002); Starr (2012: 84–89, with ills.); Webb & Starr (2015: 81–82, with ills.). **Distr**: SW USA, NW Mexico.

The protologue cites specimens from Hitchcock and Palmer (= syntypes; specimens located at F, GH, MO [2 sheets and printed material], NY, PH); Gentry (1978: 16) adds that both were collected on Rancho San Felipe, San Diego County. No attempt for a formal lectotypification seems to have been made so far.

A large and variable complex with hard-to-define limits, difficult to separate from *A. cerulata*, and also close to *A. subsimplex* (Gentry 1982: 405) (see there for differences). Moreover, also the recognized subspecies are not always clearly separable on morphological grounds, and a molecular study of 14 samples embracing all 3 subspecies did not find a clear correlation with Gentry's infraspecific concept as used here (Navarro-Quezada & al. 2003). Gentry's (1982) ssp. *pringlei* is here recognized at species rank (as *A. pringlei*) following Webb & Starr (2015).

**A. deserti** ssp. **deserti** — **Lit**: Trelease (1912b: 45, 52–53, tt. 41–42); Berger (1915: 262–263); Gentry (1978: 15–25, t. 1, with ills.); Gentry (1982: 376–380, with ills.); Hodgson (1999a: 5–6, as *A. deserti*); Reveal & Hodgson (2002:



**Fig. 20** *Agave deserti* ssp. *deserti* (Eggl s.n.: USA; California, Anza Borrego State Park). (Copyright: U. Eggl)

**Fig. 21** *Agave deserti* ssp. *deserti* (Eggl s.n.: USA; California, Anza Borrego State Park). (Copyright: U. Eggl)



with ills., as var.); Starr (2012: 84–89, ills.); Webb & Starr (2015: 77, 81–82, with ill.). **Distr:** USA (S California), Mexico (N & C Baja California); sandy to gravelly or rocky places, in desert scrub and pinyon-juniper woodlands, 500–1500 m; flowers mainly April to July, also November to January and in September. **I:** Irish & Irish (2000: t. 14); Heller (2006: 30); Richter (2011: 80, 125); Pilbeam (2013: 72); Hochstätter (2015: V: 9). – Figs. 20 and 21.

**Incl.** *Agave deserti* Orcutt (1883) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave consociata* Trelease (1912).

[2i] **Ros** mostly 30–70 × 40–80 cm, rather open, sparingly or prolifically suckering; **L** variable, ascending, narrowly triangular-lanceolate to lanceolate to linear-lanceolate, thick, rigid, scarcely narrowed above the broad clasping convex base, acuminate to long-acuminate, deeply guttered towards the apex, mostly 25–70 × 4.5–10 cm, 4–7 × as long as broad, greyish-white, grey, blue-glaucous to (yellowish-) green, often lightly cross-zoned, margins usually straight but sometimes undulate or crenate; **marginal teeth** usually regularly spaced, loosely to firmly attached, variously curved or reflexed, smaller teeth 2–3 mm, longer teeth 5–10 mm, grey, mostly 10–30 mm apart, slender-tipped, brown to pruinose-grey, sometimes with a brown ring at the base; **terminal Sp** subulate to acicular, openly grooved, strong, generally

20–40 mm, light brown to greyish, decurrent to the 1. or 2. tooth to mid-blade; **Inf** 2–6 m, paniculate, peduncle slender to thick, green to glaucous, with scarious triangular **Bra** 8–15 cm long, fertile part usually narrowly to somewhat broadly paniculate, part-**Inf** short, small, 6–15 in the upper 1/5–1/4 of the inflorescence; **Fl** 30–60 mm; **Te** yellow, tube shallow, angular, openly funnel-shaped, 3–10 × 9–15 mm, pale green to yellow, lined with a thick nectariferous disk, lobes (broadly) linear, erect to spreading, rounded and abruptly hooked inwards at the apex, equal, 13–20 × 4–6.5 mm, (light) yellow, wilting at anthesis; **Fil** 25–42 mm, unequally inserted 2.75–3.75 mm above the tube base, or subequally at the base of the lobes, pale yellow; **Anth** 13–21 mm, yellow; **Ov** 15–30 (–38) mm, greenish, neck slightly narrowed to constricted, 4–6 mm, yellow to pale green; **Sty** 24–29 mm, pale yellow; **Fr** ovoid to oblong or obovoid, mostly 35–55 × 12–20 mm, shortly stipitate, apex beaked or shortly rounded to rostrate; **Se** 5–6 × 4–4.5 mm, black. — **Cytology:** 2n = 59, 60, 118 (Cave 1964, Simpson & al. 2011).

Field experiments (Jordan & Nobel 1979) showed that successful seedling establishment takes only place in 1 out of 17 years. The length of the first drought period is the limiting factor for establishment, with water-stress in the seedling stage as the single most important factor. For a



**Fig. 22** *Agave deserti* ssp. *simplex* (Etter & Kristen 250: USA; Arizona, Maricopa County, Saddle Mountain, 350 m). (Copyright: J. Etter & M. Kristen)



summary of many further ecological and ecophysiological studies on *A. deserti* see Nobel (1988).

**A. deserti** ssp. **simplex** Gentry (Occas. Pap. Calif. Acad. Sci. 130: 22, ill. (pp. 23–24), 1978). **Type:** USA, Arizona (Gentry 23404 [US, ARIZ, ASU, DES, MEXU]). — **Lit:** Gentry (1982: 382–385, with ill.); Hodgson (1999a: 6); Reveal & Hodgson (2002: as var.); Starr (2012: 84–89, with ill.); Webb & Starr (2015: 77, 81–82, with ill.); Parker (2017: 256, 260, with ill., as var.). **Distr:** USA (SW Arizona, SE California), Mexico (NW Sonora); sandy to gravelly or rocky places, in desert scrub and pinyon-juniper woodlands, 300–1500 m; flowers mainly May and June, also in November and February. **I:** Heller (2006: 80); Pilbeam (2013: 74); Ettelt (2014: 123); Hochstätter (2015: V: 11). — Fig. 22.

≡ *Agave deserti* var. *simplex* (Gentry) W. C. Hodgson & Reveal (2001).

[2i] Differs from ssp. *deserti*: **Ros** usually solitary, rarely with 1–3 offsets; **L** lanceolate, moderately acuminate, light green to light glaucous-grey, margins repand to crenate; **marginal teeth** friable; **Inf** 4–6 m; part-**Inf** in the upper 1/3 of the inflorescence. — **Cytology:** 2n = 60 (Reveal & Hodgson 2002).

Ssp. *simplex* refers to the N and E populations of the species from hot, dry and low elevations, characterized by a predominantly solitary habit (Gentry 1982, Parker 2017). It hybridizes with *A. schottii* ssp. *schottii*, and possibly with *A.*

*mckelveyana* (Hodgson 1999a, Reveal & Hodgson 2002). It is esp. well-suited for hot and dry gardens in the SW USA (Parker 2017).

**A. desmetiana** Jacobi (Hamburg. Gart.- & Blumenzeit. 22: 217, fig. 32, 1866). **Type** [neo]: Mexico, Sinaloa (Gentry 11569 [US, ARIZ, MEXU]). — **Lit:** Berger (1915: 234, as *A. miradorensis*); Gentry (1972: 94–99, with ill.); Gentry (1982: 622–624, with ill.); Reveal & Hodgson (2002); Franck (2012: 7–8, with ill.). **Distr:** Cultivated only; flowers September to November. **I:** Irish & Irish (2000: tt. 15–16); Pilbeam (2013: 75); Hochstätter (2015: VII: 40, as *A. demeesteriana*); Moore (2016: 267, 268).

**Incl.** *Agave demeesteriana* Jacobi (1866); **incl.** *Agave regeliana* Jacobi (1866) ≡ *Agave miradorensis* var. *regeliana* (Jacobi) A. Terracciano (1885) (*incorrect name*, ICN Art. 11.4); **incl.** *Agave ananassoides* Jacobi (1868); **incl.** *Agave miradorensis* Jacobi (1868).

[2c] Stems short, trunk <0.5 m, commonly suckering in early years; **Ros** 0.7–0.9 (–1.2) × 0.7–0.9 (–1.8) m; **L** linear-lanceolate, spreading and arching, openly ascending, brittle, firm, abruptly or gradually narrowed towards the base, guttered, 50–90 (–105) × 7–13 cm, dark to glaucous-green, not cross-zoned, margins straight, smooth, finely and sparsely fibrous, without distinct colouration; **marginal teeth** typically none, or small, regular, 1–2 mm, chestnut-brown, 10 to

>20 mm apart or few and irregularly spaced; **terminal Sp** subulate, shortly and broadly grooved above, 20–30 mm, dark brown to reddish-brown; **Inf** 2.5–3 m, paniculate, peduncle with persistent triangular **Bra** 0.5–2 cm long, fertile part long, narrow and compact, often bulbiferous, part-**Inf** ascending, congested, 20–36 in the upper  $\frac{1}{2}$ – $\frac{2}{3}$  of the inflorescence, with 15–21 flowers, >10 cm long; **Fl** erect, 40–60 mm; **Tep** green in bud, pale yellow at anthesis, drying ferruginous, tube salverform, 10–12 × 14–17 mm, distinctly flanged inside below the inner tepals, deeply grooved and ridged on the outside, lobes erect, nearly equal, 13–15 mm; **OTep** 1 mm longer; **ITep** sharply involute; **St** long-exserted; **Fil** erect, 30–40 mm, yellow, inserted near the mouth of the tube; **Anth** centric, 13–26 mm, yellow; **Ov** 15–25 mm, 6-grooved in the upper part, shortly stipitate, neck 1–3 mm, not constricted; **Fr** and **Se** unknown. — **Cytology**:  $2n = 60$  (Reveal & Hodgson 2002).

Distinguished by its smooth unarmed arching leaves and the short compact inflorescences with small flowers with a very short ovary and a broad tube (Gentry 1982: 623). According to Ullrich (1990d), it was originally introduced from Cuba as *A. anomala*, where it may have originated (see also under that species). Trelease (1920: 121) assumed an origin from El Mirador (Huatusco, Veracruz), based on the epithet of the synonymous *A. miradorensis*. Gentry (1972) and Gentry (1982) found it cultivated in Sonora and Sinaloa.

Its systematic position is unclear, since it does not fit well into any section; Gentry's placement in Sect. *Sisalanae* (as Group) is regarded as artificial by Ullrich (1990d). Here, Reveal & Hodgson (2002) and Govaerts (2014+) are followed who regard the species as a sterile, possibly ancient cultivar possibly derived from *A. sisalana*/*A. kewensis* or *A. kewensis*, respectively. It is consequently placed in Sect. *Sisalanae*. Govaerts (2014+) considers the earlier *A. demeesteriana* as correct name for the species. A conservation proposal is thus necessary to retain the established name *A. desmetiana*. The epithet honours the Belgian nurseryman De Smet but is frequently misspelled 'desmettiana'. The species is naturalized in Florida (Franck 2012). The plant depicted as naturalized in Spain (Guillot Ortiz &

Meer 2009a) has larger, cross-banded leaves and may merely represent *A. sisalana*. 'Joe Hoak' is a variegated cultivar traded in the USA (Starr 2014: 222, with ill.). Guillot Ortiz & Meer (2016d) discuss variegated and normal-leaved cultivars cultivated in Spain. Variegated plants are also shown by Moore (2016).

**A. difformis** A. Berger (Agaven, 95–96, 1915).

**Type**: Ex cult. (Berger s.n. [US, K]). — **Lit**: Gentry (1982: 135–138); Eguiarte & Scheinvar (2008: 44–47); both with ill.; Trejo-Salazar & al. (2015: pollination); López-Pujol & al. (2016). **Distr**: Mexico (W-C San Luis Potosí, N-C Querétaro, Hidalgo); coarse limestone rocky soils, in desert and submontane scrub on the arid side of the Sierra Madre Oriental, 1560–2100 m; flowers May to August; neophyte in Spain. **I**: Curtis's Bot. Mag. 139: t. 8481, 1912, as *A. haynaldii*; Heller (2006: 82); Richter (2011: 68); Pilbeam (2013: 76); Hochstätter (2015: IX: 82); Greulich (2016c: 151).

**Incl.** *Agave haynaldii* Todaro (1878).

[lg] Stems short; **Ros** open, rather vigorous, variable, 0.7–1 × 1–1.5 m, freely suckering; **L** 25–50, polymorphic, straight or falcate or sinuous, stiffly ascending, thickly convex below, concave above, 50–80 × 4–6 cm, (dark) green to yellow-green, margins straight or repand, firm or detachable, predominantly light grey; **marginal teeth** variable, generally 5–10 mm, dark brown to grey, 20–30 mm apart, rarely double, sometimes with smaller intermittent teeth, or reduced or entirely lacking; **terminal Sp** conical-subulate, stout, with a short open groove above, 15–30 mm, dark brown to grey; **Inf** 3.5–6 m, 'spicate', peduncle waxy-glaucous, with thin, narrow, chartaceous, deflected **Bra**, fertile part slender, in the upper  $\frac{1}{3}$ – $\frac{1}{2}$  of the inflorescence; fertile **Bra** mostly longer than the flowers; **Fl** 30–40 mm; **Tep** light green to yellow and pink, tube flaring, 2.5–3.5 mm, lobes mostly erect, equal, sharply hooded at the apex, 15–18 × 3–4 mm, pale yellow or tinged pink, clasping the filaments at anthesis; **Fil** 35–45 mm, pale green (Gentry: pale to pinkish), inserted on the rim of the tube; **Anth** excentric, 15–18 mm, yellow or bronze-coloured; **Ov** 15–21 mm, waxy green, neck short; **Sty** slender, pale green, somewhat darker below the



stigma; **Sti** slightly thickened; **Fr** oblong, transversely rugose, 22–26 × 12–15 mm, dark brown, shortly beaked, sessile; **Se** crescent-shaped, 5 × 3 mm, somewhat wavy on the faces, wing low, hilar notch small.

A robust species, within Sect. *Heteracanthae* (as Group *Marginatae*) characterized by its very polymorphic long-ensiform leaves. Some forms resemble *A. lechuguilla* (Gentry 1982: 137). Magallán Hernández & Hernández Sandoval (2001) provide a new record for Querétaro. — The 5 type specimens at US bear 4 different dates and thus represent different gatherings. *A. haynaldii*, if really conspecific, antedates the established name *A. difformis*, and a formal proposal to conserve the established name is necessary.

From 740 flowers produced at average, only 47% develop into fruits. These may have 117 ovules of which only 37% form viable seeds. When the fruits of an inflorescence open, they release about 23,100 viable seeds dispersed by wind. Nocturnal nectar-feeding bats are the most important flower visitors. In the morning, bees, hummingbirds, hymenopterans and bumblebees visit the flowers, and at sunset various hawk-moths. The species shows relatively high levels of genetic diversity with little differentiation among the populations which is possibly generated by high gene flow provided by the pollinators (Eguarte & Scheinvar 2008).

The pollination biology of this and further sympatric species was studied by Rocha & al. (2005) and Trejo-Salazar & al. (2015), recording bats and sphingids as primary pollinators. López-Pujol & al. (2016) report the species as neophyte from Spain.

**A. doctorensis** L. Hernández & Magallán (Brittonia 67(1): 1–3, ill., 2014). **Type:** Mexico, Querétaro (Hernández 6094 [QMEX, ENCB, IEB, MEXU, TEX, XAL]). — **Distr:** Mexico (E-C Querétaro: Sierra del Doctor); on gentle slopes and flatlands on a superficial calcareous substrate, in rosette scrub or in juniper forests, 2400–2600 m; flowers in November (?). **I:** Hochstätter (2015: IX: 28).

[1g × 2a?] **Ros** open, 1–1.2 × 0.8–1 m, surculose; **L** 15–25 (–30), erect, lanceolate to

narrowly elliptic, rigid, smooth, 50–75 (–95) × 4–9.5 cm in the middle, pale green with imprints from the next inner leaves, margins corneous, easily detached, straight, to 1 mm wide, reddish, covered with narrow lines of wax that can be lost with age; **marginal teeth** deltoid or hooked, bases wide, retrorse, brittle, flat, 1–2 (–8) × 1 mm, 15–45 mm apart, abundant close to the base, absent near the leaf tip, with small interstitial teeth, greyish, or occasionally toothless; **terminal Sp** subulate, curved to straight, grooved above, 27–43 mm, slightly decurrent; **Inf** 4.2–4.5 m, ‘racemose-paniculate’, peduncle with broadly acuminate papyraceous to chartaceous **Bra** 17–28 × 2.5–6.5 cm, beige to greenish, spine-tipped, reflexed, fertile part only 12–25% of the total inflorescence height, **part-Inf** 70–80, compact, conical, dorsiventrally flattened, with 6–7 flowers, the lower 7 cm, diminishing to 1.8 cm towards the tip; **Ped** 5–30 mm; **Fl** 42–54 mm; **Top** yellowish-green, tube funnel-shaped, 4–10 × 5–8 mm, lobes oblong to linear, channelled, unequal, 13–23 × 16–25 mm, outer 3–4 mm longer than the inner, margins involute, apex dark brown to reddish, thick, inner lobes cucullate; **Fil** dorsiventrally flattened, 35–45 mm, the outer inserted 5–7 mm from base of the tube, the inner 4–6 mm from the base of the tube; **Anth** 18–24 mm, yellow; **Ov** broadly elliptic, (20–) 24–28 (–33) mm, neck constricted; **Sty** ± as long as the filaments; **Fr** usually oblong, 27–35 × 13–15 mm, beaked, dark brown, perianth persisting almost to maturity; **Se** crescent-shaped to deltoid, 5–6 × 1–2 mm, shiny black.

Placed in Sect. *Heteracanthae* (as Group *Marginatae*) in the protologue and compared with *A. ×glomeruliflora*, which is the name used for a series of natural intersubgeneric hybrids between Subgen. *Littaea* and Subgen. *Agave* with intermediate ‘racemose-paniculate’ inflorescences (see there), as well as with *A. montium-sancticaroli* with similar intermediate inflorescences (and thus supposedly another intersubgeneric hybrid; see there). *A. doctorensis* also has these intermediate ‘racemose-paniculate’ inflorescences and possibly represents the hybrid between the sympatric *A. americana* (Subgen. *Agave*) and *A. funkiana* (Subgen. *Littaea*).

**A. dolichantha** Thiede & Eggli (Kakt. and Sukk. 50(5): 111, 1999). **Type** [syn]: Mexico, Jalisco (*Rose & Hay* 6290 [US, GH, NY, P]). — **Lit**: *Rose* (1903a: 10); *McVaugh* (1989: 253–254); *Cedano & al.* (1995); *Cházaro Basáñez & Machuca Núñez* (1995: with ill.); *García-Mendoza* (2003); *Cházaro Basáñez & al.* (2010b: with ill.); *Machuca Núñez & Cházaro Basáñez* (2015: with ill.); all as *Polianthes longiflora*. **Distr**: Mexico (Jalisco, Michoacán); wet meadows, in ill-drained clayish soils or at disturbed places, in pine/oak or tropical deciduous forests, 1400–2700 m; flowers July to August. **I**: *Feria-Arroyo & al.* (2010: 19); *Castro-Castro & al.* (2016: 721); *Castro-Castro* (2017: 137); all as *Polianthes longiflora*.

≡ *Polianthes longiflora* *Rose* (1903); **incl.** *Polianthes michoacana* *Cedano & al.* (1995) ≡ *Agave michoacana* (*Cedano & al.*) *Thiede & Eggli* (1999).

[3b1] Herbaceous; corm cylindrical, to 5.5 × 2.5 cm, with many spirally arranged, deltoid, white leaf scars; bulb ovoid to oblong, (2–) 3–5 × 1.3–1.8 (–2.5) cm, covered with fibrous dry leaf bases lacerate at the apex; **R** fibrous, white when young, turning brownish-grey with age; **L** (2–) 4–6 (–10), recurved, narrowly oblanceolate to linear, semi-amplexicaul, glabrous, apex acute, (14–) 26–37.5 × (0.2–) 0.4–1.6 cm, green, with purple dots near the base, upper ones appressed to ascending, linear, carinate, broadly acuminate, 12–18.5 × 0.6–1 cm, margins hyaline, papillose or denticulate, rarely entire; **Inf** erect, (14–) 30–70 cm, spike-like, fertile part with 2–5 (–8) floral nodes, internode length decreasing distally; **Ped** none; **Fl** geminate, fragrant, ± (75–) 85–120 mm; **Tep** white, pink, sometimes red with age, buds whitish to rose, tube erect or nearly so in the basal part, narrowly tubular, 2 mm Ø, gradually widening in the distal ½ or ⅓, there funnel-shaped, curved outwards at or above the middle, tube at the base or sometimes whole tube with purple to pink dots, (63–) 70–106 × 2–6 (–8) mm, mouth oblique, lobes (somewhat) extended or arched-reflexed; **OTep** oblong to ovate, attenuate towards the rounded apex, 15–27 × 6 mm; **ITep** lanceolate, fleshy, margins somewhat wavy, apex cucullate, with short white hairs, 12–27 × 3–8 mm; **Fil** filiform, white, 5.6–10 mm, inserted near the

mouth of the tube; **Anth** linear, (7–) 12–17 mm, apex scarcely surpassing the tube; **Ov** cylindrical, 7–10 × 2.5–5 mm; **Sty** filiform, 48–87 (–100) mm, included at anthesis, white; **Sti** 3-lobate, lobes oblong, internally ciliolate; **Fr** globose, (13–) 20–30 × 10–16 mm; **Se** semicircular, 4.4 × 3.1 mm, shiny or dull.

*Machuca Núñez & Cházaro Basáñez* (2015) report 22 populations from 16 municipios in Jalisco, and in addition known from 3 populations in Michoacán. Since its description by *Rose* (1903a: 10), the species was long known only from incomplete specimens offered for sale as cut flowers (*McVaugh* 1989: 253) until its recent discovery in the wild at several localities in Jalisco (*Cedano & al.* 1995, *Cházaro Basáñez & Machuca Núñez* 1995). *Cedano & al.* (1995) published similar plants from Michoacán as *Polianthes michoacana*, but its differences fall within the range of variability in *A. dolichantha* so that the populations from Michoacán were included in the latter (*García-Mendoza* 2003, *Cházaro Basáñez & al.* 2010b, *Feria-Arroyo & al.* 2010, *Castro-Castro & al.* 2016: 722; all as *Polianthes longiflora*). *A. dolichantha* is locally harvested for the cut-flower trade; its habitats are threatened by grazing (*Cházaro Basáñez & al.* 2010b, *Machuca Núñez & Cházaro Basáñez* 2015, both as *P. longiflora*). The geographical distribution, niche modelling and extinction risk of the species are dealt with by *Solano & Feria* (2007) and *Feria-Arroyo & al.* (2010). — The “holotype” at US consists of 2 sheets which are not cross-labelled and thus represent syntypes; US 396106 is the true species, whereas US 396105 is *Polianthes sessiliflora* (here treated as *A. apedicellata*) according to a label by E. Solano C. placed on the specimen in the year 2000 (see also *McVaugh* 1989: 254). — When placed in *Agave*, a new name was necessary to avoid homonymy with *A. longiflora* (*Rose*) G. D. Rowley (1977).

**A. durangensis** *Gentry* (*Agaves Cont. North Amer.*, 433–436, ill., 1982). **Type**: Mexico, Durango (*Gentry & Gilly* 10576 [US, ARIZ, MEXU, MICH]). — **Lit**: *Cházaro Basáñez & Vázquez-García* (2006: with ill.); *Vázquez-García & al.* (2007b: 51–52, t. H); *González-*

Elizondo & al. (2009: 65–68, with ills.); Almaraz-Abarca & al. (2013b: genetic variability). **Distr:** Mexico (S Durango, N & C Zacatecas); rocky slopes and gravelly bajadas in grama grasslands, pine-oak or sometimes tropical deciduous forests, 1700–2600 m; flowers April to July, also in November. **I:** Etter & Kristen (2007b: 177); Klopper & al. (2010: 60); Richter (2011: 52); Pilbeam (2013: 77); Hochstätter (2015: IV: 8).

[2h] Stems short; **Ros** (0.6–) 0.8–1.2 (–1.8) × (0.7–) 1.2–1.8 (–3.1) m, solitary or caespitose; **L** broadly lanceolate, narrowed above the broad base, widest in the middle, straight to outcurving, flat to concave esp. towards the apex, thick and convex towards the base, asperous, mostly 40–90 (–130) × 14–22 cm, glaucous-grey, pruinose, margins heavily armed, deeply crenate-mamillate; **marginal teeth** variously curved, prominent, broadly flattened, 10–20 mm, generally 10–20 mm apart; **terminal Sp** strong, broadly channelled above, (30–) 40–60 mm, pruinose-grey over brown; **Inf** 7–8 m, paniculate, peduncle short, with scarious remote reflexed **Bra** 15–25 cm long, fertile part long, lax, axis flexuous or zig-zag, part-**Inf** 18–30, sinuously spreading, trifurcate, small, in the upper  $\frac{3}{4}$  of the inflorescence; **Fl** 60–80 mm; **Tep** yellow, tube cylindrical, broad and fleshy, lightly grooved, 15–22 × 12–17 mm, lobes strictly appressed to the filaments, becoming leathery, unequal; **OTep** larger, 10–12 mm, thickly rounded on the back and overlapping the inner, apex conspicuously papillate, almost horny, reddish; **ITep** smaller, sharply keeled; **Fil** somewhat flattened, 48–60 mm, inserted at 2 levels 8–12 and 6–10 mm above the tube base; **Anth** 18–25 mm; **Ov** 30–45 mm (incl. the unconstricted neck); **Sty** somewhat longer than the tepals; **Sti** capitate; **Fr** oblong, 45–60 × 16–18 mm, rounded and shortly beaked, obscurely stipitate; **Se** small, crescent-shaped to obovate or tear-shaped, 4.5–6 × 3.5–5 mm, with a broad but little raised rim wing.

Distinguished by the large, rigid, broadly lanceolate leaves heavily armed with flexuous teeth on deeply crenate margins, and the large, long, lax panicle with a flexuous or zigzag axis, a short peduncle, and without close relationship to other species of Sect. *Ditepalae* (as Group) according

to Gentry (1982). Vegetatively, it may be confused with the sympatric *A. scabra* of Sect. *Agave* (Gentry 1982: 436, as Group *Americanae*). *A. temacapulinensis*, also of Sect. *Ditepalae*, is very similar (see there).

*A. durangensis* is economically important for the mescal industry in Durango (Contreras-Hernández & al. 2016). Molecular studies of 3 natural populations found evidence for genetic differences between the populations, some incongruence between molecular data and morphology, and advanced diversification in 1 of the 3 populations (Almaraz-Abarca & al. 2013b). Seed morphology, germinability and phenolic profiles varied among 3 natural populations (Barriada-Bernal & al. 2013). Pollen and foliar phenol profiles indicate the presence of several chemotypes and allow the separation of the 2 studied populations (Almaraz-Abarca & al. 2009). The edible flowers of *A. durangensis* represent an important source of antioxidant flavonols (Barriada-Bernal & al. 2014). The arthropod communities associated with the species were studied by González-Castillo & al. (2011).

**A. eggersiana** Trelease (Mem. Nation. Acad. Sci. 11: 28, tt. 31–33, 1913). **Type:** US Virgin Islands, St. Croix (*Ricksecker* 282 [MO, US]). — **Lit:** Berger (1915: 220); Britton & Wilson (1923: 156); Proctor & Acevedo-Rodríguez (2005: 118); Chamorro & al. (2016: with ills.). **Distr:** US Virgin Islands (St. Croix); coastal cliffs and dry coastal shrubland, in open-canopy and open-understorey habitats exposed to full sun. **I:** Hochstätter (2015: VII: 60).

[2s] Acaulescent, not surculose; **L** numerous, narrowly lanceolate, nearly straight and erect, gradually acute, concave, mostly 120–200 × 10–15 cm, dull green, transiently slightly glaucous; **marginal teeth** straight or upcurved, narrowly triangular, 1–1.5 mm, usually 10 mm apart, with broadly lenticular blackish-brown base, intervening margin nearly straight, at first reddish; **terminal Sp** conically subulate, usually somewhat upcurved, often laterally compressed, smooth, 15–20 mm, brown, rather glossy, with slender dull-brown involute basal thickening to 3 × 10–15 mm, decurrent for its length or more and

dorsally intruded into the green leaf tissue; **Inf** 5–7 m, ‘paniculate’, peduncle with distant, deltate, spreading or reflexed **Bra**, fertile part densely flowered, part-**Inf** (slightly) ascending,  $\pm 25$ , freely bulbiferous, in the upper  $\frac{1}{4}$  of the inflorescence; **Ped** 20–25 mm; **Fl** 50–60 mm, pumpkin-scented; **Tep** deep yellow, tube broadly open, 5–7 mm, lobes 20–25  $\times$  5–8 mm; **Fil** 45–50 mm, inserted nearly in the throat; **Anth** not described; **Ov** oblong-fusiform, 20–30 mm; **Fr** and **Se** not produced.

For the typification, see Smith & Figueiredo (2014c: 233). Endemic to St. Croix in the US Virgin Islands where it now appears to be largely extinct in the wild, but persisting as relatively few cultivated plants on St. Croix as well as on St. Thomas (Proctor & Acevedo-Rodríguez 2005: 118). The species is threatened by the Agave Snout Weevil (*Scyphophorus acupunctatus*) recently reported from St. Croix; Chamorro & al. (2016) provide management recommendations.

In the first edition of this handbook, *A. eggersiana* was placed in the synonymy of *A. missionum* (the only other native *Agave* species on the US Virgin Islands) based on Álvarez de Zayas (1995), but it is here recognized as a distinct species following Proctor & Acevedo-Rodríguez (2005). *Agave missionum* differs from *A. eggersiana* by broader leaves and longer marginal teeth (Proctor & Acevedo-Rodríguez 2005: 117).

**A. ellemeetiana** K. Koch (Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 8: 103 [1. April], 1865). **Type** [neo]: Ex cult. (*Anonymus* s.n. [K 524804, K [524802 + 524803]]). — **Lit**: Gentry (1982: 94–97); Thiede (2014b); both with ills. **Distr**: Mexico (C Veracruz, N & W Oaxaca).

**Incl.** *Agave ellemeetiana* Regel (1865) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave ellemeetiana* Jacobi (1865) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave ellemeetiana* [?] *obovata* Hort. Sutherland (1875) (*nom. inval.*, ICN Art. 38.1a).

*A. ellemeetiana* was previously ascribed to Jacobi (Hamburg. Gart.- & Blumenzeit. 21: 457, 1865), but was first published as cited above (Thiede 2014b). Ullrich’s (1991k) notion that the species might possibly represent hardly more than

a garden clone of *A. attenuata* ssp. *dentata* (as *A. pedunculifera*) must be dismissed. *A. ellemeetiana* differs from *A. attenuata* esp. in its nearly stemless habit with even fewer, bright green leaves, and its eastern distribution. For the history, rediscovery, distribution and habitats of the species, see Thiede (2014b).

**A. ellemeetiana** ssp. **ellemeetiana** — **Lit**: Berger (1915: 125–126); Gentry (1982: 94–97); Alsemgeest (2004); Cházaro Basáñez & al. (2012); Thiede (2014b); all with ills. **Distr**: Mexico (C Veracruz, N Oaxaca); on often near-vertical cliffs and rock-faces, in cloud or tropical subdeciduous forests, in the cloud belt, rarely epiphytic, 400–1460 m; flowers February to May. **I**: Refug. Bot. 3: t. 163, 1869; Baker (1888b); Heller (2006: 83); Richter (2011: 62); Hochstätter (2015: VIII: 36); Castillo-Hernández & Flores-Olvera (2017: 541, as *A. gomezpompae*).

[1c] Stems nearly none; **Ros** open, 0.35–0.5  $\times$  0.7–1 m, surculose; **L** rather few, ovate to oblong, somewhat recurved, reclining at maturity, thickly soft-succulent, widest in the middle, acuminate, flat beyond the thick base, concave to flat above, smooth, 50–70  $\times$  12–20 cm, light bright green, margins thin, friable, smooth, unarmed, white, sometimes reddish, sometimes finely serrulate towards the leaf tip; **terminal Sp** none, but leaf tip shortly acuminate and slightly calloused; **Inf** erect, 3–4.5 m, ‘spicate’, peduncle with ovate caudate-acuminate **Bra** 8–10 cm long, fertile part densely flowered from near the base, part-**Inf** usually with 4 flowers; **Ped** united in pairs, 15–20 mm; **Fl** campanulate, 28–40 mm; **Tep** pale greenish-yellow, tube very short, 1–2 mm, lobes lanceolate, concave, somewhat hooded at the tip, 13–15  $\times$  5 mm, inner somewhat wider; **Fil** long exerted, 50–60 mm, inserted on the rim of the tube together with the lobes; **Anth** 10–12 mm, yellow; **Ov** bottle-shaped, 13–20 mm, neck conspicuously elongate; **Sty** slender, as long as the filaments; **Sti** thickened; **Fr** trigonous, rounded at the base, 13–15  $\times$  10 mm, light brown, beaked; **Se** numerous, 3 mm, black, shiny.

Introduced into cultivation from Mexico in 1862 or before, and persisting in cultivation esp. in Europe up to the present. Its natural habitats



**Fig. 23** *Agave ellemetiana* ssp. *subdentata* (Etter & Kristen 3905: Mexico; Oaxaca, ± 10 km S of Yosonicaje, 2320 m). (Copyright: J. Etter & M. Kristen)



remained unknown until the recent past. At present, ssp. *ellemetiana* is known from 3 areas in the Sierra Madre Oriental of C Veracruz and NE Oaxaca (Thiede 2014b), namely from the Sierra de Zongolica in C Veracruz (Cházaro Basáñez & al. 2012), and in N Oaxaca from the Sierra Mazateca (= Sierra de Huautla) (Lorea Hernández & Munn-Estrada 2005) and from near San Bartolomé Ayautla where it was first observed by A. B. Lau (Ullrich 2007: fig. 6, as “*A. attenuata*?”).

**A. ellemetiana** ssp. *subdentata* (Trelease) Thiede (Bradleya 32: 157, 2014). **Type** [neo]: Mexico, Oaxaca (*Spath & Griffin* s.n. [ZSS]). — **Lit**: Köhres (2008: with ill., as *A. ellemetiana*). **Dist**: Mexico (W Oaxaca: Putla/Tlaxiaco/Santiago Nuyoó area); volcanic rocks in cloud or tropical subdeciduous forests, 2300–2600 m; flowers in January. **I**: Pilbeam (2013: 78, as *A. ellemetiana*); Hochstätter (2015: VIII. 37). — Fig. 23.

≡ *Agave ellemetiana* var. *subdentata* Trellease (1914).

[1c] Differs from ssp. *ellemetiana*: **L** margins whitish or reddish, finely but clearly denticulate throughout; **L** of adult plants have a wax bloom absent from ssp. *ellemetiana* and appear to be partly broader, but measurements are not available (Thiede 2014b).

Köhres (2008) reported plants of *A. ellemetiana* from the W slopes of the Sierra Madre del Sur in Oaxaca above Santiago Nuyoó, and

published the first habitat photographs of it. Since these plants differ from typical *A. ellemetiana* by leaf margins being finely denticulate throughout, Thiede (2014b) re-established the forgotten name var. *subdentata* Trellease (described as having the “leaves very minutely denticulate”) at subspecific rank. Localities of the subspecies in the Putla/Tlaxiaco/Santiago Nuyoó area were also visited by other collectors, and plants belonging here are commercially offered in the USA and Europe. A preliminary investigation using AFLP data placed material from Putla probably belonging to ssp. *subdentata* separate from *A. ellemetiana* (Gil-Vega & al. 2007: as *A. aff. pedunculifera*). Further studies are needed to establish the status of ssp. *subdentata* and its differences from ssp. *ellemetiana*.

**A. × engelmannii** Trellease *pro sp.* (Annual Rep. Missouri Bot. Gard. 3: 167, tt. 55–56, 1892). **Type**: Ex cult. Missouri BG (*Anonymous* s.n. [K [2 sheets, cross-labelled]]). — **Lit**: Anonymous (1892: 398); Berger (1915: 184–185); both as *A. engelmannii*. **Dist**: Cultivated only.

**Incl.** *Agave attenuata* var. *subdentata* Hort. Hoopes *ex* Trellease (1892) (*nom. inval.*, ICN Art. 38.1a).

[1b? × 2] Raised from seed by J. Hoopes and flowered and fruited at the Missouri Botanical Garden 1890–1891. Seedlings from Missouri flowered later at La Mortola and were described

by Berger (1915). Placed close to *A. horrida* ssp. *perotensis* (as “*A. polyacantha*”) by Trelease (1920: 135) and in the synonymy of that species by Gentry (1982: 228). With inflorescences intermediate between the subgenera, with distinctly stalked part-inflorescences with up to 7 flowers (protologue t. 55, sheet K 001096501!) and thus obviously of intersubgeneric hybrid origin involving a species of Subgen. *Littaea* (possibly *A. attenuata*) and one of Subgen. *Agave*.

**A. ensifera** Jacobi (Nachtr. Versuch syst. Glied. Agaveen 1: 13–14, 1868). **Type** [neo]: Ex cult. La Mortola (*Berger* s.n. [US 1023791]). — **Lit:** Baker (1877a: 369, with ill., as *A. heteracantha*); Berger (1915: 99); Gentry (1982: 139); Meer & Puche (2014: as *A. univittata* var. *ensifera*, *A. lophantha* var. *latifolia* and *A. heteracantha*). **Distr:** Known from cultivation only. **I:** Roosbroeck (2014); Hochstätter (2015: VII: 29).

≡ *Agave univittata* var. *ensifera* (Jacobi) P. Van der Meer & C. Puche (2014); **incl.** *Agave heteracantha* Baker (1877) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave lophantha* var. *latifolia* A. Berger (1915) ≡ *Agave univittata* var. *latifolia* (A. Berger) Breitung (1959).

[lg] **Ros** dense, caespitose; **L** linear-lanceolate, ensiform, leathery-fleshy, strongly convex below and above, upwards becoming concave to the apex, at the base 1.5–1.7 cm thick, smooth, 50–60 × 4–5 (3.8–4 near the base) cm, dark green with a distinct light longitudinal central stripe 5–7 mm wide up to the middle, margins with a narrow grey border 0.5–1 mm wide; **marginal teeth** mostly antrorsely curved, 4–6 mm, light grey, closely set, 10–20 mm apart, mostly with broad bases, interspersed with smaller teeth, altogether 30–40 teeth per leaf side; **terminal Sp** short, basal groove above short and opening broadly with decurrent border, 10–15 mm, brown to grey; **Inf** 2–2.5 m, ‘spicate’, peduncle with deflected subulate **Bra** 6–10 cm long, part-**Inf** mostly with geminate flowers; **Ped** 2–3 mm; **Fl** 35–42 mm; **Te** light green, tube open, short, 2–3 mm, lobes linear, involute around the filaments at anthesis, subequal, 14–17 mm, light yellowish, outer overlapping the inner at the base; **Fil** slender, 40–45 mm, inserted on the tube rim;

**Anth** 16 mm, yellow; **Ov** 20–24 mm, neck constricted, ±3 mm; **Sty** whitish, equalling the anthers; **Fr** and **Se** unknown.

Of unknown origin and commonly cultivated along the Mediterranean Riviera at Berger’s time; apparently related to the *A. lechuguilla* – *A. difformis* group and recognized specifically by its long narrow leaves with numerous teeth of 2 sizes regularly spaced along the narrow margins, and the short, mostly weak terminal spine (Gentry 1982: 139). Meer & Puche (2014) classified the plant as *A. univittata* var. *ensifera*, but the name *A. univittata* var. *latifolia* (A. Berger) Breitung would take priority. The plants depicted as *A. lophantha* var. *latifolia* by Guillot Ortiz & Meer (2012: 33) and as *A. univittata* var. *ensifera*, *A. lophantha* var. *latifolia* and *A. heteracantha* by Meer & Puche (2014: 59–62, 64) have lanceolate leaves with teeth on distinct prominences and are most probably misidentified.

Gentry (1982: 139) selected two specimens of Berger (Château Grimaldi, *Berger* s.n., 19. 6. 1909, US 1023791 & 1023763) as “lectotype”, but since Jacobi did not cite any material, this is interpreted as first-step neotypification (ICN Art. 9.17) as they are not cross-labelled. Meer & Puche (2014: 59) designated US 1023791 as “lectotypus” (but actually representing a neotype), and US 1023763 as well as a third specimen (*Berger* s.n., 19. 6. 1909, ARIZ 268297) as “isolectotype”. These specimens are both not cross-labelled and are thus interpreted to represent different gatherings and not isoneotypes.

**A. evadens** Trelease (Mem. Nation. Acad. Sci. 11: 20–21, tt. 9–10, 116, 1913). **Type:** Trinidad (*Crueger* 1333 [B †, K 000524793, MO, NY, U, UPS, US]). — **Lit:** Berger (1915: 225); Britton & Wilson (1923: 157); Hummelinck (1938: 23–24). **Distr:** Trinidad (along the coast and on Isla de Chacachacare and Isla Monos), Venezuela (Isla de Patos); littoral deciduous seasonal forests; flowers in March. **I:** Richter (2011: 97); Hochstätter (2015: VII: 41).

**Incl.** *Agave polyacantha* Baker (1888) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave vivipara* Hart (1890) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave polyantha* Dodge (1897).



[2u] **Ros** shortly caulescent, not surculose; **L** narrowly oblanceolate, gradually acute, openly concave or somewhat conduplicate, or with inrolled margins above, 70–100 cm, green, margins almost straight; **marginal teeth** small, on low broadly conical prominences, 0.5–1.5 mm, 6–15 mm apart, margins between the teeth convex; **terminal Sp** conical, straight or somewhat recurved, slightly involute at the base, 10–14 × 2–3 mm, slightly or not decurrent; **Inf** paniculate, fertile part lax, slender, part-**Inf** few, ascending, tripartite, not known to be bulbiferous; **Ped** rather slender, (6–) 8–10 (–12) mm; **Fl** 47–55 mm; **Tep** bright yellow, tube open, 2–3.5 mm, lobes 19–25 × 4 mm; **Fil** 35–42 mm, inserted 0–0.5 mm below the tube throat; **Anth** 17–25 mm; **Ov** oblong-fusiform, 22–25 × 3–4 mm; **Sty** 32–38 mm; **Fr** broadly ellipsoid, 30–34 × 20–24 mm, slightly beaked, distinctly stipitate; **Se** D-shaped, angled, 6–8 × 4–6 mm, shiny black.

According to the protologue intermediate in foliage between *A. cocui* and *A. boldinghiana* and known to Trelease from photographs and dissociated flowers only. If the name *A. polyantha* Dodge really proves to be conspecific, it would have priority.

The characters regarded in the protologue as most important were taken by Trelease from his plate 9: Shortly caulescent, leaves narrowly oblanceolate, inflorescence laxly paniced at the end with few ascending branches. Hummelinck (1938: 24) assumed that these data have no value: the short stem appears to result from the bases of the plants being washed free, the narrowly oblanceolate leaves may be due to external circumstances, and the laxly paniced inflorescence may result from the great reduction of the picture which made flowerless branches invisible.

Apart from Trinidad (main island), *A. evadens* is also reported from Isla de Chacachacare (Hummelinck 1938: 23, Adams & Baksh-Comeau 2005: 9) and Isla Monos (Chalmers 1965) and from Isla de Patos (Williams 1924: 278), which since 1942 belongs to Venezuela. Preserved flowers from Isla Margarita (Venezuela) placed here with reservation by Trelease may belong to *A. cocui* or *A. vicina* (as *A. vivipara*; Hummelinck (1938)). Material from Puerto Santo (Venezuela)

“may possibly belong to *A. evadens*” (Hummelinck 1938: 24). Several specimens from the Venezuelan mainland placed here (*Pittier* 10238, US 1187053; *Steyermark* 107981, US 2706466; *Steyermark* 108044, US 2706464) need verification. The species was (is?) cultivated on St. Thomas (US Virgin Islands; Britton & Wilson (1923: 157)). Baksh-Comeau & al. (2016: 33) assign the species to the IUCN category “Vulnerable”.

**A. felgeri** Gentry (US Dept. Agric. Handb. 399: 60–62, ills., 1972). **Type:** Mexico, Sonora (*Gentry* 11343 [US, ARIZ, MEXU, MICH]). — **Lit:** Gentry (1982: 107–110, with ills.); Ullrich (1991j; with ills.); Turner & al. (1995); Smith & Figueiredo (2014b: with ills.). **Dist:** Mexico (Sonora, esp. Bahía San Carlos); arid desert lowlands and rocky hillsides near the coast, to 200 m; flowers May to August, also October and December. **I:** Richter (2011: 63); Pilbeam (2013: 79); Hochstätter (2015: VIII: 45).

[1d] **Ros** small, rather open, 20–50 cm Ø, surculose, forming rather densely caespitose groups; **L** rather few, erect to rigidly spreading, linear to narrowly lanceolate, straight or falcate, widest at the amplexicaul base, convex below, flat above in the lower ¼, concave in the upper ¾, epidermis rugose or scabrous above, 25–35 × 0.7–1.5 cm, matt light green to yellow-green, turning light yellow during and after flowering, with faint imprints from the central bud, frequently with pale median longitudinal stripe, margins with weakly filiferous narrow brown border, smooth, threads ± absent from older leaves; **terminal Sp** weak, small, slightly grooved at the base, 6–15 mm, grey or dark brown; **Inf** 1.2–2.5 m, ‘spicate’, peduncle light green, 7–15 mm Ø near the base, with chartaceous laxly arranged **Bra**, the lower very narrow and 2–3 cm, fertile part in the upper ¼, part-**Inf** with 1–2 flowers; **Ped** strong, 2–5 mm; **Fil** 25–30 mm; **Tep** light green, lateral sections creamy-white, the very margins purple, tube 2–4 mm, lobes linear, ± equal, 10–12 × 3–4 mm, strongly recurved to rolled back during the male phase, less so and straight with the onset of the female phase; **Fil** 20–25 mm, light shiny pinkish-purple, inserted 2 mm above the tube

base; **Anth** 8–9 mm, dull yellow; **Ov** terete, 12–14 × 4–5 mm, abruptly tapering apically, neck distinctly constricted; **Sty** stout, terete, 30–35 mm, light green; **Sti** prominent, white; **Fr** oblong, cylindrical or obovoid to globose, narrowed towards the base, 15–20 × 9–14 mm, distinctly beaked, light green to yellowish-green; **Se** irregular, thick, D-shaped, angled, wrinkled, hilar notch narrow and deep, 4–5 × 3 mm. — **Cytology**:  $n = 30$  (Baker & al. 2009).

Very similar to *A. schottii* from Sect. *Parviflorae* in vegetative features, but placed in Sect. *Littaea* (as Group *Filiferae*) due to its open shallow flower tube and long lobes, in which it occupies the most arid habitats. The type locality was destroyed for recreational development (Gentry 1982). Additional data on the reproductive morphology and phenology were provided by Smith & Figueiredo (2014b). Geographically it is closest to the broad-flowered form of *A. schidigera* which forms a more robust non-suckering colony on the Cerros del Fuerte in N Sinaloa (Gentry 1982). Ullrich (1991j) emphasizes vegetative and geographical criteria and suggests a placement in Sect. *Parviflorae* (as Group), but this is not followed here.

**A. filifera** Salm-Dyck (Hort. Dyck., 309, 1834). **Type**: [neo — icono]: Ill. Hort. 7(4): t. 243, 1860. — **Lit**: Berger (1915: 73–74); Gentry (1982: 110–111); Vázquez-García & al. (2007a: 51–52, t. I); Starr (2012: 90–93, 317–319); all with ill. except Berger. **Distr**: Mexico (Aguascalientes, Jalisco, Guanajuato, Querétaro, Hidalgo, México); on rocks, in desert scrub, thorn, oak and oak-juniper forests, 2340–3100 m; flowers June to September. **I**: Heller (2006: 84); Richter (2011: 63); Pilbeam (2013: 80, as ssp. *filifera*); Hochstätter (2015: IX: 30).

**Incl.** *Agave filifera* ssp. *filifera*; **incl.** *Agave filamentosa* Salm-Dyck (1859) ≡ *Bonapartea filamentosa* (Salm-Dyck) Boucén (1868) (*incorrect name*, ICN Art. 11.4) ≡ *Agave filifera* var. *filamentosa* (Salm-Dyck) Baker (1877); **incl.** *Agave filifera* var. *superba* J. Croucher ex R. Hogg (1874); **incl.** *Agave pseudofilifera* Ross & Lanza (1892); **incl.** *Agave filifera* var. *candida superba* Hort. Besaucèle ex A. Berger (1915)

(*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave filifera* var. *elatio*r Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave filifera* var. *immaculata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave filifera* var. *longifolia* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave filifera* var. *mediopicta* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave filifera* var. *splendens* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave filifera* var. *viridis* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[1d] **Ros** small, green, dense, surculose, forming large clumps; **L** many, lanceolate, straight, thick, broadest in the middle, acuminate, thickened and convex above and below from the base to the middle, smooth, 15–30 × (1–) 2–4 cm, green, with white imprints from the central bud, margins finely filiferous; **terminal Sp** flat above, rounded below, 10–20 mm, greyish; **Inf** 2–2.5 m, ‘spicate’, peduncle densely covered with long-caudate recurving **Bra**, fertile part tall, in the upper ½ of the inflorescence, tapering, densely flowered; **Ped** short, thick; **Fl** mostly geminate, 30–35 mm, ascending-outcurving; **Tep** reddish, tube funnel-shaped, furrowed, 5–6 × 8 mm, mouth bulging at the filament insertions, lobes recurving, lanceolate, apiculate, equal, 14 × 4 mm, inner a little wider, with prominent keel; **Fil** slender, 30–35 mm, reddish, inserted on the tube rim; **Anth** centric, 7–12 mm, reddish; **Ov** fusiform, angled, 13–15 mm, neck furrowed; **Sty** strong, longer than the filaments; **Sti** 3-lobate; **Fr** oblong-ellipsoid to oblong-obovoid, acute, 15–17 × 12 mm; **Se** semicrescent-shaped. — **Cytology**:  $2n = 60$  (Cave 1964, Simpson & al. 2011).

Separable from the closely related *A. schidigera* by its caespitose habit, smaller rosettes, shorter and thicker leaves, and smaller reddish-purple flowers with a shorter tube (Gentry 1982, Starr 2012). Ullrich (1992h) reduced *A. schidigera* and *A. multifilifera* to subspecies of *A. filifera*, but was not followed by Vázquez-García & al. (2007b), Starr (2012) and Govaerts (2014+: accessed April 2014). The species was recently recorded from E Jalisco (Hernández-Vera & al. 2007a). A record

from C Zacatecas (Ramírez Prieto 2014: 54) may refer to *A. schidigera*.

**A. flexispina** Trelease (Contr. US Nation. Herb. 23: 133, 1920). **Type** [syn]: Mexico, Durango (Palmer 330 [MO, US, CM, GH, K, NY, UC]). — **Lit:** Gentry (1982: 436–438); González-Elizondo & al. (2009: 77–79); Klopper & al. (2010: 58, 60–61); Alsemgeest & Roosbroeck (2010: 68–70); all with ills. **Distr:** Mexico (S Chihuahua, N Durango, Zacatecas, N Nayarit); rocky slopes and hillsides, in grama or oak-juniper grasslands and oak woodlands, 1300–2440 m; flowers July, October and November. **I:** Breitung (1963: 121, right-hand figure); Pilbeam (2013: 84); Ettelt (2014: 124); Hochstätter (2015: IV: 9).

[2h] **Ros** open, small, 25–35 (–45) × 50–70 cm, solitary or caespitose; **L** 35–40, ovate, acuminate, nearly flat to concave above, 16–30 × 6–8 (–12.7) cm, glaucous- to yellowish-green, margins repand to crenate; **marginal teeth** mostly retrorse, larger teeth mostly 5–8 mm, brown to pruinose, 10–15 mm apart, on small prominences, sometimes with small intermittent teeth; **terminal Sp** acicular, usually flexuous, flat to openly grooved near the base, 25–35 mm, brown to pruinose-grey, decurrent to the upper teeth; **Inf** 2–3.5 m, paniculate, peduncle with small, dry, appressed, hardly persistent **Bra**, fertile part slender, rather open, frequently narrow, part-**Inf** small, 6–12 (–16), few-flowered; **Ped** nearly none; **Fl** 50–70 mm; **Tep** greenish-yellow, with red tinge on buds and lobes, tube cylindrical to urceolate, bulging in the middle, slightly or narrowly grooved, 10–18 mm, lobes lanceolate to linear, broad, broadly rounded at the apex, unequal, outer larger, strongly overlapping the inner, 10–18 mm, persisting erect and drying leathery, inner with high narrow keel; **Fil** sometimes broadly flattened, 40–50 mm, with red tinge, inserted at one level, sometimes irregularly so; **Anth** 17–23 mm, yellow or bronze-coloured; **Ov** cylindrical, slightly angled, 22–35 mm, neck short, obscure; **Sty** longer than the filaments; **Sti** capitate, 3-lobate; **Fr** oblong, strongly trigonous, round at the apex, tardily dehiscent, 35–45 × 15–17 mm, abruptly stipitate; **Se** obovate to crescent-shaped, 5.5–7 × 4–5 mm, rim wing low.

In appearance like a small *A. shrevei* or *A. palmeri*, but differing in having the filaments inserted at a single level in the tube (vs. 2 distinct levels in the species mentioned, and indeed in most members of Sect. *Ditepalae*). Rosettes and inflorescences of *A. flexispina* are consistently smaller than normally found in other species of Sect. *Ditepalae* (as Group) (Gentry 1982). The holotype is at MO according to the protologue, but the 2 sheets (MO 3346761, leaves; MO 3346762, inflorescence) are not cross-labelled and represent syntypes (Smith & Figueiredo 2014c: 234). The specimen *Flores F. & al.* 2079 (MEXU 520551!) provides a new record from Nayarit.

The left-hand figure in Breitung (1963: 121) is incorrectly labelled and represents *A. parryi* var. *truncata* (Alsemgeest & Roosbroeck 2010: 69).

**A. fortiflora** Gentry (US Dept. Agric. Handb. 399: 122–126, ills., 1972). **Type:** Mexico, Sonora (Gentry 19808 [US, ARIZ, DES, MEXU]). — **Lit:** Gentry (1982: 421, 438–440, with ills.); Klopper & al. (2010: 61). **Distr:** Mexico (NW Sonora); on isolated mountain ranges, mostly on volcanic rocks or also on limestone ridges, in desert scrub; flowers in cultivation (California) June to July. **I:** Heller (2006: 85); Pilbeam (2013: 85).

[2h] **Ros** open, to 1 × 1.8 m, mostly solitary, occasionally suckering; **L** straightly ascending or outcurving and conduplicate, long-acuminate, gradually narrowed above the dilated base, widest in the middle, finely tuberculate-rugose (incl. teeth and terminal spine), to 50–100 × 8–12 cm, light grey-glaucous, usually cross-zoned, margins straight or teeth in the middle of the lamina on small prominences; **marginal teeth** curved downwards or erect, 5–10 mm (middle of the lamina), 10–30 mm apart, smaller and variously flexed above and below the middle, with irregularly arranged smaller intermittent teeth; **terminal Sp** subulate, rounded below, narrowly grooved above, 30–50 mm, chestnut-brown to light grey, decurrent along the margin to the uppermost teeth; **Inf** 4–6 m, paniculate, peduncle with short, triangular, chartaceous **Bra** 5–6 cm long at the lower branches, fertile part open and long-ovoid, part-**Inf** nearly horizontal, 8–15, densely 12-

18-flowered; **Ped** 4–20 mm; **Fl** long-lived, 72–82 mm; **Tep** yellow, tube broadly bulging, sinuses overlapping and deeply grooved below, 11–13 × 18–20 mm, pale yellow, lobes erect, 20–23 × 7–8 mm, yellow, outer rounded, linear-lanceolate, with an involute margin, obtuse, inner with high narrow keel and involute hyaline margins, broadly hooded at the tip; **Fil** strong, elliptic in cross section, 60 mm, persisting erect after anthesis; **Anth** centrally affixed, 20–22 mm, yellow; **Ov** 45–50 mm, pale green, conspicuously angled below the outer tepals; **Sty** finally to slightly shorter than the filaments; **Sti** capitate, 3-lobed; **Fr** and **Se** unknown.

The species is highly distinct in its floral morphology: The large flowers are sturdy (hence the name), and long-lasting, persisting erect for long after anthesis, and the flattening of the filaments is extreme, making them almost strap-shaped and quite the broadest in the genus. With these features, *A. fortiflora* does not show relations to other species of Sect. *Ditepalae* (as Group), but the erect tepal lobes dry in the same way as found in other species of the section (Gentry 1982).

Plants from near Bahía San Carlos (Sonora) placed here in the protologue (Gentry 1972: 124, 125: upper photo) (Gentry & Arguelles 19881, Felger & Russell 11455) belong to *A. colorata* (Gentry 1982: 432–433, Starr 2012: 79). — The species is very rare, known only from the Sierra Jojoba and the Sierrita de López, and has apparently not been recollected since Gentry, but Kristen & Etter (photograph in Pilbeam (2013)) recently visited the habitat. Photographs from Nacapule Canyon labelled *A. aff. fortiflora* in Greulich (2017b) appear to represent *A. chrysoglossa* (on p. 40) and *A. colorata* (on p. 46).

**A. fourcroydes** Lemaire (Ill. Hort. 11(Misc.): 65, 1864). **Type:** not typified. — **Lit:** Berger (1915: 238–240, with ill.); Gentry (1972: 138–139); Gentry (1982: 573–576, with ill.); Lott & García-Mendoza (1994: online version with ill.). **Distr:** Cultivated only; mainly E Mexico; locally naturalized in the Caribbean, Costa Rica, and the Mediterranean. **I:** Curtis’s Bot. Mag. 144: t. 8746, 1918; Heller (2006: 86);

Sánchez Gullón (2013: 51); Hochstätter (2015: VII: 42).

**Incl.** *Agave rigida* var. *longifolia* Engelmann (1875); **incl.** *Agave ixtli* var. *elongata* Baker (1877) ≡ *Agave rigida* var. *elongata* (Baker) Baker (1881) ≡ *Agave elongata* (Baker) A. Berger (1912) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave longifolia* hort. ex A. Berger (1915); **incl.** *Agave ixtli* hort. ex A. Berger (1915) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave sullivanii* Trelease (1920); **incl.** *Agave fourcroydes* var. *espiculata* L. H. Dewey (1929).

[2g] Stems thick, 1–2 × ±0.25 m; **Ros** large, suckering; **L** straight, linear, rigid, sword-like, thickly rounded at the base, acuminate, guttered, 120–180 (–250) × 7–12 cm, grey-green, margins straight; **marginal teeth** slender, 3–6 mm, dark brown, regularly spaced, 20–35 mm apart; **terminal Sp** conical, stout, openly short-grooved above at the base, mostly 20–30 mm, dark brown, somewhat decurrent; **Inf** 4–7 m, paniculate, part-**Inf** 10–18 in the upper ½, freely bulbiferous; **Fl** (50–) 60–70 mm; **Tep** greenish-yellow, tube urceolate, thick-walled, grooved, 12–16 × 12–15 mm, lobes linear, at first erect then sharply reflexing, closely overlapping, subequal, 16–18 × 3–5 mm, outer with flat outer face, inner keeled; **Fil** stout, tapered towards the apex, 45–60 mm, inserted 6–8 mm above the tube bottom; **Anth** slender, excentric, 20–24 mm, pale yellow; **Ov** fusiform, roundly-trigonous, tapered towards the base, (20–) 30–40 mm, neck briefly constricted; **Sty** stout, clearly longer than the tepals; **Sti** capitate, 3-lobate; **Fr** and **Se** normally not produced, **Fr** elongate-clavate, obtusely triangular, 3-sulcate, shortly stipitate, acutely rostrate; **Se** nearly crescent-shaped, 9–10 mm. — **Cytology:** 2n = 60, 90, 138, ±140, 150 (Doughty 1936, Castorena Sanchez & al. 1991, Lv & al. 2009, Simpson & al. 2011), in cultivars 2n = 90, 150 (Robert & al. 2008).

Widely cultivated for fibre (“Henequén”) esp. in E Mexico and Yucatán (Gentry 1982), but also used to produce an alcoholic beverage similar to mescal marketed under the registered trademark “sisal” (Larqué Saavedra 2007). The origin of *A. fourcroydes* is in Yucatán according to Lott & García-Mendoza (1994). The different cultivars subsumed under *A. fourcroydes* show different

degrees of similarity with its wild progenitor *A. angustifolia*. ‘Sac Ki’ and ‘Yaax Ki’, cultivated for cordage, show four syndromes of domestication: gigantism, greater fibrosity, less pronounced thorniness, and less reproductive capacity (Colunga-García Marín & al. 1996, Colunga-García Marín & May-Pat 1997). The major differences of *A. fourcroydes* from its wild progenitor *A. angustifolia* (thicker and longer stems, longer and broader leaves, and its sterility) reflect these domestication syndromes.

Morphological data (Colunga-García Marín & al. 1999) and combined morphological/molecular isozyme data (Colunga-García Marín 2003) indicated *A. fourcroydes* to represent a polyphyletic assemblage of different cultivars independently derived from within the variable *A. angustifolia*. However, with molecular AFLP data, several cultivars as well as variants of the progenitor species *A. angustifolia* (see there) cluster independently, so that Infante (2006) suggest the need for a revised classification. *A. fourcroydes* normally does not produce seeds and is only asexually propagated via rhizomes for plantation use, according to most authors. The sole descriptions of fruit and seed are given by Berger (1915) and Berger (1918). Offsets of a given mother plant are genetically variable so that selection of special genotypes for the improvement of Henequén is possible (Infante & al. 2003).

Locally naturalized in the Caribbean (Cayman Islands, Cuba, Dominican Republic, Haiti, Leeward Islands), Costa Rica, Italy (Govaerts 2014+), Spain (Sánchez Gullón 2013), the Balearic Islands (Sáez & al. 2016) and the Canary Islands (Acebes Ginovés & al. 2010).

**A. franzosinii** (Sprenger) Sewell (Gard. Chron., ser. 3, 6: 639, 1889). **Type:** [neo — icono]: Curtis’s Bot. Mag. 136: t. 8317, 1910. — **Lit:** Baker (1892: with ills.); Berger (1915: 157–160, with ills.); Gentry (1982: 291–292, with ills.); Guillot Ortiz & al. (2008: 50–52); Thiede (2017b). **Distr:** Known from cultivation only; locally naturalized in Spain. **I:** Irish & Irish (2000: t. 17); Lyons (2002: 162); Heller (2006: 26, 87, 157, 159); Smith & Figueiredo (2008: 57); Richter (2011: 41, 70); Pilbeam (2013: 86);

Hochstätter (2015: VII: 82, as *A. beaulueriana*); Mesquida & al. (2016: 48–49); Moore (2016: 209, 233, 234).

≡ *Agave americana* var. *franzosinii* Sprenger (1885); **incl.** *Agave beaulueriana* Jacobi (1869).

[2a] **Ros** very large, 2–2.7 (–3) × to 4.5 m, freely suckering; **L** to ±40, lanceolate, widely spreading, recurved or sharply reflexed, narrowed at the base, thickened and convex below towards the base, guttered above, somewhat asperous, 180–220 × 22–35 cm, light glaucous-grey or bluish-glaucous variously marked with green below the middle of the lamina, margins straight to repand; larger **marginal teeth** (middle of the lamina) 8–10 mm, dark brown, remote, on fleshy prominences, sometimes with smaller intermittent teeth; **terminal Sp** with short open groove above, 30–60 mm, dark brown, decurrent along the inrolled leaf tip; **Inf** 8–11.4 m, paniculate, peduncle strong, fertile part broadly cylindrical, to 2.9 m broad, part-**Inf** broadly spreading, several times compound; **Fl** large, 83–100 mm; **Tep** yellow, soon withering, tube 18–22 mm, lobes 30–32 mm, outer linear, inner keeled on the back, grooved, with 2 ribs within; **Fil** stout, 65–80 mm, yellow, inserted at mid-tube; **Anth** 38–40 mm, yellow; **Ov** 35–45 × 10–13 mm, light bright green, neck slightly narrower; **Sty** stout, to 120 mm; **Sti** clavate, 3-lobed; **Fr** elongate-clavate, 55–70 mm; **Se** to 12 × 8–9 mm, black, shiny.

A very distinctive species not easily confused with, but obviously related to, *A. americana* (Gentry 1982), although it might be viewed as a larger version of the latter with greyish to glaucous leaves. The name is commonly ascribed to Baker (Bull. Misc. Inform. Kew 1892: 3, 1892), but was first mentioned by della Valle di Casanova (Garden [London, 1871–1927] 11: 63 (1877)) at the eponymous Villa Franzosini at the Lago Maggiore (Italy). The epithet was first published at varietal rank by Sprenger (in Deutsche Gärt.-Zeitung 9: 130, 1885), which has been overlooked so far. Howard (in Howard & Thompson-Mills (1979: 489)) first established that *A. franzosinii* is antedated by *A. beaulueriana*. To conserve the established *A. franzosinii* against *A. beaulueriana*, a formal proposal to conserve was published, together with notes on typification, by Thiede



(2017b). The species is naturalized in Spain (Guillot Ortiz & al. 2008, Sáez & al. 2014).

In the USA, two different “forms” are cultivated under this name: The typical form (e.g., at Lotusland), which is also propagated by tissue culture (Gomez Rhine 2009), and a clearly different, much smaller plant with stiffer leaves with more closely spaced teeth and a different colour, which is referable to *A. ×winteriana* (see there).

**A. funkiana** K. Koch & C. D. Bouché (Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 3: 47, 1860). **Type** [neo]: Mexico, Hidalgo (*Gentry* 12273 [[neo — syntypes]: ARIZ, MEXU, US]). — **Lit**: Berger (1915: 91); *Gentry* (1982: 139–141, with ills.); Guillot Ortiz & al. (2008: 51, 54, with ills.). **Distr**: Mexico (C Nuevo León, W & SW Tamaulipas, San Luis Potosí, N Querétaro, Hidalgo, SW México); rocky hillsides and slopes, in oak forests and mixed woodlands, 250–1800 m; flowers in August. **I**: Heller (2006: 88); Pilbeam (2013: 87); Hochstätter (2015: VII: 82).

[1g] Acaulescent; **Ros** open, 0.6–0.9 × 1.2–1.8 m, freely suckering; **L** linear, radiating, firm, straight or somewhat falcate, patulous, base broadly clasping, convexly thickened below, concave above, mostly 60–80 × 3.5–5.5 cm, yellowish-green to dark green, frequently with pale median stripe, margins horny, nearly straight, firm, thin, brown to grey; **marginal teeth** mostly directed downwards, regular, slender, 3–5 mm, 10–25 mm apart, with a few small irregularly arranged intermittent teeth; **terminal Sp** conical-subulate, with a narrow to open groove above, 10–30 mm, brown to white; **Inf** slender, 3.5–4.5 m, ‘spicate’, peduncle glaucous-grey, the small **Bra** apparently caducous, fertile part laxly flowered in the upper ½ of the inflorescence; **Ped** ±10 mm; **Fl** geminate, 40–45 mm; **Tep** pale glaucous-green, tube conspicuously grooved and knobby-angled, 3.5–4 mm, lobes linear, mucronate with a small hood, at first spreading to ascending, 18–19 mm, appressed and clasping the filaments after anthesis; **Fil** 30–35 mm, red or pink, inserted on the tube rim; **Anth** 20 mm, yellow with pink flush towards the tips; **Ov** oblong-fusiform, 20–24 mm, neck grooved,

constricted; **Sty** somewhat longer than the tepals, red; **Sti** capitate; **Fr** transversely wavy-ridged, strong-walled, 25–30 × 15 mm, light pruinose-grey, abruptly apiculate; **Se** thick, shape very variable, 5–6 × 3.5–4.5 mm, wavy-lined on the faces, hilar notch large.

The neotype cited above was designated by *Gentry* (1982: 140). Obviously related to *A. lophantha*, but differing in its larger size, regular and linear slightly concave leaves with nearly straight fine margins, and numerous regular fine teeth. The species is not well known in habitat, and the few individuals observed show little variation (*Gentry* 1982: 140). The specimens cited by *Gentry* (1982: 189) from Chiapas (*Gentry* 12195, DES, MEXU) belong to *A. ghiesbreghtii* (Lott & García-Mendoza 1994). The following selection of specimens represent new state records: *G. B. Hinton & al.* 18722 (MO) for Nuevo León, *Hernández & Martínez* 4298 (MEXU) for Querétaro, *García Mendoza* 4393 (MEXU) for México State, and *Gentry & al.* 20095 (MEXU) for San Luis Potosí (Portal Datos Abiertos UNAM 2018+). Guillot Ortiz & al. (2008) report the species as naturalized in Spain. — ‘Fatal Attraction’ and ‘Blue Haze’ are horticultural selections, and ‘Hakuro Shiro Fukurin’ is a variegated cultivar with leaves with white margins.

**A. fusca** (Ravenna) Thiede & Egli (Kakt. and. Sukk. 52(6): 166, 2001). **Type**: Guatemala (*Ravenna* 325 [Herb. Ravenna]). — **Lit**: Ravenna (1987: with ill.); Castañeda Rojas & al. (2005: 70–71); Castillejos-Cruz (2009: [133]–[138], with ills.); all as *Manfreda*. **Distr**: Guatemala (Chimaltenango, Comalapa); sandy plains and embankments, in pine-oak forests, 1920–2410 m; flowers June to July. **I**: Lott & García-Mendoza (1994: online version); Hochstätter (2016: I: 19); both as *Manfreda*.

≡ *Manfreda fusca* Ravenna (1987).

[3a3] Plants herbaceous; corm 3–9 × 2–5 cm, subcylindrical, bulb 3–4.5 × 1.5–3 cm, shortly cylindrical to ovoid, nearly completely covered with dry leaf bases 4–12 cm long, these membranous at the base and fibrous above; **R** fleshy and fibrous, contractile; **L** drought-deciduous, 5–15, 30–60 × (1–) 2.2–3.2 cm, light green, prostrate or



semi-erect, linear-lanceolate, narrowed towards the base, semisucculent, canaliculate, lower face carinate to slightly scabrous, upper face glabrous, apex acute-acuminate, margins entire, with a papillose-denticulate hyaline band; **Inf** 77–200 cm, ‘spicate’, peduncle stiff, **Bra** 8–12, rather distant, fertile part 5–25 cm, with 7–21 flowers; floral **Bra** 0.2–1.1 × 0.3–0.6 cm; **Fl** 37–47 mm, solitary, sessile, ascending, with foetid odour; **Tep** glaucous-green to reddish on the outer face, semisucculent, forming a tube 14–24 × 5–6 mm, lobes narrowly oblong to lanceolate, extended to revolute, 15–17 × 4–6 mm, tip apiculate, with a bundle of short white hairs; **Fil** sparsely glandular-pilose, 39–42 mm, erect at anthesis, exceeding the tube for 10–20 mm, inserted at mid-tube all on the same level, yellowish-green with purple dots; **Anth** 10–11 mm, yellow; **Ov** oblong, 12–18 × (5–) 6–6.6 mm, greenish, prolonging 1 mm into the tube, not constricted above; **Sty** 37–57 mm, yellowish-green with purple dots; **Sti** capitately 3-lobed; **Fr** subglobose, 15–21 × 9–15 mm, with a scar near the apex, tepals persistent; **Se** deltoid, plane-concave, with narrow margin, 4–5 × 3–4.5 mm, shiny black.

In the protologue, no differential diagnosis is given nor is the relationship indicated. García-Mendoza & al. (2000) clearly place the species in Ser. *Guttatae* (as *A. guttata* Group) of *Manfreda* Sect. *Manfreda*, based on a study of additional specimens at MEXU. This placement is confirmed by Castañeda Rojas & al. (2005) and Castillejos-Cruz (2009) (both as *Manfreda*), who provide additional morphological data. *A. fusca* (presently known from the inaccessible holotype and 2 further gatherings only) is distinct esp. in its flower colour and foetid odour. The species was erroneously omitted from the treatment of the family for the ‘Flora Mesoamericana’ (Lott & García-Mendoza 1994), but the online-version includes photographs.

**A. galvaniae** (Castañeda & al.) Etter & Kristen (Haseltonia 12: 70, 2007). **Type:** Mexico, México (Castañeda Rojas & al. 108 [MEXU, ENCB, IEB, MEXU, MO]). — **Lit:** Castañeda Rojas & al. (2005); Castillejos-Cruz (2009: [139]–[144]); both with ill. and as *Manfreda*. **Dist:** Mexico

(S México); in disturbed tropical deciduous forests and ecotone with pine forests, 1450–1900 m; flowers in July. **I:** Hochstätter (2016: I: 20, as *Manfreda*).

≡ *Manfreda galvaniae* A. Castañeda & al. (2005).

[3a3] Plants herbaceous; corm 3–5 × 2–4 cm, subglobose to subcylindrical, bulb 2.7–4 × 1.3–2.5 cm, cylindrical, nearly completely covered with dried leaf bases 4.5–7.3 cm long, these membranous at the base and fibrous above; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, 2–5 (–7), prostrate or semi-erect, linear-lanceolate, 22–62 × 0.6–2.6 cm, light green, narrowed towards the base to a pseudopetiole 3–4 × 1 cm, semisucculent, slightly canaliculate, glabrous on both faces, apex acuminate, margins entire, with a hyaline band not visible to the naked eye; **Inf** 77–154 cm, ‘spicate’, erect, somewhat arched, reddish to greenish with purple tinge, peduncular **Bra** 5–8, similar to the leaves but smaller, fertile part 23–67 cm, lax, with 7–21 flowers; floral **Bra** 0.8–3.1 × 0.3–1 cm; **Fl** 27–42 mm, solitary, sessile, ascending; **Tep** reddish with purple tinge, semisucculent, forming a tube 13–24 × 4–5 mm, lobes narrowly elliptic to ovate, extended, 9–14 × 3–7 mm, tip cucullate, with a bundle of short white trichomes; **Fil** 15–24 mm, erect at anthesis, exceeding the tube for 10–20 mm, inserted at the upper ¼ of the tube all on the same level, yellowish-green; **Anth** 8–12 mm, yellow; **Ov** cylindrical, (5–) 8–12 × 2–4 (–5) mm, reddish with purple tinge, prolonging 1 mm into the tube, not constricted above; **Sty** 28–37 mm, whitish with purple tinge to yellowish-green; **Sti** capitately 3-lobed; **Fr** subglobose, 13–20 × 9–15 mm, with a scar near the apex, tepals persistent; **Se** deltoid, plane-concave, with narrow margin, 3–5 × 2–4 mm, shiny black.

In the protologue placed in Ser. *Guttatae* (as *A. guttata* Group) of Sect. *Herbaceae*, and characterized by its globose corm nearly always completely covered with dry leaf bases, linear-lanceolate pseudopetiolate leaves, short and lax inflorescences with reddish to yellowish-green with purple tinge, narrowly elliptic to ovate perianth lobes, and a shortly projecting ovary. It is morphologically closest to *A. fusca* and *A. debilis*

(= *Manfreda pringlei*), but differs in its hyaline leaf margin, the lax flower arrangement, the semi-succulence and colour of its flowers, the shape and orientation of its perianth lobes, and its short filaments.

**A. garciae-mendozae** Galván & L. Hernández (Cact. Succ. J. (US) 74(4): 188, ills. (pp. 189–190), 2002). **Type:** Mexico, Hidalgo (*Galván & Galván* 4646 [ENCB, CHAPA, MEXU, MO, QMEX, UAMIZ]). — **Lit:** Eguiarte & Scheinvar (2008: 35–39, with ills.); Trejo-Salazar & al. (2015: pollination). **Distr:** Mexico (San Luis Potosí, Querétaro, Hidalgo); mountain slopes and rocky outcrops, often in canyon bottoms, in limestone soils, in sclerophyllous scrub or oak/pine-oak forests, 1800–2650 m; flowers June to August. **I:** Pilbeam (2013: 88); Hochstätter (2015: IX: 31).

[lg] Stems short; **Ros** openly spreading, 0.75–1.15 (–1.3) × 1–1.75 m, single or somewhat caespitose; **L** (30–) 50–80, lanceolate, straight or incurved, fleshy, thin, flexible mainly in the upper ½, flat or slightly convex below, flat to somewhat concave above, (33–) 48–78 × 6–13 cm, dark green to glaucous-green, margins horny, continuous, 0.5–2 mm wide, grey to dark reddish-brown, easily separated; **marginal teeth** variable, straight to curved, narrowly acuminate, deltoid, flattened, 7–14 mm, grey with reddish-brown tip, (7–) 10–40 mm apart, often with intermittent smaller teeth; **terminal Sp** conical to subulate, sometimes somewhat reflexed, widely grooved on the upper face, keeled abaxially, 27–48 mm, grey, decurrent; **Inf** 3.2–5.5 m, ‘spicate’, peduncle reddish to glaucous-green, with long-deltoid, chartaceous to papery **Bra** 7.5–23 cm long, fertile part in the upper ½–⅔ of the inflorescence; **Ped** 2–3 mm; **Fl** geminate, 28–39 mm; **Tep** light green to yellowish-green and somewhat glaucous, tube 1.5–2.5 × 5–6 (–7) mm, lobes oblong, involute, acute, slightly cucullate and hairy, 12.5–16 × 4–5 mm, sometimes reddish, inner with a wide keel; **Fil** 38–45 mm, inserted at the base of the lobes; **Anth** 10–13 mm, yellow or greenish-yellow; **Ov** cylindrical, 8–12 × 3.5 mm, neck constricted, 2–3 × 1.2–1.8 mm; **Sty** slightly longer than the filaments; **Fr** oblong or oblong-ellipsoid, (15–)

17–20 × 9–11 mm, shortly apiculate; **Se** semicircular, black, 3–4.9 × 2–2.7 mm, marginal wing 0.8–1 mm wide, hilar notch shallow.

Showing affinities with *A. horrida* and *A. kerchovei* according to the protologue, and thus placed in Sect. *Heteracanthae* (as Group *Marginatae*). It differs from the former in its open rosettes, the colour and larger size of its flexible leaves with a grooved terminal spine, its shorter ovary and more shallow tube; and from the latter in its shorter rosettes, fewer leaves with a different colour and flexibility, its shorter ovary and shallower tube.

The inflorescences of *A. garciae-mendozae* consist on average of 3623 flowers, of which 426 are producing pollen or nectar at any one day. Only 60% of the flowers have a high probability to develop into fruits. From the total seeds per infructescence (471,120 on average), only ⅓ (142,725 on average) are viable. The plants are self-compatible, but cross-pollination is most effective for fruit set, indicating a strong inbreeding depression. Most flower visitors are nectarivorous bats, honey bees and bumblebees are infrequent, and hawkmoths rare. The species appears to have a generalist pollination system with bats as main pollinators, and bees and bumblebees ensuring reproductive success when bats are missing. Relatively high levels of genetic diversity and small genetic distances between different populations have been found (González 2004, Eguiarte & Scheinvar 2008, Eguiarte & al. 2013: 491, Trejo-Salazar & al. 2015).

The unpublished *A. hidalgensis* (also as “*hidalguensis*”) (Eguiarte & Scheinvar 2008, Arzate García 2009, both with ills.), one of the largest representatives of Subgen. *Littaea* (rosettes to 2.5 m Ø, leaves 70–90 cm, inflorescences exceeding 7 m) from the N Barranca de Metztitlán, appears to belong here.

**A. garciaruii** A. Vázquez & al. (Phytotaxa [in press], ills., 2019). **Type:** Mexico, Michoacán (*Vázquez-García & al.* 10140 [IBUG, CIMI, MEXU]). — **Distr:** Mexico (SE Jalisco, N Michoacán); rocky cliffs of the Itzicuario-Apupátaro watershed, in tropical deciduous forests, 900–1000 m; flowers in March. **I:** Vázquez-

García & al. (2007b: 41–42, t. B1–B4, as *A. angustiarum*).

[1g] Subcaulescent; **Ros** open, 0.9–1.1 m, solitary; **L** 20–34, linear to lanceolate, openly spreading, straight, thick, firm, long-acuminate, flat to concave above, convex below, 50–80 × 6–10.6 cm, green to dark green, pale green median stripe above inconspicuous or lacking, margins whitish-grey, continuous; **marginal teeth** straight or inclined in the lower part of the leaf, curved upwards or bent in the upper part, flattened, the largest somewhat scattered, 4–7 mm, dark brown to grey, (3–) 10–30 mm apart, 8–14 teeth per 10 cm, teeth absent from the topmost 5–10% of the leaf, intervening margin nearly straight; **terminal Sp** acicular, narrowly grooved above, 30–40 mm; **Inf** 3–4.2 m, ‘spicate’, flexible, peduncle with toothless triangular **Bra** 10.5–13.5 cm long, fertile part in the upper 33–40%, 15–18 cm Ø (infructescence 10–14 cm Ø); **Ped** 8–10 mm (fruiting 18–20 mm); **Fl** 57–64 mm, geminate; **Tep** pale yellow to yellowish-green, tube very short, 2–3 × 6–7 mm, lobes 17–18 × 4–5 mm, pale yellow to yellow, glaucous-greenish in bud; **Fil** 38–44 mm, yellow; **Anth** 16–21 mm, yellow; **Ov** 16–17 mm, neck narrow; **Sty** slightly longer than the filaments; **Sti** capitate; **Fr** 24–26 × 10–12 mm, fruit valves curved outwards, apically acute; **Se** crescent-shaped, 2–3 × 3–5 mm.

A local endemic, according to the protologue closest to *A. angustiarum* and differing esp. in having an inconspicuous or absent median stripe on the upper face of the leaves, denser marginal teeth, longer anthers, longer fruiting pedicels, a larger infructescence diameter, and larger capsules with acute fruit valves curved outwards. *A. garciaruzii* is also close to *A. arcedianoensis* and differs esp. in having an inconspicuous or absent median stripe on the upper leaf face, denser marginal teeth, a shorter fertile inflorescence part, pale yellow to yellowish-green flowers with larger anthers and longer pedicels, and smaller fruits with apically acute, spreading fruit valves. The records and specimens for *A. angustiarum* from SE Jalisco (Hernández-Vera & al. 2007a) and from SE Jalisco and N Michoacán (Vázquez-García & al. 2007b) belong here. The fruit valves

curved outwards are reported only for *A. garciaruzii* and *A. impressa*.

**A. geminiflora** (Tagliabue) Ker Gawler (J. Sci. Arts (London) 2: 86–90, 1817). **Type:** [icono]: Bibliot. Ital. Giorn. Lett. 1: t. inter pp. 112, 1816. — **Lit:** Berger (1915: 69–70); Gentry (1968); Gentry (1982: 113–115); McVaugh (1989); Ullrich (1995a); Cházaro Basáñez & al. (2004b); Vázquez-García & al. (2007b: 52–53, t. J); Starr (2012: 94–97, 317–319); all with ills. except Berger. **Distr:** Mexico (C Nayarit, N-C Jalisco); on rocks along arroyos, in oak woodland, 1000–1400 m; flowers October to December. **I:** Bot. Reg. 14: t. 1145, 1828; Irish & Irish (2000: t. 18); Guillot Ortiz & Meer (2008c); Richter (2011: 28, 29); Etter & Kristen (2012: 94); Pilbeam (2013: 89–90).

≡ *Littaea geminiflora* Tagliabue (1816); **incl.** *Bonapartea juncea* Haworth (1812) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca boscii* Hort. Panorm. ex Hornemann (1813) (*nomen rejiciendum*, Art. 56.1) ≡ *Dracaena boscii* (Hornemann) J. Zeyher (1818) ≡ *Agave boscii* (Hornemann) Anonymous (2013) (*nom. inval.*, ICN Art. 29.1, 34.1b); **incl.** *Bonapartea juncea* Willdenow (1814) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca boscii* Desfontaines (1815) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Dracaena filamentosa* Scannagatta ex Ker-Gawler (1817) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Bonapartea flagelliformis* Henckel (1820) (*incorrect name*, ICN Art. 11.4); **incl.** *Tillandsia juncea* Willdenow ex Steudel (1841) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave geminiflora* var. *filamentosa* Hooker (1856); **incl.** *Littaea juncea* É. Morren (1866); **incl.** *Agave angustissima* Engelm. (1875); **incl.** *Agave geminiflora* var. *filifera* A. Terracciano (1885); **incl.** *Agave knightiana* J. R. Drummond (1909); **incl.** *Dracaena boscii* Hort. J. F. Cels ex A. Berger (1915) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave geminiflora* var. *stricta-viridis* Hort. Besauçèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[1d] Stems short; **Ros** dense, 0.7–1 m, somewhat broader than tall, solitary; **L** many, linear, eventually arching, flexible, narrow, pliable, abruptly acute, roundly convex below and above, smooth, 45–60 × 0.6–0.8 cm, green,

margins finely filiferous or rarely naked; **terminal Sp** shortly subulate, 5–7 mm, greyish; **Inf** 4–7 m, ‘spicate’, peduncle long-tapering, stout at the base (9–12 cm Ø), with narrow ascending-reflexed **Bra**, fertile part in the upper  $\frac{2}{3}$ – $\frac{3}{4}$  of the inflorescence, part-**Inf** with mostly geminate flowers; **Ped** slender, 5–8 mm; **Fl** 40–52 mm; **Tep** pale yellowish-greenish below, tinged above with red or purple, tube narrowly funnel-shaped, 6-grooved, 6–11 mm, lobes linear-lanceolate, recurving, slightly unequal, 18–21 × 4–5 mm, tinged with red, inner slightly shorter, distinctly keeled; **Fil** 35–46 mm, colourless or reddish, inserted on the tube rim; **Anth** excentric, 20–22 mm; **Ov** slender, fusiform-angled, 16–20 mm, neck grooved; **Sty** thickened above, slightly shorter than the filaments; **Sti** not thickened; **Fr** oblong, trigonous, tough, persistent, 18–20 × 9–10 mm, shortly stipitate, shortly beaked, reddish when young; **Se** crescent-shaped, thick, irregularly veined on the faces, 3–4 × 2–3 mm, with conspicuous marginal wing.

Distinct within Sect. *Littaea* (as Group *Filiferae*) by its relatively large simple stem with innumerable, very narrow, pliable, smooth leaves and large ‘spikes’ with relatively remote long flowers. It is most closely related to *A. ornithobroma* which differs esp. in its asymmetrical, few-leaved, surculose rosettes (Gentry 1982: 112). The species was of unknown wild origin until Gentry (1968) reported it from a small area N of Ocotillo, Nayarit. Recently, 2 further populations in Nayarit (Sierra de Álica, La Galinda) and a first occurrence in Jalisco at Xiloasco were found (Cházaro Basáñez & al. 2004b, Hernández-Vera & al. 2007a, Vázquez-García & al. 2007a). The report of a specimen of this taxon from S Sinaloa by McVaugh (1989: 135) is erroneous, since the collection cited (Gentry 18358) is the type collection of *A. ornithobroma*.

The plant came in 1797 from the Botanical Garden Bologna to Milano (Italy), where it first flowered in the garden of Duke Litta of Lainate in 1815, after whom it was named in a new genus as *Littaea geminiflora* (Berger 1915) (see also the historical account by Richter 2011: 24–32). The epithet of *A. geminiflora* (dating from 1816) is antedated by the name *Yucca bosicii* (1813),

which would therefore be the correct epithet for the species (Govaerts 2014+). A proposal to conserve the long-established name *A. geminiflora* was consequently published by Figueiredo & Smith (2013b) and was recommended for acceptance (Applequist 2014: 1366).

**A. gentryi** B. Ullrich (Succulenta 69(10): 210–214, ill., 1990). **Type:** Mexico, Nuevo León (Gentry 20159 [ARIZ, US]). — **Lit:** Gentry (1982: 598–601, figs. 21.8, 21.9, as *A. macroculmis*); Villarreal (1996); González-Elizondo & al. (2009: 80–84, with ill.); Starr (2012: 98–105, 325–328, with ill.); Greulich (2012c: with ill.). **Distr:** Mexico (Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosí, Guanajuato (?), Querétaro, Hidalgo, Puebla); mountain regions in open pine-oak forests, 1800–3400 m; flowers in April. **I:** Heller (2006: 89); Spracklin (2007: 148); Richter (2011: 72); Pilbeam (2013: 91); Nájera Quezada & al. (2015: 5); Hochstätter (2015: III: 3); Greulich (2016b: 38).

[2m] **Ros** 0.9–1.5 (–1.8) × (0.6–) 0.9–1.8 (–2.2) m, solitary or clustering with rhizomatous offsets; **L** 30–45, either broad from the base to above the middle before quickly tapering to the sharp tip, or long triangular and widest at the base before gradually narrowing to the tip, concave, 60–120 × 15–26 cm, light yellowish-green to deep rich green, with strong imprints from the central bud created by the marginal teeth; **marginal teeth** nearly straight, small to large, 8–12 mm, 20–40 mm apart; **terminal Sp** stout, 45–75 mm; **Inf** 2.5–5.5 m, paniculate, peduncle with overlapping, thick and succulent, entire **Bra**, fertile part elliptic, covered in a bulb-like manner by fleshy bracts before anthesis, **Fl** densely clustered in 10–18 (–21) short-stalked part-**Inf**; **Fl** 70–110 mm; **Tep** yellow, reddish in bud, tube funnel-shaped, 11–16 mm, lobes 22–28 mm; **Ov** 35–50 mm; **Fr** 60–75 × 20–25 mm; **Se** 7–8 × 6 mm.

The usage of the name *A. macroculmis* by Gentry (1982: 598) must be rejected, since this name is a synonym of *A. atrovirens* (Ullrich 1990i). This left Gentry’s distinctive plant without a name, which led Ullrich (1990i) to describe it as a new species, *A. gentryi*, using Gentry’s



**Fig. 24** *Agave ghiesbreghtii*. (Copyright: J. Etter & M. Kristen)



description of *A. macroculmis*. However, this description also includes features of the subsequently separated *A. montana*. The description given above for *A. gentryi* is based on a combination of data from Villarreal (1996), Starr (2012), and Greulich (2012c). See under *A. montana* for differences and the classification of both species.

*A. gentryi* includes 3 distinct and geographically separated forms (Starr 2012). It moreover appears to form hybrids with *A. americana* ssp. *protoamericana*, *A. asperrima*, *A. salmiana* ssp. *crassispina*, *A. mapisaga*, and *A. montana* (Starr 2012, Greulich 2012c). González-Elizondo & al. (2009) report the species from Durango. The report of “*A. macroculmis*” from Guanajuato (Zamudio & Galván Villanueva 2011) may refer to *A. gentryi*. — ‘Jaws’ is a cultivar with exceptionally large teeth (Starr 2012: 105). Greulich (2012c) depicts flowering specimens of it and considers ‘Jaws’ to be a long-leaved transitional form to *A. salmiana* with longer stalked and compound part-inflorescences. ‘La Pena Colorada’ is a variegated cultivar (Starr 2014: 222, with ill.).

The flowers are visited at day by birds and insects and at night, when nectar production and sugar content increases, by bats and insects (Castillo-Hernández & Treviño-Carreón 2014). The maroon-fronted parrot (*Rhynchopsitta terrisi*) feeds on flowers and fruits of the species during the breeding season (Ortiz-Maciel & al. 2010).

**A. ghiesbreghtii** Verschaffelt (Cat., 71: 3, 1862). **Type** [neo]: Cult. BG La Mortola (Berger s.n. [US [neo/syn?]]). — **Lit**: Berger (1915: 116–117, with ill.); Standley & Steyermark (1952: as *A. huehueteca*); Gentry (1982: 141–142, with ill.); Lott & García-Mendoza (1994: online-version with ill.); García-Mendoza (2011a: 26–27, 30). **Dist**: Mexico (México, Guerrero, Puebla, Oaxaca, Veracruz, Chiapas), W Guatemala; limestone rock slopes and outcrops in desert scrub, tropical deciduous forests, and pine-oak forests, 975–2500 m; flowers mainly June to September, also October, November and January. **I**: Heller (2006: 40, 90, 91, 156); Richter (2011: 48, as *A. purpusorum*, 66, 113); Pilbeam (2013: 92). — Fig. 24.

**Incl.** *Agave rohanii* Jacobi (1864); **incl.** *Agave leguayana* Verschaffelt (1868); **incl.** *Agave gilbeyi* Hort. Haage & Schmidt (1873) ≡ *Agave horrida* var. *gilbeyi* (Hort. Haage & Schmidt) Baker (1877) ≡ *Agave roezliana* var. *gilbeyi* (Hort. Haage & Schmidt) Trelease (1914); **incl.** *Agave roezliana* Baker (1877); **incl.** *Agave roezliana* var. *inghamii* hort. ex Baker (1877); **incl.** *Agave purpusorum* A. Berger (1915); **incl.** *Agave roezlii* hort. ex A. Berger (1915) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave huehueteca* Standley & Steyermark (1943).

[1g] Acaulescent; **Ros** compact, 0.4–0.7 × 0.6–0.8 m, solitary or copiously suckering; **L** 70–90, broadly lanceolate, ovate or deltoid,



erect, straight or upcurving, thick, rigid, narrowed above the thick base, broadest at the base or in the middle, apex acuminate, convex below, flat to slightly concave or guttered above, smooth, (20–) 30–40 (–65) × (5–) 7–12 cm, or more rarely broadly linear and 35–38 × 5.5–6 cm, dark or light green to yellow-green, sometimes with a lighter mid-stripe, margins horny, relatively straight, narrow, continuous, brown or greyish; **marginal teeth** triangular, strong, frequently straight, sometimes curved upwards or downwards, 5–8 (–15) × 3–6 (–7) mm, brown to greyish, (10–) 25–40 (–60) mm apart, with some intermittent small teeth, reduced at the leaf tip for 2.5–4.5 (–12) cm; **terminal Sp** conical or subulate, shortly shallowly grooved above, rounded below, (10–) 25–35 (–40) × 4–6 (–10) mm, brown to grey, decurrent on the lower face for 2–4 mm; **Inf** (3–) 3.5–5 (–6) m, ‘spicate’, peduncle green with purple tinge, with linear papery brown **Bra** 13–17 cm long, fertile part in the upper  $\frac{1}{2}$ – $\frac{1}{3}$ , densely flowered; **Ped** geminate, 1–4 (fruiting 5–8) mm, thick; **Fl** campanulate, 30–40 (–50) mm; **Tep** purple to greenish-red, inside yellowish, tube broadly funnel-shaped, grooved, 2–5 (–10) × 5–7 (–10) mm, lobes broadly linear to oblong, apex rounded, thickly apiculate, at first outcurving, later involute and clasping the filaments, subequal, 15–21 × 3–5 (–8) mm, inner narrower and with broad low keel; **Fil** (35–) 40–45 mm, inserted on the rim of the tube at the lobe bases, reddish; **Anth** centric, 10–15 (–22) mm, brownish to brownish-red; **Ov** cylindrical, 15–20 × 3–5 (–8) mm, green, neck 2–4 mm, constricted; **Sty** 45 to >70 mm, thickened below the stigma, brown or reddish; **Sti** capitate; **Fr** oblong, globose-ovoid or ellipsoid to obovoid, 17–23 × 8–15 mm, brownish; **Se** semicircular, finely punctiform, wing inconspicuous, (3–) 4–5 × 2–3.5 mm, shiny black. — **Cytology**: 2n = 120 (Simpson & al. 2011: p.p., as *A. gilbeyi*).

The neotype cited above was designated by Gentry (1982: 142). A species of uncertain circumscription, closely related to *A. kerchovei*, but different by its shorter and broader leaves with fewer and smaller teeth on narrower and darker horny margins (Gentry 1982: 142, García-Mendoza 2011a). Characterized by its small rosettes, deltoid or broadly

lanceolate leaves, narrow margins with few short and widely spaced teeth, short tepals, long filaments, and punctiform seeds (García-Mendoza 2011a). The species was introduced by Ghiesbreght and brought into the trade by Verschaffelt in 1862 (Berger 1915). The species (vernacular names: “pichomel”, “jabalf”) is used for living fences, and strips of dried leaves are used to make ties (García-Mendoza 2011a). Rivera-Hernández & al. (2015) provide a new record from W-C Veracruz. See also notes under *A. angustiarum*, *A. funkiana*, *A. horrida* ssp. *horrida*, and *A. kerchovei*.

**A. gigantensis** Gentry (Occas. Pap. Calif. Acad. Sci. 130: 63–67, ill. (pp. 65–66 [bottom], 68, t. 2 [top]), 1978). **Type** [syn]: Mexico, Baja California Sur (Gentry & McGill 23320 [US, ARIZ, ASU, CAS, DES, MEXU, MICH, SD]). — **Lit**: Gentry (1982: 386–388, ill. pp. 387, 388 [bottom]); Webb & Starr (2014a: 94); Webb & Starr (2014b: 7–8); Webb & Starr (2015: 73); all with ill. **Distr**: Mexico (C Baja California Sur: N Sierra de la Giganta [Cerro El Potrero & Sierra de las Palmas]); mountain slopes, mesas and cliffs, 900–1520 m; flowers April to May and November.

[2j] Acaulescent; **Ros** rather open, 0.5–1 × 0.8–1.2 m, solitary; **L** few, broadly lanceolate, flat, rigid, thick, fleshy, markedly narrowed at the base, widest at or above the middle, acuminate, smooth, 40–75 × 11–16 cm, dark green to occasionally glaucous grey-green, with distinct imprints from the central bud, turning red to purplish when plants are flowering, margins repand to prominently mammillate; **marginal teeth** variously curved, basis thick, sometimes grotesquely so, frequently 2–3 teeth on the same base, confluent along the upper leaf margins, 10–20 mm and more, brown to light greyish, generally remote and to 60–80 mm apart; **terminal Sp** strongly subulate, straight or sinuous, deeply sulcate above, 30–60 mm, grey, long decurrent as pronounced horny margin, sometimes to mid-leaf; **Inf** 4–5 m, paniculate, peduncle with narrowly lanceolate, thickly chartaceous **Bra**, fertile part rather stout, compact and narrow, part-**Inf** nearly horizontal, 18–25 in the upper  $\frac{1}{3}$  of the inflorescence; **Fl**

slender, 48–60 mm; **Tep** bright pale yellow, buds whitish or pale green, tube shortly discoid, spreading, thickened at the lobe bases, 4–5 × 11–13 mm, lobes linear, spreading, rounded and shortly hooded at the apex, 18–25 × 5–6 mm, inner with prominent keel, grooved within and strongly overlapped at the base by the outer; **Fil** slender, 30–45 mm, variable in length, inserted on the rim of the tube at the lobe bases; **Anth** somewhat excentric, 18–25 mm; **Ov** slender, fusiform, neck short, slightly grooved, constricted; **Sty** slightly longer than the filaments; **Sti** capitate; **Fr** oblong, 35–40 × 12–15 mm, neither beaked nor stipitate; **Se** unknown. — **Cytology**: 2n = 60 (Simpson & al. 2011).

Gentry's holotype indicated in the protologue for US consists of 3 sheets which are not cross-labelled, thus representing syntypes. Recent field and herbarium studies (Webb & Starr 2014a, b) showed that Gentry (1978) and Gentry (1982) included material with glaucous-blue to blue-green leaves in fact belonging to *A. sobria* ssp. *sobria* in his original concept of *A. gigantensis*. Webb & Starr (2014b) restricted the concept of *A. gigantensis* to plants with dark-green leaves and occurring only at higher elevations on the Cerro El Potrero and Sierra de las Palmas. In the above description based on Gentry (1982), the leaf colour is corrected to dark green and some further data were added from Webb & Starr (2014b) and Webb & Starr (2015), but it may still include incorrect data from *A. sobria*. Some of Gentry's photographs labelled "*A. gigantensis*" (1978: p. 66 top; 1982: p. 388 top) belong to *A. sobria* (Webb & Starr 2014b), and "*A. gigantensis*" plants with bluish leaves (Richter 2011: 79, 105, Pilbeam 2013: 93, Moore 2016: 277) apparently belong to *A. sobria*. According to Gentry (1982), the closest relatives appear to be *A. avellanidens* (with leaves not or scarcely narrowed towards the base) and *A. moranii* (with much longer leaves), both disjunct to the north. These three taxa as well as *A. turneri* are now placed in a new Sect. *Conicae* (see under *A. avellanidens*).

**A. gilbertii** A. Berger (Monatsschr. Kakt.-kunde 14: 126, 1904). **Type** [lecto]: Ex cult.

(*Anonymous* s.n. [K [sub *A. bakeri*]]). — **Lit**: Watson (1902: protologue *A. bakeri*); Hooker (1903: as *A. bakeri*); Berger (1915: 41–42); Gentry (1982: 71–72); Roosbroeck (2004); all with ills. **Distr**: Known from cultivation only. **I**: Heller (2006: 93); Richter (2011: 60, as *A. bakeri*); Hochstätter (2015: VIII: 21); Meer (2016c: 144).

**Incl.** *Agave bakeri* W. Watson (1902) (*nom. illeg.*, ICN Art. 53.1).

[1b] Stems short; **Ros** solitary, not suckering; **L** many, lanceolate, recurving, coriaceous, narrowed and thickened near the base, broadest in the middle, tapering to the base to 6.25 cm, tapering to the apex to a sharp point, convex below, concave to flat above, 90–100 × 10–12 cm, glaucous-green, with paler median stripe, margins thin, with continuous narrow brown border; **marginal teeth** none; **terminal Sp** slender, 5–20 mm, brown; **Inf** to 3 m, 'spicate', peduncle short, with linear-lanceolate **Bra** longer than the lowest flowers, fertile part cylindrical, densely flowered from near the base; **Fl** 50–60 mm, geminate; **Tep** pale greenish-yellow outside, whitish within, tube 6-furrowed, 11–12 mm, lobes reflexed or revolute, obtuse, 20 mm, greenish outside, whitish within, inner broader, with dark green keel; **Fil** rigid, 40–50 mm, whitish, inserted at the orifice of the tube 1 mm above the tube base; **Anth** 14 mm, golden-yellow; **Ov** fusiform, slender, ±20 mm, neck slender, 6-sulcate; **Sty** rigid, shorter than the filaments but longer at the female phase (Watson 1902); **Sti** 3-lobed; **Fr** and **Se** unknown (although Berger (1904) reported that the plant which flowered at Kew in 1902 yielded many seeds, which were widely distributed).

The illegitimate name and replaced synonym *A. bakeri* is usually ascribed to Hooker (1903), but was published earlier by W. Watson (Watson 1902), based on a flowering plant at Kew purchased at the sale of the *Agave* collection of the late Mr. Peacock in 1889. The notion of Gentry (1982) that the species "disappeared in cultivation" is erroneous; it is cultivated in Europe (see references) and the USA, but has never been located in habitat (Gentry 1982). The recently published *A. chazaroi* is somewhat similar, but stemless and with broader leaves with a longer terminal spine.

**A. ×glomeruliflora** (Engelmann) A. Berger *pro sp.* (Hort. Mortol. 12, 1912). **Type:** [lecto — icono]: Gard. Chron. ser. nov., 1883: 19, fig. 6. — **Lit:** Berger (1915: 94–95, as *A. glomeruliflora*); Muller (1939: with ill., as *A. chisoensis*); Gentry (1982: 142–144, with ills., as *A. glomeruliflora*); Reveal & Hodgson (2002: as *A. glomeruliflora*); Greulich (2016a: with many ills.). **Distr:** USA (W Texas), Mexico (Coahuila); gravelly calcareous slopes in grasslands and oak-juniper woodlands, 600–1600 m; flowers mid-spring to early fall. **I:** Kümmel & Klügling (2006: as *A. lechuguilla*); Richter (2011: 86); Pilbeam (2013: 94–95); Hochstätter (2015: IX: 47).

≡ *Agave heteracantha* var. *glomeruliflora* Engelmann (1883) ≡ *Agave lechuguilla* fa. *glomeruliflora* (Engelmann) Trelease (1920); **incl.** *Agave chisosensis* C. H. Muller (1939).

[1g × 2l] Obviously of intersubgeneric hybrid origin with morphological gradations between *A. lechuguilla* and *A. ×gracilipes*, *A. (parryi ssp.) neomexicana* and/or *A. havardiana* (Gentry 1982: 143) and thus only representing an aggregate of different habitually similar natural hybrids. According to Reveal & Hodgson (2002), the name *A. ×glomeruliflora* “should probably be more appropriately applied only to crosses and back-crosses between *A. lechuguilla* and *A. havardiana*”. Gentry’s selection of a neotype is superseded by his simultaneous selection of a lectotype (Gentry 1982: 143). Baker & al. (2009: 283) report a chromosome count of  $n = 60$  which is congruent with a spontaneous origin between *A. lechuguilla* × *A. parryi ssp. neomexicana*, both with  $2n = 120$ ; counts for the remaining two possible parental taxa are unknown. Few if any substantial threats were identified, and substantial populations in Big Bend and Guadalupe Mountains National Parks are under protection (Reichenbacher 1985: 103–105). Magallán Hernández & Hernández Sandoval (2001: 108) report “*A. aff. glomeruliflora*” from Municipio Cadereyta in Coahuila. Plants have survived 30 years outdoors in a mild climate in Germany with rain protection in winter (Kümmel & Klügling 2006: as *A. lechuguilla*, Greulich 2016a).

**A. gomezpompae** Cházaro & Jimeno-Sevilla (Cact.-Avent. Int. 88: 2–11, ills., 2010). **Type:** Mexico, Veracruz (*Jimeno-Sevilla & al.* 247 [XAL, CHAP, CHAPA, ENCB, IBUG, IEB, MEXU]). — **Lit:** Jimeno-Sevilla (2010: 97–99, with ills.). **Distr:** Mexico (C Veracruz: near Córdoba); karstic limestone rocks and outcrops, 850 & 1400 m, in tropical “subperennial” (semi-deciduous) or cloud forests; flowers May to July; only known from 4 populations. **I:** Richter (2011: 56); Meer (2012); Pilbeam (2013: 96); Hochstätter (2015: VIII: 21).

[1f] Caulescent, stems creeping, to >150 × 8–15 cm, bifurcating 3× or more, each stem with a repeatedly flowering **Ros** that turns upright, not surculose; **L** few, lanceolate to oblanceolate, flexible, fleshy, concave above, convex below, 80–85 × 10–13 cm, dark green, margins denticulate throughout; **marginal teeth** none; **terminal Sp** 20 mm or longer, dark; **Inf** lateral according to the protologue but actually likely terminal on rudimentary lateral rosettes, erect, to 2.7 m, ‘spicate’, peduncle with triangular **Bra** 12–16 × 3–5 mm, fertile part only ±50 cm; **Ped** 3–4 mm, single or geminate; **Fl** 32–49 mm (74 mm with stamens); **Tep** spatulate, 20–28 × 2–4 (at the base) mm, green or creamish-yellow inside, tube ± ½ as long as the obtuse lobes; **Fil** to 43 mm; **Anth** 7–9 mm, yellowish; **Ov** ovoid or barrel-shaped, 15–21 × 3–5 mm, greenish, not constricted; **Sty** slender, to 43 mm; **Sti** slightly thickened; **Fr** trigonous, 20 mm with a 5 mm long stipe, blackish; **Se** 3–4 × 2 mm, black, shiny.

Placed in Sect. *Micracanthae* (as Group *Polycephalae*) according to the protologue, and closest to the allopatric *A. pendula* with which it shares long and bifurcating stems and seemingly lateral inflorescences, but differs by thicker stems, broader and pure green leaves without yellow mid-stripe and denticulate all along the margins, and longer inflorescences.

**A. ×gonzaloii** D. Guillot & P. Van der Meer *pro sp.* (Flora Montiber. 27: 55–56, 2004). **Type:** Spain, Valencia (*Guillot & Van der Meer s.n.* [VAL 151000]). — **Distr:** Cultivated only.

≡ × *Mangave gonzaloi* (D. Guillot & P. Van der Meer) hort. (s.a.) (*nom. inval.*, ICN Art. 29.1).

[1 × 3a] A commercially offered garden hybrid with spotted leaves, most probably between a species of Subg. *Manfreda* (*A. maculosa* or *A. variegata*?) and an unknown species of Subg. *Littaea* (and thus belonging to the synonymized nothogenus × *Mangave*), found at the Botanical Garden of Valencia (Spain).

**A. graciellae** Galván & Zamudio (Acta Bot. Mex. 105: 2–4, ills., (pp. 3, 6–7), 2013). **Type:** Mexico, Querétaro (*González 569* [IEB, ENCB, MEXU, XAL]). — **Dist:** Mexico (SE San Luis Potosí, NE Querétaro); on karstic limestone rocks, in pine-oak or cloud forests, 1200–2400 m; flowers April to July. **I:** Magallán Hernández & al. (2012: 26, as *Agave* sp. 1); Hochstätter (2015: VIII: 21); Perez Badillo (2016: 120); De-Nova & al. (2018: 24).

[1a] Stems short; **Ros** hemispherical, 16–60 (–70) × 35–75 cm, caespitose, forming dense groups/clusters; **L** (65–) 100–230, linear, at the base with a deltoid sheath 2.5–5 × 1.8–2.5 (–3) cm at the base, whitish, fleshy, lamina straight to slightly incurved at maturity, fleshy-coriaceous, flexible, keeled below, flat or slightly concave above, esp. towards the apex, smooth on both faces, 13.5–55 (–60) × (1–) 1.2 (–1.5) cm, light green, striated when dried, margins corneous, 3–5 mm wide, with hyaline or yellowish border, minutely serrulate, denticles sometimes bicuspid, sometimes reddish or only at the tip; **marginal teeth** none; **terminal Sp** conical-subulate, weak, keeled below, somewhat flat above, 4–6.5 mm, reddish-brown, slightly decurrent; **Inf** 1.5–2.45 m, ‘spicate’, straight, peduncle 95–185 cm, green, often tinged reddish or reddish-brown, with linear, reddish-brown, often decurrent **Bra** 2–5 cm long, fertile part ± in the upper ¼–½, 35–75 cm; **Fl** geminate, 22–27 mm, sessile; **Tep** green or yellowish-green, often tinged purple, tube slightly flaring, 8–13 × 4–5 mm, grooved, lobes slightly spreading, ovate-oblong, unequal, 7–11 × 3–4.5 mm, cucullate, apex with a tuft of hairs; **OTep** acute; **ITep** somewhat shorter, rounded, with a broad keel; **Fil** 30–40 mm, green with reddish tinge or purple, inserted at 2 levels in the

upper ⅓ of the tube; **Anth** slightly eccentric, ±10 mm, yellow or purple; **Ov** cylindrical, grooved, 6–8 × 4–5 mm, neckless, intruding the tepal tube; **Sty** 48–55 mm, shorter than the filaments, green with reddish tinge, purple at the apex; **Sti** slightly thickened; **Fr** ovoid-ellipsoid, 15–17 × 10–12 mm, shortly beaked, dark brown; **Se** semicircular, 3.8–5 × 2.2–2.5 mm, black, shiny, with marginal wing, hilar notch shallow.

According to the protologue closest to *A. dasyliroides* and *A. petrophila*, differing from both esp. in its smooth leaves without striae in fresh condition, larger marginal denticles, and flowers tubular below and campanulate above. *A. dasyliroides* differs further in its usually solitary rosettes, its arching inflorescences, and its occurrence on igneous rocks, and *A. petrophila* in its campanulate flowers with a shorter tube, globular fruits and its occurrence in tropical deciduous forests. *A. graciellae* is also similar to *A. rzedowskiana*, which differs in its smaller inflorescences and its inclined to decumbent peduncle, shorter tepal lobes and the occurrence on igneous rocks. *A. kavandivi* is a further close relative (see there for differences). The floral buds are eaten as vegetable, and the young inflorescences are cooked and eaten as sweets according to the protologue. The specimen *Rzedowski 7128a* from San Luis Potosí, placed in *A. dasyliroides* by Gentry (1982: 249) may belong here according to the protologue.

**A. gracilipes** Trelease (Annual Rep. Missouri Bot. Gard. 22: 95, 1912). **Type** [syn]: USA, Texas (*Mulford 293 + 293a* [MO, ILL, NY]). — **Lit:** Berger (1915: 180–181); Breitung (1963: 120–121, with ills.); Gentry (1982: 526–530, 536, with ills.); Reveal & Hodgson (2002); González-Elizondo & al. (2009: 85–87, with ills.). **Dist:** USA (SE New Mexico, W Texas); Mexico (Chihuahua); gravelly to rocky, often calcareous places in grasslands, desert scrub, and pinyon-juniper woodlands, 1200–1900 m; flowers summer to early fall. **I:** Pilbeam (2013: 97); Hochstätter (2015: VII: 100); Greulich (2016a: 35).

[2l × 1g?] Acaulescent; **Ros** compact, small, 0.6–0.8 m Ø, sparingly and closely suckering; **L** 60–100, lanceolate, thick at the base, rigid,

gradually acuminate, convex below, openly concave above, smooth, 18–30 × 5–7 cm, mostly glaucous-green, margins nearly straight to wavy because of the teeth bases, slightly narrowed above the base; **marginal teeth** narrowly triangular, mostly rather straight or curved, regular, abruptly lenticular and often confluent at the base, larger along mid-leaf and 2–10 mm, light grey, 15–25 mm apart, regularly spaced, 8–12 per side, intervening margin usually slightly concave; **terminal Sp** usually straight, narrowly to openly grooved above, 20–50 (–100) × 4–5 mm, dark reddish-brown to light grey, long-decurrent; **Inf** 1.8–5 m, paniculate, peduncle slender, with scarious lanceolate **Bra**, fertile part frequently narrow and deep, with 30–40 ascending part-**Inf** in the upper  $\frac{1}{2}$ – $\frac{1}{3}$  of the inflorescence, or fertile part short, with only 10–12 ascending part-**Inf** in the upper  $\frac{1}{4}$  of the inflorescence **Ped** < 5 mm, very slender; **Fl** 35–55 mm; **Top** yellow at anthesis, red in bud, tube shallow, broadly campanulate, 4–7 × 9–15 mm, knobby by the base of the filaments, grooved below the sinuses, lobes spreading to ascending at anthesis, overlapping at the base with thin margins becoming involute above, soon narrowing, withering and sinuses spreading, slightly unequal, 14–18 mm; **Fil** 30–45 mm, slender, inserted just below the rim of the tube, yellow, sometimes red; **Anth** 16–20 mm, yellow; **Ov** slender to broadly cylindrical to fusiform, 20–32 mm, neck constricted; **Sty** intermediate in length between lobes and filaments, yellow, sometimes red; **Sti** capitate; **Fr** oblong to ovoid, 35–40 × 20 mm, sessile or shortly stipitate, straw-coloured; **Se** 5–6.5 × 4 mm. — **Cytology**: 2n = 60 (Reveal & Hodgson 2002).

A very variable complex, hypothetically of ancient hybrid (allopolyploid?) origin between *A. (parryi ssp.) neomexicana* × *A. lechuguilla*, but presently back-crossing with *A. lechuguilla*, which explains the dimorphic variation (Gentry 1982). Pinkava & Baker (1985) list the taxon as putative intersubgeneric hybrid *A. neomexicana* × *A. lechuguilla*. Reveal & Hodgson (2002) are reluctant to designate the taxon as nothospecies until populations are studied cytologically in detail, and this view is followed here. The fact that *A. parryi ssp. neomexicana* is absent from

major parts of the area of *A. × gracilipes* excludes a spontaneous hybrid origin with *A. lechuguilla* and would favour the hypothesis of an allopolyploid origin. The diploid chromosome number, however, dismisses an allopolyploid origin, since both putative parental species are tetraploid. For the time being, *A. gracilipes* must be upheld as valid species, but its origin and status needs further study.

*A. gracilipes* is very similar in habit to *A. applanata* (Berger 1915) and was formerly included in the concept of the latter as “Texas form”, e.g. by Mulford (1896: 83), but differs from that species in its much smaller flowers with much shorter tubes (Berger 1915). In the protologue, Mulford, 293, 293a, 1895 are designated as “the types” (plus several paratypes), so that all four specimens of both gatherings (ILL 00009818, ILL 00009819, MO 202075, NY 00170405) represent syntypes. Similar plants from N Durango are provisionally placed here by González-Elizondo & al. (2009) as “*A. aff. gracilipes*”.

**A. gracillima** A. Berger (Agaven, 33, 288 [erratum], 1915). **Type**: Mexico, Durango (Rose 2341b [US]). — **Lit**: Rose (1903c: 21); Verhoeck-Williams (1975: 283–286); Piña Luján (1986: 13–15); McVaugh (1989: 229–230); Castillejos-Cruz (2009: [127]–[132], with ills.); all as *Manfreda elongata*. **Distr**: Mexico (S Durango, S Nayarit, S Zacatecas (?), C Jalisco); valleys and grassy plains in the mountain region, in oak and tropical deciduous forests and grasslands, 1000–1380 m; flowers mid-August to September. **I**: Hochstätter (2016: I: 18); Castro-Castro & al. (2017: 62); both as *Manfreda elongata*.

≡ *Manfreda elongata* Rose (1903) ≡ *Polianthes elongata* (Rose) Shinnars (1966) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave gracilis* A. Berger (1915) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Polianthes rosei* Shinnars (1967) (*nom. illeg.*, ICN Art. 52.1).

[3a2] Herbaceous; corm 5–10 × 2.5–4 cm, cylindrical, bulb 4–6.5 × 2.5–3 cm, ovoid to cylindrical, covered with fibrous dry leaf bases 6–12 cm long; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, 2–5, recurvate to arching, extended, linear-lanceolate,



slightly canaliculate, glabrous on both faces, apex acute, with a short soft tip, 40–60 (–95) × 2–4 (–5) cm, light green, shiny, margins entire, with a hyaline band, slightly revolute; **Inf** 120–140 (–160) cm, erect, glaucous-green, ‘spicate’, **Bra** 8–10, similar to the leaves but smaller, fertile **Inf** part 20–40 (–70) cm, lax, with 20–30 flowers; floral **Bra** (0.6–) 1.4–2 × 0.3–0.7 cm, narrowly deltoid; **Fl** 28–32 mm, solitary, sessile, ascending; **Tep** yellowish-green to reddish-green, forming a funnel-shaped tube (9–) 13–18 × 4–5 mm, slightly recurved, lobes oblong, extended to revolute, 11–16 × 3–6 mm, tip cucullate, with a soft tip and a bundle of short white trichomes; **Fil** 25–35 mm, erect at anthesis, exceeding the tube for 24–28 mm, inserted in the upper part of the tube on the same level, greenish-yellow with purple dots; **Anth** 10–12 mm, greenish-yellow; **Ov** cylindrical, 12–16 × 4–5 mm, greenish, not extending into the tube, not constricted above; **Sty** 30–42 mm, yellowish-green with purple dots; **Sti** capitately 3-lobed; **Fr** cylindrical, 20–26 × 12–14 mm, slightly apiculate, tepals persisting; **Se** deltoid, plane-concave, 3–4 × 3–5 mm, dull black.

Distinguished by its long, recurving, channelled leaves, the long-acuminate floral bracts, and the styles, which are usually much longer than the stamens. The flowers of *A. gracillima* are similar to those of *A. scabra* but with a proportionately longer style and a bluntly angled perianth tube (Verhoek-Williams 1975: 285, as *Manfreda elongata* and *M. scabra*).

The protologue wrongly cites the number of the type collection as “2341” (Verhoek-Williams 1975: 283). The map in Castillejos-Cruz (2009) shows a locality in S Zacatecas, but does not cite a specimen from that state.

**A. graminifolia** (Rose) Govaerts & Thiede (Willdenowia 43(2): 332, 2013). **Type:** Mexico, Jalisco (*Rose* 2571 [US, GH, K, MO, NY]). — **Lit:** *Rose* (1903a: 11–12, as *Polianthes*); *McVaugh* (1989: 251–252, as *Polianthes geminiflora* var.); *Solano Camacho & García-Mendoza* (1998: 476–477, as *Polianthes*). **Distr:** Mexico (S Zacatecas, Aguascalientes, Jalisco); grasslands, rocky slopes and grassy openings in oak forests, (1400?–) 2000–2250 m; flowers July to September. **I:**

*Castro-Castro & al.* (2015: 145); *Castro-Castro & al.* (2016: 721); *Hochstätter* (2016: II: 14); all as *Polianthes*.

≡ *Polianthes graminifolia* *Rose* (1903) ≡ *Bravoa graminifolia* (*Rose*) *Conzatti* (1903) ≡ *Polianthes geminiflora* var. *graminifolia* (*Rose*) *McVaugh* (1989) ≡ *Agave duplicata* ssp. *graminifolia* (*Rose*) *Thiede & Eggli* (1999) (*incorrect name*, ICN Art. 11.4).

[3b2] Herbaceous; corm short, ±0.8 × 0.8 cm, bulb oblong, ±3 × 1.6–1.7 cm, covered with dry leaf bases; **R** contractile, thickened; **L** ±6, linear, ascending or drooping, involute, ± densely pubescent on the lower face on the nerves and margins and on exposed portions of the leaf sheath, glabrous on the upper face, 15–20 (–30 (–60)) × 0.1–0.2 (–0.8) cm; **Inf** (20–) 50–85 cm, ‘spicate’, peduncle with narrow subulate-tipped **Bra** 2–6 cm long, pubescent in the lower part, fertile **Inf** part 15–30 cm, with 8–15 widely spaced flowering nodes, lower ones often on 1 cm long peduncles, lower internode 5–7 cm, internode length decreasing towards the distal portion; **Ped** 3 mm, elongating in fruit to 4–4.5 (–10?) mm; **Fl** geminate, ±25 mm; **Tep** rose to dark red, forming a tube curved downwards near the base, widening between the curvature and the base of the lobes, ±22–25 × 3–4 (at the tip) mm, lobes unequal, outer 2–3 × (1.5–) 3–4 mm, inner 1.5–3 × 1.5–2.5 mm, apex obtuse to rounded, rose; **St** included; **Fil** filiform, inserted low in the tube 3.5–8 mm above the tip of the ovary; **Anth** not described; **Ov** cylindrical, ±5 × 1.5 mm; **Sty** not exerted at anthesis; **Sti** 3-lobate, with 3 flat suborbicular lobes, ± reaching the anther tips; **Fr** and **Se** not described.

For some time considered to represent merely an infraspecific taxon of *A. coetocapnia* (*McVaugh* 1989: as *Polianthes geminiflora* var., *Thiede & Eggli* 1999: as *A. duplicata* ssp.), it is here accepted at species rank based on *Solano Camacho* (2002) (where it represents an independent clade in the morphological analysis), *García-Mendoza & Solano* (2007), and *Solano & García-Mendoza* (2013) (all as *Polianthes*). Its most characteristic feature is the pubescence of distinct, upright, stiff hairs to ±0.2 mm that cover the veins and margins of the leaf sheath and lamina and the lower part of

the peduncle (McVaugh 1989: as *Polianthes geminiflora* var. *graminifolia*). Albeit well collected (29 records from 12 localities; Solano & Feria 2007: 1888), no detailed morphological description is yet available.

**A. grisea** Trelease (Mem. Nation. Acad. Sci. 11: 34–35, tt. 54–56, 1913). **Type:** Cuba, Santa Clara (*Grey* 1 [MO [4 sheets, syn?]]). — **Lit:** Berger (1915: 208–209); Álvarez de Zayas (1996: 118–119, 123, with ills.); Guillot Ortiz & Meer (2011). **Distr:** S-C Cuba (Bahía de Cienfuegos); on calcareous coastal cliffs; flowers January to March. **I:** Hochstätter (2015: VII: 70).

**Incl.** *Agave grisea* var. *grisea*; **incl.** *Agave grisea* var. *cienfuegosana* Trelease (1913); **incl.** *Agave grisea* var. *obesispina* Trelease (1913).

[2p] Acaulescent, not surculose; **Ros** semi-globular, solitary; **L** lanceolate, somewhat concave, or oblanceolate, (100–) 110–130 (–160) × (10–) 12–16 (–20) cm, yellowish grey-green, passing into glaucous, or grey, rather dull, margins between the teeth from nearly straight to conspicuously concave; **marginal teeth** gently curved, broadly triangular, or acuminate tapered from the hardened tops of asymmetrical green prominences, sometimes wider or sublenticular at the leaf base, 2–5 (–10) × 1–4 mm, 10–25 mm apart; **terminal Sp** triquetrously conical or somewhat subulate, slightly curved, flattened or shallowly concave to or beyond the middle or becoming subinvolute, smooth, (10–) 12–22 (–25) × 3–6 mm, reddish chestnut-brown or brown, ± dull, decurrent for its length or more; **Inf** 4–6 (–8) m, paniculate, fertile part oblong, part-**Inf** in the upper  $\frac{2}{3}$  of the inflorescence, 45–50 cm, not bulbiferous; **Ped** 5–10 mm; **Fl** 42–47 (–50) mm; **Tep** golden-yellow, tube 4–8 × 7–9 mm, lobes 14–16 (–19) × 4–5 mm; **Fil** 30–36 (–40) mm, inserted nearly in the tube throat; **Anth** 14–18 mm; **Ov** fusiform, trigonous, 25–30 mm; **Sty** longer than the filaments; **Sti** capitate; **Fr** cylindrical, sometimes subpyriform, 35–40 × 14–17 (–20) mm, beaked, shortly stipitate; **Se** subtriangular, 6–7 × 5–7 mm.

The 4 type specimens at MO are cross-labelled, but the cross-labels do not appear to be original (Smith & Figueiredo 2014c: 235). A polymorphic

species. Since the 2 published varieties merely differ gradually and in addition appear to be connected by transitional forms (Berger 1915: 209), they were included in the synonymy by Álvarez de Zayas (1996) and in the first edition of this handbook. *A. grisea* differs from *A. brittoniana* and *A. acicularis* esp. in its longer leaves, and from *A. offoyana* (as *A. legrelliana*) in its greyish leaves and golden-yellow flowers (Álvarez de Zayas 1996). The omnivorous bat *Phyllonycteris poeyi* feeds predominantly on the nectar of the species (Mancina 2010). According to the IUCN Red List categories, the species is considered as “Endangered” (Berazaín & al. 2005, González-Torres & al. 2016). The plant depicted by Guillot Ortiz & Meer (2011: 12) has teeth on distinct prominences and is most probably misidentified.

**A. guadalajarana** Trelease (Contr. US Nation. Herb. 23: 123, 1920). **Type:** Mexico, Jalisco (*Pringle* 4473 [MO, BR, COLO, E, F, JE, K, MEXU, NY, NDG, RM, S, US, VT]). — **Lit:** Gentry (1982: 531–532, with ills.); McVaugh (1989: 135, 137); Cházaro Basáñez & Mostul (1999: with ills.); Kemble (2006: with ills.); Hernández-Vera & al. (2007b); Starr (2012: 312–313, with ill.). **Distr:** Mexico (Jalisco, known only from the region of Guadalajara; S Nayarit); grassy slopes in oak woodlands and ecotone with tropical deciduous forests, in volcanic rocky soils, 1400–2000 m; flowers April to November. **I:** Kemble (2004: 208); Heller (2006: 16, 93); Etter & Kristen (2012: 83); Pilbeam (2013: 99–101); Hochstätter (2015: IV: 22); Moore (2016: 279); Castro-Castro (2017: 136).

[21] **Ros** compact, 25–50 (–70) cm Ø, broader than tall, solitary, rarely suckering; **L** numerous, obovate to oblong, rigid, closely imbricate, obtuse, flat to incurved, 20–30 × 8–12 cm, inner leaves shiny but glaucous, outer leaves dull grey, margins nearly straight, upper part with prominences; upper **marginal teeth** (5–) 8–10 mm, remote, on strong prominences, those below mid-leaf much smaller, 3–4 mm, reddish-brown to dusty grey, 5–10 mm apart; **terminal Sp** subulate, straight to sinuous, flat to shallowly hollowed above, roundly keeled below, 25 mm, greyish; **Inf**

3–5 m, paniculate, peduncle slender, pruinose, fertile part very lax, part-**Inf** nearly horizontal, small, remote, 15–25 in the upper  $\frac{1}{2}$  of the inflorescence, pale reddish; **Fl** 60 mm; **Tep** lobes slender, much longer than the short tube,  $\pm 20$  mm, tips cucullate, greenish or yellow-green to pale yellow, tips in bud sometimes purplish, in flower tips of **OTep** rose to purple, tips of **ITep** less so; **Fil** slightly exerted, rose to purplish; **Ov** fusiform,  $\pm 25$  mm, green, neck short, slightly constricted and slightly sulcate; **Sty** longer than the tepals, rose to purplish; **Sti** capitate; **Fr** narrowly oblong, thick-walled,  $38\text{--}45 \times 15\text{--}18$  mm, shortly beaked, stipitate, dark brown; **Se** crescent-shaped,  $6 \times 4$  mm.

The protologue is rather short, and the description in Gentry (1982) is incomplete, lacking data on filaments and ovary, which were added here from Cházaro Basáñez & Mostul (1999), Kemble (2006) and Etter & Kristen (1997+: accessed Dec. 2015). The specimen Norris & Taranto 14380 (MICH) from Nayarit doubtfully assigned here by Gentry (1982: 546), is listed under *A. guadalajarana* by McVaugh (1989). Portal Datos Abiertos UNAM (2018+: accessed Jan. 2019) lists three further specimens from S Nayarit (MEXU 606850, 615834, 878517).

Resembling the other members of Sect. *Parryanae* in the compact rosettes with closely imbricate, short, broad, rigid leaves with the largest teeth confined to the upper third of the margin, and the proportions of flower tube and lobes. The short obtuse leaves resemble those of *A. parryi* var. *truncata*, but the conspicuous prominences along the leaf margins and the lax panicles distinguish *A. guadalajarana* from that species and all others of Sect. *Parryanae* (as Group) (Gentry 1982). — Hummingbirds are (occasional?) flower visitors (photo in Cházaro Basáñez & Mostul 1999: 12).

**A.  $\times$  guemensis** D. Guillot & P. Van der Meer (Stud. Bot. (Salamanca) 24: 87–89, 2006). **Type:** Spain (*Anonymous* s.n. in VAL 169523 [VAL]). — **Distr:** Cultivated only.

[1f  $\times$  1f] This is the garden hybrid *A. horrida* ssp. *perotensis* (as “*A. polyacantha*”)  $\times$  *A. warelliana*.

**A. guerrerensis** (Matuda) G. D. Rowley (Repert. Pl. Succ. 26: 4, 1977). **Type:** Mexico, Guerrero (*González Medrano & al.* s.n. [MEXU 231698, MEXU 526057]). — **Lit:** Matuda (1975: protologue, with ill.); García-Mendoza (2003); Castillejos-Cruz (2009: [145]–[149], with ills.); all as *Manfreda*. **Distr:** Mexico (Guerrero); oak forests, 1250 m; flowers in October.

$\equiv$  *Manfreda guerrerensis* Matuda (1975).

[3a3] Plants herbaceous; corm  $4\text{--}8.2 \times 2.2\text{--}3.5$  cm, succulent, cylindrical, bulb  $3\text{--}4.2 \times 1.5\text{--}3.5$  cm, conical to ovoid, covered with dried fibrous leaf bases  $1.5\text{--}6.5$  cm long; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, 2–3,  $40\text{--}45 \times 6\text{--}8$  cm, prostrate to semi-erect, linear-lanceolate, narrowed towards the base, semi-amplexicaul, slightly pubescent at the leaf base, apex acute to obtuse, dark green to glaucous-green, with cherry to purple dots, margins entire; **Inf** (120–)  $150\text{--}260$  cm, erect, glabrous with purple dots at the base, ‘spicate’, peduncular **Bra** 5–12, lower similar to the leaves, fertile **Inf** part 35–40 cm, lax, with 6–12 flowers; floral **Bra**  $0.7\text{--}3.5 \times 0.4\text{--}0.8$  cm; **Fl** 40–50 mm, solitary, ascending, sessile or the basal ones shortly stipitate; **Tep** reddish-green, semisucculent, forming a tube  $27\text{--}33 \times 5\text{--}7$  mm, lobes narrowly elliptic to oblong, erect to extended,  $13\text{--}17 \times 5\text{--}7$  mm, tip cucullate, with a bundle of short white trichomes; **Fil** 30–47 mm, erect at anthesis, exceeding the tube for 23–40 mm, inserted at  $\frac{3}{4}$  of the tube length on the same level, reddish-green; **Anth** 8–11 mm, yellow with reddish dots; **Ov** cylindrical, (6–)  $8\text{--}12 \times 3\text{--}5$  mm, not prolonging into the tube, not constricted above; **Sty** 30–38 mm, yellowish-green; **Sti** capitate 3-lobed; **Fr** oblong-ellipsoid,  $15\text{--}21 \times 9\text{--}18$  mm, without scar near the apex, tepals persisting; **Se** deltoid, plane-concave,  $4\text{--}5 \times 3\text{--}4$  mm, shiny black.

According to the protologue, the species keys out near *A. debilis* (as *Manfreda pringlei*) in the key to *Manfreda* of Rose (1903c). A full description complementing the partly sparse data from the protologue was provided by Castillejos-Cruz (2009). The species is remarkable for its pubescent leaves (although the pubescence is less pronounced than in *A. maculata* and *A. pubescens*),

**Fig. 25** *Agave guiengola*  
(Etter & Kristen 83:  
Mexico; Oaxaca, Presa Lic.  
Benito Juárez, 190 m).  
(Copyright: J. Etter &  
M. Kristen)



and is characterized by its broad, ovate-lanceolate leaves gradually narrowing towards the base. Morphologically it is closest to *A. scabra* and *A. pubescens*. At present known from 4 collections only (Castillejos-Cruz 2009). — For details of the typification see González Medrano (1991). — The species is erroneously omitted from the *Manfreda* accounts of Piña Luján (1985), Piña Luján (1986), and Hochstätter (2016). It has to be considered as “Rare” in the IUCN Red List Categories

**A. guiengola** Gentry (Brittonia 12: 98–100, ills., 1960). **Type:** Mexico, Oaxaca (*Gentry* 16436 [US, ARIZ, DES, MEXU, MICH]). — **Lit:** Gentry (1982: 97–99, with ills.); Ullrich (1991k: with ills.); García-Mendoza (2003: with ill.); (García-Mendoza & al. 2019: 8). **Distr:** Mexico (Oaxaca: Cerro Guiengola); limestone rocks in short-tree forests, 100–1000 m, flowers in March. **I:** MacDougall (1956: as ‘blue Agave’); MacDougall (1966: as *A. guiengolensis*); MacDougall (1970: as *A. guiengolensis*); Irish & Irish (2000: t. 19); Heller (2006: 95, 160); Richter (2011: 62); Pilbeam (2013: 102–103); Greulich (2013); Gonzales & Mera (2015: 12); Moore (2016: 226, 227). — Fig. 25.

[1c] Acaulescent; **Ros** open, mostly solitary; **L** few, at maturity 9–16 (to 25–30 in cultivation), broadly lanceolate, sometimes ovate, openly ascending, fleshy-leathery, short-acuminate, nearly

flat above but briefly and narrowly channelled apically, 30–50 × 14–25 cm (larger in cultivation), light grey or white-glaucous, with transversal bands, epidermis finely and densely papillate, margins repand, discontinuous, variously serrate; **marginal teeth** flattened, blunt, fine or coarse, unequal, 1- to 3-cuspidate, 1–10 × 2–9 mm, (5–) 15–20 mm apart, often basally confluent, dark brown, on prominences or on a lenticular base; **terminal Sp** acicular, rounded above and below, pungent, 6–8 (–15) mm, dark brown, not decurrent; **Inf** erect, (1.6–) 2–4 (–5) m, ‘spicate’, peduncle with recurved, long attenuate upper **Bra** and bracteoles, **Bra** scarious, with a dark midvein, subulate-lanceolate, 10–20 × 3 mm at the deltoid base, fertile **Inf** part from near the base, part-**Inf** with 2–3 flowers; **Ped** 5–8 mm; **Fl** inconspicuous, 30–45 mm; **Tep** greenish-yellow, pale yellow or yellowish-white, tips reddish or rose on the outer face, 17–18 × 4–5 mm, erect or slightly incurved, tube funnel-shaped, 2–4 mm (García-Mendoza 2003; “virtually tubeless” according to the protologue), lobes elliptic to lanceolate, openly ascending, straight; **Fil** 15–21 mm, yellowish, inserted at the lobe bases; **Anth** excentric, versatile, 13 mm, yellow; **Ov** cylindrical to obconical, sulcate, 10–14 mm, neck narrowly constricted, green; **Sty** longer than the filaments; **Sti** thickened; **Fr** oblong-ovate, thin-walled, 11–18 × 5–6 mm (from *García-Mendoza* 6062,



ASU0000570!; protologue: 22–24 mm), shortly beaked; **Se** “small”, without further data.

A strikingly ornamental and very distinct species esp. due to its broad, thick, white-glaucous leaves. In the protologue, where the flowers are described as “nearly tubeless”, placed in Sect. *Choritepalae* (as Group), but differing from the other species (*A. bracteosa*, *A. ellemetiana*, *A. gypsicola*) geographically as well as in the shape and colouration of the toothed leaves, its strictly monocarpic rather than polycarpic habit (protologue), and its seed morphology (Ullrich 1991k). Ullrich (1991k) therefore regards Sect. *Choritepalae* (as Group) as artificial (see also the introduction to the genus). The description by García-Mendoza (2003) differs from the protologue, esp. by giving a tube length of 2–4 mm. The fruits, as described above, are among the smallest in the genus. — For the closely related *A. gypsicola* see there.

The type locality Cerro Guiengola is a karstic limestone formation  $\pm 20$  km NW Tehuantepec, where the species grows “on sheer cliff-faces in prodigious numbers, resembling dense colonies of sea-stars” (Trager 2011) and even on the ancient Zapotec pyramids (MacDougall 1956, Ullrich 1991k). The species was also collected at the microwave tower at Santa María Jalapa del Marqués slightly further northwest (MEXU AGA807760). Well-nourished plants in cultivation may develop much larger rosettes and inflorescences (Greulich 2013). *A. guiengola* is propagated via tissue culture at the Huntington Botanical Garden (Gomez Rhine 2009). ‘Moto Sierra’ K. Griffin (= ISI 2011–14) is a cultivar with confluent teeth giving the leaf-margin a chain-saw-like appearance (Trager 2011), and ‘Creme Brulee’ is a variegated cultivar with cream-coloured margins (Starr 2014: 222, for illustrations see Moore 2016: 227).

**A. ×guignardii** Trelease (in L. H. Bailey, Stand. Cycl. Hort. 1: 233, 235, 1914). **Nom. inval.**, ICN Art. 38.1a. **Type:** not typified. — **Distr:** Cultivated only.

[1b × 2o] This is the artificial intersubgeneric hybrid *A. attenuata* × *A. potatorum* (as *A. verschaffeltii*). Apparently lost from cultivation.

**A. guttata** Jacobi & C. D. Bouché (Hamburg. Gart.- & Blumenzeit. 21: 561, 1865). **Type:** not typified. — **Lit:** Rose (1903c: 21–22); Verhoek-Williams (1975: 233–244); Piña Luján (1985: 35, 85–86, with ill.); McVaugh (1989: 230–231); Castillejos-Cruz (2009: [150]–[156], with ills.); all as *Manfreda*. **Distr:** Mexico (Chihuahua, Durango, Zacatecas, San Luis Potosí, Aguascalientes, Nayarit, Jalisco, Guanajuato, Querétaro, Hidalgo, Michoacán); open grassy roadsides, rocky fields, summit of hills, roadcuts, in oak, pine-oak and tropical deciduous forests, desert scrub and grasslands, 1220–2440 m; flowers mid-July to September. **I:** Curtis’s Bot. Mag. 86: t. 8429, 1912, as *A. protuberans*; Anonymous (1940); Rodríguez & Castro-Castro (2006: 624); Rodríguez & Castro-Castro (2007: 9); Richter (2007: 42); Hochstätter (2016: I: 21); Castro-Castro & al. (2017: 62); all as *Manfreda*.

≡ *Manfreda guttata* (Jacobi & C. D. Bouché) Rose (1903) ≡ *Polianthes guttata* (Jacobi & C. D. Bouché) Shinnars (1966); **incl.** *Agave protuberans* Engelm. ex Baker (1888) ≡ *Leichtlinia protuberans* (Engelm. ex Baker) H. Ross (1894); **incl.** *Leichtlinia commutata* H. Ross (1896).

[3a3] Plants herbaceous; corm 2–5 × 2–4.5 cm, oblong to subcylindrical, succulent, stoloniferous; bulb 1.8–3 × 1.8–3.5 cm, cylindrical, nearly completely covered with dried leaf bases 4.5–6 cm long, these slightly membranous at the base and fibrous above; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, 2–7 (–13), extended, lanceolate to lanceolate-elliptic, narrowed towards the base, semisucculent, canaliculate, slightly wavy, lower face slightly papillose above the veins, upper face glabrous, apex obtuse, apiculate, (8–) 17–34 × (0.9–) 1.2–3.5 cm, light green to glaucous, sometimes with small to large confluent dark-green to purple dots, margins entire, with a cartilaginous, finely denticulate to erose hyaline band; **Inf** 60–160 cm, erect, light green to yellowish, ‘spicate’; **Bra** 8–12, lower ones similar to the leaves; fertile **Inf** part (2.3–) 4–14 cm, dense, with (2–) 4–25 (–33) flowers; floral **Bra** 0.8–3.1 × 0.3–1 cm; **Fl** 27–42 mm, solitary, sessile, ascending; **Tep** yellowish-green to reddish with purple tinge, semisucculent, forming a tube 7–11 × 4–5 mm, lobes oblong to



narrowly elliptic, recurved to revolute, 10–15 (–17) × 4–5 mm, tip cucullate, with a bundle of short white trichomes; **Fil** 26–38 (–46) mm, arching upwards at anthesis, exceeding the perianth tube for 19–32 (–42) mm, inserted at the upper end of the tube on the same level, reddish-green with small purple dots; **Anth** (9–) 12–15 mm, yellow; **Ov** cylindrical to slightly ellipsoid, 7–13 × 4–7 mm, greenish, prolonging 1–5 mm into the perianth tube, slightly constricted above; **Sty** 36–52 mm, yellowish-green; **Sti** capitate 3-lobed; **Fr** ellipsoid, 13–22 (–25) × 10–18 mm, with a scar near the apex, base of tepals and style persisting; **Se** deltoid, plane-concave, with narrow margin, 3–4 × 2–3 mm, shiny black.

The cylindrical storage rhizome and the presence of spreading rhizomes, the denticulate-erose leaf margin, dense inflorescence, and the stubby flowers with revolute lobes and exerted stamens and styles are diagnostic for this widespread species (Verhoek-Williams 1975: 238, Castillejos-Cruz (2009). Morphologically closest to *A. planifolia* (as *Manfreda*) esp. in its flowers, and to an as yet undescribed species “*Manfreda valsequillana*” (Castillejos-Cruz 2009); the latter appears to be the same as the undescribed *M. riosramirii* from Mpio. Valsequillo in Puebla, dealt with in the same publication.

**A. gypsicola** García-Mendoza & D. Sandoval (Acta Bot. Mex. 126: e1461: 6, ills. (pp. 7, 15), 2019). **Type:** Mexico, Oaxaca (*García-Mendoza & Franco Martínez* 11218 [MEXU [2 parts], IEB, MEXU, MO]). — **Distr:** Mexico (W-C Oaxaca: Tlaxiaco Distr., upper Río Verde basin); on gypsisols in xerophytic scrub, 1350–1600 m; flowers January to March.

[1c] Acaulescent; **Ros** open, solitary, 0.7–1 × 1–1.4 m; **L** 20–40, broadly ovate to semi-orbicular, erect, soft, thickened at the base, with acute apex or caudate, flattened, 45–60 × 20–26 cm, 1.8–2.5 × longer than broad, glaucous or glaucous-yellowish, epidermis densely papillate, margins straight, horny, continuous, reddish-brown or whitish-yellow when young, dentate; **marginal teeth** deltoid, straight or antrorse, 1–3 (–4) × 2–4 mm, brownish-red, <5 mm apart;

**terminal Sp** 25–55 × 3–7 mm, brownish-reddish, decurrent for (15–) 40–70 mm; **Inf** inclined above, 4.5–5 (–6) m, ‘spicate’, peduncle green-yellowish, ± erect, with chartaceous long triangular **Bra** (12–) 15–19 × 3–5 cm, fertile part ± inclined to overhanging, dense, in the upper ½ of the inflorescence; floral **Bra** 0.8–1.5 × 0.2–0.3 cm, filiform; **Ped** short; **Fl** 30–35 (–37) mm; **Te** greenish-yellowish, tube none, replaced by a discoid receptacle, lobes oblong, slightly recurved at anthesis, 17–18 × 2–4 mm; **Fil** 40–45 mm, pale yellow, inserted at the lobe bases; **Anth** 10–15 mm, yellow; **Ov** cylindrical, 15–17 × 3–4 mm, neck 3–4 mm; **Sty** 40–45 mm, whitish-yellowish; **Sti** filiform to clavate; **Fr** clavate or ellipsoid, (20–) 30–32 × 12–14 mm; **Se** semicircular, unwinged, 3–4 × 2–3 mm, black.

In the protologue placed in Sect. *Choritepalae* (as Group), and compared with *A. guiengola* from which it differs in having more and broadly ovate to semi-orbicular, glaucous or glaucous-yellowish leaves with smaller and narrower marginal teeth and a longer, decurrent terminal spine, its inclined inflorescences with greenish-yellowish flowers with lobes recurved at anthesis, larger fruits, and its occurrence at higher altitudes on soils rich in gypsum.

Vernacular name: “maguey blanco” (Zapotec: “xavi kuiji”). Fresh leaves are cooked and flowers and buds are eaten as stew or dried; the dried inflorescences are used for fences. The species is assigned to the “Endangered” IUCN Red List Category.

**A. gypsophila** Gentry (Agaves Cont. North Amer., 510–512, ills., 1982). **Type:** Mexico, Guerrero (*Floyd & Ryan* 103 [MICH, ARIZ, UC]). — **Lit:** McVaugh (1989: 137); Vázquez-García & al. (2013). **Distr:** Mexico (S Guerrero); limestone outcrops, in thorn and tropical dry forests, occasionally near the ecotone with pine-oak forests, 600–900 m; flowers February to June. **I:** Etter & Kristen (1997+: accessed 2016). – Fig. 26.

[2n] Acaulescent; **Ros** 0.8–1 × 0.9 m tall, solitary, not surculose; **L** 8–11, narrowly lanceolate to obtusulate, firm but brittle, smooth, 70–100 (–125) × 8–19 cm, light to dark green, not

**Fig. 26** *Agave gypsophila*

(Etter & Kristen 1671:  
Mexico; Guerrero, S of  
Acahuizotla, 860 m).  
(Copyright: J. Etter &  
M. Kristen)



evidently cross-zoned, margins repand; **marginal teeth** 1–2 mm, on low prominences 2–4 × 4–6 mm, 5–16 (–25) mm apart at mid-leaf, intervening margin concave; **terminal Sp** 5–11 mm; **Inf** 5–6 m, paniculate, not bulbiferous, peduncle slender, ±7–10 mm Ø; **Fl** 31–34 mm; **Tep** orange-yellow, tube 4–5 × 9 mm, lobes ± equal, triangular, 10–11 × 3–4 mm; **Fil** 20–23 mm, inserted 1–2 mm above the tube base, orange-yellow; **Anth** 11–12 mm, orange-yellow; **Ov** ±15 × 3.5–4 mm, greenish, neck slightly constricted; **Fr** 28–30 × 17–20 mm; **Se** 3–3.7 × 1.7–2.4 mm.

The recent study of the *A. gypsophila* complex by Vázquez-García & al. (2013) has led to a re-circumscription of *A. gypsophila* and the publication of 4 new species (*A. abisaii*, *A. andreae*, *A. kristenii*, *A. pablocarrilloi*). Gentry's protologue of *A. gypsophila* cites 3 specimens from Guerrero that correspond to the narrowed circumscription of the species, 1 specimen from Jalisco (Gentry 23532) now placed in *A. abisaii*, and 3 specimens from Colima (Gentry 19563, 22193, 23533) now placed in *A. pablocarrilloi* (Vázquez-García & al. 2013).

At present, no full description of *A. gypsophila* s.s. is available, and the data above are taken from the comparative table in Vázquez-García & al. (2013), augmented from Etter & Kristen (1997+: accessed 2016), and the holotype. The diagnostic characters for *A. gypsophila* s.s. include narrowly lanceolate to obovate, smooth, flexible, green, and not evidently cross-zoned leaves.

Nearly all illustrations available published or in the web under the name of *A. gypsophila* are misidentified. The illustrations in Vázquez-García & al. (2007b: M5–M8) are *A. abisaii*, the illustrations in Cházaro Basáñez & al. (2006a) and Vázquez-García & al. (2007b: M1, M3) are *A. andreae*, the illustrations in Vázquez-García & al. (2007b: M2, M9, M10) are *A. kristenii*, and the illustrations in Gentry (1982: 511: figs. 18.4 & 18.5), Newton (1999), García-Mendoza (2003), Newton (2004), Richter (2011: 82), Pilbeam (2013: 104), Guillot Ortiz & Meer (2016c: 28: fig. 2, 29: figs. 3–5), and Moore (2016: 268, 269) represent *A. pablocarrilloi*. The new record from coastal Michoacán (Ullrich 1991b) is *A. kristenii*, but the plant depicted appears to be *A. pablocarrilloi*. The only correctly labelled illustrations of *A. gypsophila* at present appear to be those on the web page of Etter & Kristen (1997+: accessed Dec. 2016).

**A. harrisii** Trelease (Mem. Nation. Acad. Sci. 11: 34, tt. 50–51, 1913). **Type** [syn]: Jamaica (*Harris* s.n. [MO [4 sheets from 1907, 1909 and 1911]]). — **Lit**: Berger (1915: 208); Adams (1972: 81). **Dist**: Jamaica; arid coastal to densely wooded interior limestone, 10–50 (–700) m; flowers March to April. **I**: Richter (2011: 137); Hochstätter (2015: VII: 71).

[2p] Acaulescent; **Ros** solitary; **L** narrowly lanceolate, ± sigmoidally curved, upper ¼ recurved, gradually acute, slightly guttered, 100–200 ×

15–35 cm, rather glossy dark green, margins between the teeth straight or concave; **marginal teeth** straight or curved, narrowly triangular, scarcely 2 mm, 10–20 mm apart, often from the tops of green prominences; **terminal Sp** conical, somewhat flexuous or recurved, narrowly channelled towards the base, smooth, 10–15 × 2 mm, reddish-brown, glossy, not decurrent; **Inf** 8–10 m, paniculate, not known to be bulbiferous, part-**Inf** ±60 cm; **Ped** 5–10 mm; **Fl** 45–50 mm; **Tep** ±20 mm, yellow, tube open, 7–8 mm, lobes erect, 12–15 × 4 mm; **Fil** 30–35 mm, inserted near the bottom of the tube; **Ov** fusiform, 25–30 mm; **Sty** ± as long as the filaments; **Fr** narrowly oblong, 45–50 × 15–20 mm, shortly beaked, turbinate narrowed rather than stipitate; **Se** crescent-shaped, 7 × 4–5 mm.

The protologue cites types with three different collection dates thus representing syntypes (Smith & Figueiredo 2014e: 236). *A. harrisii* is one of only three native Jamaican agaves. It differs from *A. sobolifera* in its longer ovary (25–30 vs. 15–20 (–25) mm) and from *A. longipes* in its shorter pedicels (5–10 vs. 20 mm) and shorter flowers (45–50 vs. 60–70 mm) (Adams 1972).

**A. hauniensis** J. B. Petersen (Bot. Tidsskr. 48: 158–159, ill., 1948). **Type:** Cult. BG Kobenhaven (*Anonymous* P1875/459 [C]). — **Lit:** Verhoek-Williams (1975: 227–232); Piña Luján (1985: 84–85, 87); Castillejos-Cruz (2009: [157]–[163], with ill.); all as *Manfreda*. **Distr:** Mexico (Michoacán, México, Morelos, Guerrero, Oaxaca); lava fields, rocky slopes in juniper, oak and pine-oak and tropical deciduous forests or in full sun in glades, 700–2150 m; flowers October to January. **I:** Rodríguez & Castro-Castro (2006: 623, 625); Hochstätter (2016: I: 22); both as *Manfreda*.

≡ *Manfreda hauniensis* (J. B. Petersen) Verhoek-Williams (1978); **incl.** *Manfreda tlatlayensis* Matuda (1965) (*nom. inval.*, ICN Art. 29.1); **incl.** *Manfreda insignis* Matuda (1966).

[3a1?] Plants herbaceous, very large (for Subgen. *Manfreda*); rhizome cylindrical, branched, 7 cm Ø, reproducing vegetatively by lateral shoots from the storage rhizome, covered with dried leaf bases, these cartilaginous at the base and fibrous above; **R** abundant, fibrous; **L** 6–10, semi-erect to slightly arcuate, linear-lanceolate,

46–95 × 4–12 cm, green, canaliculate, somewhat coriaceous, slightly glaucous on the lower face, dark on the upper face, apex acute, with a long pungent point, margins hyaline, cartilaginous, irregularly dentate, teeth small to large, simple, bifid or trifid; **Inf** 2–3.5 (–3.8) m, erect, glaucous-green, ‘spicate’; **Bra** 7–10, diminishing in size upwards; fertile **Inf** part (20–) 45–60 cm, dense, with 20–40 flowers; floral **Bra** (2–) 2.7–3 × (0.4–) 0.7–1 cm; **Fl** 40–48 mm, solitary, sessile, ascending; **Tep** green in bud, mature brownish-green, forming a funnel-shaped perianth, straight, tube 12–22 × 4–8 mm, lobes oblong, extended to revolute, 25–32 (–37) × 5–7 mm, tip semi-succulent, cucullate, with a bundle of short white trichomes; **Fil** ±125 mm, erect to extended at anthesis, exceeding the tube for (69–) 73–85 (–89) mm, inserted at mid-tube on the same level, reddish with brown dots; **Anth** 22–29 mm, yellow to reddish; **Ov** ellipsoid to ovoid, 12–22 × 5–8 mm, reddish-green, not constricted above; **Sty** (72–) 77–108 (–112) mm, reddish-brown; **Sti** clavate, 3-lobed, reddish-brown; **Fr** ovoid to oblong, 22–35 × 12–20 mm, tepals persisting (?); **Se** plane-concave, 5–6.3 × 5 mm, rough, dull black.

*A. hauniensis* was published based on a cultivated specimen of unknown wild origin which flowered at BG Copenhagen in 1945. It is well characterized within Sect. *Herbaceae* by its considerable size, leaves with a hardened pungent tip (not found in other species) and denticulate margins, and in possessing a branched rhizome without bulb (all other species are bulbous). All these characters point towards Subgen. *Littaea*, and the species might have arisen as an allopolyploid between a species of Sect. *Herbaceae* and a species of Subgen. *Littaea*, but evidence from karyology or other sources is wanting as yet. The leaf longevity (evergreen?) is unknown. The rhizome is used for laundry (Castillejos-Cruz 2009).

**A. havardiana** Trelease (Annual Rep. Missouri Bot. Gard. 22: 91, tt. 84–86, 1912). **Type** [syn]: USA, Texas (*Havard* s.n. [MO]). — **Lit:** Berger (1915: 178); Gentry (1982: 531–535, with ill.); Reveal & Hodgson (2002); Starr (2012: 106–109, 322–323, ill.). **Distr:** USA (SW

**Fig. 27** *Agave havardiana* (Eggl s.n.: USA; Texas, Big Bend National Park, Chisos Mts., 1450 m). (Copyright: U. Eggl)



Texas: Big Bend region), Mexico (N Chihuahua, N Coahuila); rocky slopes in mountain grassland with scattered oak and juniper, frequently on limestone, 1200–2000 m; flowers June to September. **I**: Kuppen (2000: 87); Irish & Irish (2000: t. 20); Heller (2006: 96); Bulot (2010: 40); Richter (2011: 128); Pilbeam (2013: 105); Hochstätter (2015: III: 14). – Fig. 27.

[21] Acaulescent; **Ros** rather open, (0.4–) 0.5–0.8 × (0.5–) 1–1.5 m, mostly solitary, suckering sparingly; **L** lanceolate to broadly lanceolate, ascending, thick, rigid, broadest at the clasping base, slightly narrowed above the base, widest below the middle, convex below, concave above, 30–60 (–70) × 15–27 cm, rarely larger, glaucous-grey to light or grey-green, occasionally yellowish, not cross-zoned, margins straight; uppermost **marginal teeth** ± straight, other teeth reflexed, single, well defined, numerous, larger teeth towards the leaf tip, mostly (3–) 7–10 mm, gradually diminishing downwards, 15–25 (–30) mm apart; **terminal Sp** stout, straight to sinuous, subulate, roundly keeled below, broadly grooved above, mostly 30–50 (–100) × 5–7 mm, dark brown to greyish, long decurrent, sometimes as a complete horny margin; **Inf** 2–7 m, paniculate, peduncle with persistent lanceolate **Bra** (3–) 5–10 cm long, fertile part broad, dense, part-**Inf** slightly ascending, large, 12–20, with 21–48 flowers, comprising the upper  $\frac{1}{2}$ – $\frac{2}{3}$  of the inflorescence, >10 cm, not bulbiferous; **Fl** erect, 68–90 mm;

**Tep** yellow to yellow-green, tube deeply funnel-shaped, 14–22 × 15–22 mm, lobes erect, slightly unequal, 18–24 × 4–5 mm, inner shorter, narrower, involute-conduplicate, wilting early and inwards; **St** long-exserted; **Fil** erect, long-tapered to the apex, 50–65 mm, yellow, inserted rather irregularly above mid-tube; **Anth** excentric, 25–30 mm, yellow; **Ov** fusiform, 30–40 mm, green, neck short, thick, constricted; **Sty** stout, longer than the tepals; **Sti** capitate, 3-lobate; **Fr** oblong to obovoid, 40–55 × 14–20 mm, apex beaked, broadly short-stipitate, on strong pedicels; **Se** 6–7 × 4–5 mm, smoothly black, marginal wing low, hilar notch small.

Distinguished within Sect. *Parryanae* (as Group) by the very broad-based acuminate leaves with reflexed teeth, and tepals forming a deep tube and with relatively short lobes (Gentry 1982: 535). *A. havardiana* hybridizes with *A. lechuguilla* (= *A. ×glomeruliflora*), and backcrosses with that hybrid (see there). The 4 type sheets at MO are not cross-labelled and represent syntypes.

The species has a multiple pollinator syndrome and is pollinated by birds during the day and by bats during the night; nectar production and stigma receptivity is both nocturnal and diurnal (Slauson 2002a). The feeding ecology of flower-visiting hummingbirds was studied by Kuban & Neill (1980) and Kuban & al. (1983), and the nectar sugar variability by Reid & al. (1985).



**A. hiemiflora** Gentry (Agaves Cont. North Amer., 480–482, ills., 1982). **Type:** Guatemala (Gentry 23640 [US, ARIZ, DES, MEXU, MICH]). — **Lit:** Lott & García-Mendoza (1994: online version with ills.); Véliz Pérez (2013: 237–239, 479, 489, with ill.). **Distr:** Mexico (Chiapas: E mountains), Guatemala (Huehuetenango); montane slopes, often on limestone, in pine-oak or also in montane rain forests, rarely epiphytic, 800–2290 m; flowers October to December. **I:** Richter (2011: 114, 123); Pilbeam (2013: 106); Hochstätter (2015: VI: 7).

[2o] Acaulescent; **Ros** compact, 1–1.5 m Ø, solitary, not surculose; **L** 50–90, lanceolate to ovate, openly spreading, rather softly fleshy, gradually narrowed and thickened towards the base, acuminate, flat to slightly concave above, mostly 30–60 × 8–15 cm, light grey-glaucous to pale green, margins repand to deeply crenate; larger **marginal teeth** curved or retrorse, rarely straight, (1–) 5–8 mm at mid-leaf, (10–) 20–40 mm apart, light to dark brown or greyish, or teeth smaller and more distal on the repand margins, all on distinct prominences, the slender tips variously curved up or down; **terminal Sp** slender or thick, sinuous or contorted to straight, openly grooved to flat above, generally 20–40 mm, brown, decurrent; **Inf** 2–5 m, paniculate, peduncle with remote, triangular, quickly drying **Bra**, fertile part slender, narrow, part-**Inf** small, dense, densely tufted with scarious, frequently dark-coloured bractlets, 20–30 in the upper ½–¾ of the inflorescence, on very short (4–5 cm) or longer (10–20 cm) stalks; **Ped** slender, to 5 mm; **Fil** slender, 45–55 (–70) mm; **Tep** yellow, sometimes red in bud, tube broadly tubular to funnel-shaped, angled to rather knobby, lightly grooved, 5–13 mm, lobes oblong, unequal, 15–23 mm, involute; **OTep** linear-lanceolate, erect-ascending, obtuse, frequently reddish towards the tip, overlapping the inner tepals at the base; **ITep** smaller, narrower but widened at the base, keel narrow; **Fil** slender, flattened adaxially, (30–) 45–60 mm, inserted in the middle or near the mouth of the tube, reddish; **Anth** straight, regular, centric, 15–27 mm, yellow; **Ov** angled-cylindrical, 20–30 (–40) mm, neck short, smooth, little-constricted; **Sty** finally longer than the stamens; **Sti** capitate, triquetrous;

**Fr** ovoid to oblong, 30–40 × 14–20 mm, scarcely beaked; **Se** 5–6 × 3.5–4 mm.

A highland relative of *A. seemanniana* and *A. congesta*, sharing with both moderate leaf variability, and an openly grooved to flat terminal spine. It differs from *A. seemanniana* in a more regular leaf form and size with a less narrowed base, and the densely tufted bracteolate apex of the part-inflorescences, and from *A. congesta* in its small rosette, less robust and more richly branched open inflorescence with fewer part-inflorescences, and filaments more evenly inserted at a lower level in the tube (Gentry 1982: 480). The species is used for fibre. The IUCN Red List Category is “Vulnerable” according to Véliz Pérez (2013).

**A. hookeri** Jacobi (Hamburg. Gart.- & Blumenzeit. 22(4): 168, 1866). **Type** [neo]: Ex cult. Kew (*Brown* s.n. [K]). — **Lit:** Berger (1915: 162–163); Gentry (1982: 338–340, with ills.); McVaugh (1989: 137–138); Hernández-Vera & al. (2007b). **Distr:** Mexico (Jalisco, Michoacán); apparently cultivated only or as spontaneous escape (?), in mountain regions in pine-oak forests, 1920–2285 m; flowers October to January. **I:** Richter (2011: 111); Pilbeam (2013: 107); Greulich (2014a: 57–59, 61);

[2d] Stems short, thick; **Ros** to 2 m, solitary; **L** lanceolate, arching in age, thickly fleshy, gradually narrowed towards base and tip, generally concave above, 120–175 × 20–25 cm, glaucous to green or yellow-green, margins repand to crenate, esp. in the middle of the lamina, nearly straight below; **marginal teeth** straight or curved, 8–12 mm (middle of the lamina), dark brown to greyish-brown, 20–50 mm apart, with few smaller intermittent teeth, much reduced and closely spaced towards the base, broadly based on fleshy prominences; **terminal Sp** subulate, shortly openly grooved above, roundly keeled below, and with linguiform protrusion into the leaf, 35–60 mm, edges decurrent as toothless smooth horny border for 15–20 cm; **Inf** 7–8 m, paniculate, peduncle with narrow, triangular, reflexed **Bra**, part-**Inf** compact, 20–40 in the upper ½ of the inflorescence; floral **Bra** caducous; **Ped** long; **Fil** slender, 63–80 mm; **Tep** yellow, red to pink in



bud, tube grooved, 5–8 × 13–14 mm, lobes red to pink, linear, erect, elongate, conduplicate, unequal, outer 28–32 mm, rounded on the back, cucullate, inner 2–3 mm shorter, with prominent keel; **Fl** slender, flattened, 50–60 mm, inserted above mid-tube; **Anth** excentric, 26–34 mm, yellow; **Ov** cylindrical, angled, smooth, 34–41 mm, neck long, grooved, constricted; **Sty** almost as long as the filaments; **Sti** capitate; **Fr** oblong, rounded at the tip, thick-walled, 50–55 × 25 mm, stipitate; **Se** broadly crescent-shaped, rugose, 8–9 × 6–7 mm, lucid black, hilar notch broad, marginal wing broad but little raised.

Recognizable among the species of Sect. *Crenatae* (as Group) by its large size, the glaucous leaves with long-decurrent spine-bases, the short flower tube and the very long tepal lobes (Gentry 1982: 340). Gentry's "type" represents in fact a neotype (McVaugh 1989: 138). The collection *Diguét* s.n. (P) cited by McVaugh for Jalisco is likely a misidentification with *A. inaequidens*, and the collection Gentry s.n. (DES, now at ARIZ 266166) from Jalisco cited by Gentry (1982: 352) appears to represent a cultivar introduced from Michoacán according to Hernández-Vera & al. (2007a); a further collection from Jalisco (García-Mendoza & al. 6409, ASU 0000674!, MEXU AG817141) is designated as "semi-cultivada". Widely cultivated for pulque in Michoacán. Morphometric studies showed that *A. hookeri* is most similar to cultivated *A. inaequidens*, supporting the hypothesis that it could merely represent the extreme of a domestication gradient *A. inaequidens* wild → *A. inaequidens* cultivated → *A. hookeri* cultivated (Figueredo-Urbina & Casas 2012, Figueredo & al. 2014). A cluster analysis of morphological data showed *A. hookeri* to be nested within *A. inaequidens* (Figueredo-Urbina & al. 2017). For differences from *A. inaequidens* see there.

The name *A. hookeri* was independently published three times for different taxa: The oldest, *A. hookeri* K. Koch (1865), is a synonym of *A. spicata* Cavanilles (1802), the younger *A. hookeri* Jacobi (1866) was based on cultivated plants and applied by Gentry to plants he collected in Michoacán, and are described above, and the illegitimate *A. hookeri* Baker (1881) is a synonym

of *A. inaequidens* K. Koch (1860). A proposal to conserve the established name *A. hookeri* Jacobi against *A. hookeri* K. Koch was published by Figueiredo & Smith (2014) and was recommended by the relevant committee (Applequist 2014: 1368).

**A. horrida** Lemaire *ex* Jacobi (Hamburg. Gart.- & Blumenzeit. 20: 546–547, 1864). **Type** [neo]: Mexico, Morelos (*Pringle* 8206 [US, CM, E, G, MEXU, MO, NDG, NY, P, S, VT]). — **Distr**: S Mexico.

The neotype cited above was designated by Gentry (1982: 146).

**A. horrida** ssp. **horrida** — **Lit**: Berger (1915: 100–101); Gentry (1982: 144–146, with ill.); Ullrich (1993b: with ill.); Starr (2012: 110–114, with ill.). **Distr**: Mexico (México, Morelos, C Puebla, C Guerrero, NW Oaxaca); volcanic rocks and rocky slopes in mountain regions, pine-oak forests and rosette scrub, 1600–2440 m; flowers January to March and July. **I**: Curtis's Bot. Mag. 106: t. 6511, 1880; García-Mendoza (2002: 186); Heller (2006: 97, 156); Richter (2011: 68, 122); Pilbeam (2013: 108); Hochstätter (2015: IX: 33); Moore (2016: 254–255).

**Incl.** *Agave grandidentata* Hort. Belg. *ex* Jacobi (1866); **incl.** *Agave maigretiana* Jacobi (1866) ≡ *Agave horrida* var. *maigretiana* (Jacobi) Trelease (1914); **incl.** *Agave horrida* var. *laevior* Jacobi (1869); **incl.** *Agave horrida* var. *micracantha* Baker (1877); **incl.** *Agave desmetiana* hort. *ex* Baker (1877) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave regeliana* hort. *ex* Baker (1877) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave horrida* var. *macrodonta* Van Geert (1878); **incl.** *Agave artichaut* Hort. C. Besserer *ex* A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave horrida* var. *latifrons* Hort. Besaucèle *ex* A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave horrida* var. *monstruosa* Hort. Besaucèle *ex* A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave horrida* var. *recurvispina* Hort. Besaucèle *ex* A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave horrida* var. *viridis* Hort. Besaucèle *ex* A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave killischkii* hort. *ex* A. Berger (1915) (*nom. inval.*,

**Fig. 28** *Agave horrida* ssp. *perotensis* (Etter & Kristen 994: Mexico; San Luis Potosí, Sierra Alvarez, 2350 m). (Copyright: J. Etter & M. Kristen)



ICN Art. 36.1c); **incl.** *Agave regelii* Hort. Besauccèle *ex* A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[lg] Acaulescent; **Ros** compact, formidably armed, 0.3–0.6 × 0.45–0.9 m, solitary; **L** 80–100 in mature rosettes, ovate to elliptic-lanceolate, patulous, rigidly thick-fleshy, slightly narrowed above the base, short-acuminate, convex below, flat to guttered above, generally 18–35 × 4–7.5 cm, yellowish-green, green or dark olive-green, margins thickly horny, straight to sinuous between the teeth; **marginal teeth** straight to variously curved, sometimes hooked, broadly flattened at the base, massive, generally 10–15 mm, rarely much smaller, light grey, 5–10 mm apart, continuing to near the base of the terminal spine; **terminal Sp** semicircular to subdeltoid in cross-section, very pungent, flattened rather than grooved above, 25–40 mm; **Inf** 2–2.5 m, ‘spicate’, slender, peduncle 1–1.5 m, with deltoid-attenuate, narrow, appressed **Bra**, fertile part slender, part-**Inf** with 1–2 flowers; **Ped** slender, 4–8 mm; **Fl** 35–40 mm; **Tep** dark purple, red or yellow, tube shortly funnel-shaped, 3–5 × 8–9 mm, lobes linear, obtuse with small hood, equal, 15–16 × 4–6 mm, the inner broader, with a prominent keel; **Fil** slender, regular, flattened, 36–42 mm, mostly reddish, inserted near the rim of the tube; **Anth** centric, regular, 14–16 mm, bronze to red or purple; **Ov** fusiform, 17–20 mm, neck constricted, smooth or slightly grooved; **Fr** ovoid, 20–25 × 12–14 mm, beaked, on strongly

jointed pedicels 10–12 mm long; **Se** crescent-shaped, 3–4 × 2–3 mm.

Exhibited for the first time by Verschaffelt in 1862, and introduced by the collector C. Besserer as *A. artichaut* (Berger 1915). Hardly separable from some small-leaved forms of *A. ghiesbreghtii*, from which it otherwise differs by larger, more numerous leaf margin teeth continuing nearly to the base of the terminal spine (Gentry 1982). Plants with yellow or reddish flowers may occur in the same population (e.g. Gentry 23368 (DES 00009541!, ASU 131463!); García Mendoza 6143 (ASU 0000670!)). The collection Steinmann & Ramírez-Amezcuca 5771 (MEXU; det. A. García-Mendoza) is a new record for Guerrero (Portal Datos Abiertos UNAM 2018+: accessed Dec. 2018).

The species is self-compatible and mainly pollinated by a nocturnal bat, but two species of diurnal hummingbirds are also regular visitors and successful, though less efficient pollinators (Flores-Torres & Galindo-Escamilla 2017).

**A. horrida** ssp. *perotensis* B. Ullrich (Cact. Suc. Mex. 35(4): 80, ill. (p. 96), 1990). **Type:** Mexico, Veracruz (Gentry & al. 20417 [US, ARIZ, MEXU]). — **Lit:** Gentry (1982: 161–164, as *A. obscura*); Ullrich (1992f); Jimeno-Sevilla (2010: 377–378); Starr (2012: 111, 113–114); all with ills. **Distr:** Mexico (N Puebla, C Veracruz). **I:** Aalsemgeest & al. (2006b: 214); Heller (2006: 97); Richter (2011: 115); Pilbeam (2013: 109); Hochstätter (2015: IX: 34). — Fig. 28.

[1g] Differs from ssp. *horrida*: **Ros** with somewhat more leaves, small to medium-sized; **L** narrowly linear to ovate, 25–40 × 5–8 cm, pale green to green; **marginal teeth** variable, small (3–5 mm) or large (10–15 mm), straight to curved or flexuous, frequently slanted downwards and curved, <10 mm or 20–30 mm apart; **terminal Sp** conical to subulate, 30–50 mm, broadly decurrent; **Inf** long, tapering, 3–5 m, more densely flowered in the upper  $\frac{2}{3}$  in spiralling sequence, **part-Inf** with geminate flowers with shorter pedicels.

Plants belonging to this taxon were previously misinterpreted as *A. obscura* (see there) by Trelease (1920: 137), Breitung (1959: 146) and Gentry (1982).

**A. howardii** (Verhoek-Williams) Thiede & Eggl (Kakt. and. Sukk. 50(5): 112, 1999). **Type**: Mexico, Colima (*Howard & al.* 72–70 [RSA 240114]). — **Lit**: Verhoek-Williams (1976: with ill.); McVaugh (1989: 252–253); Solano Camacho & García-Mendoza (1998: 55); Guillot Ortiz & al. (2006: 64, with ill.); Feria-Arroyo & al. (2010: with ill.); all as *Polianthes*. **Distr**: Mexico (S Jalisco, Colima); well-drained soils in partial shade in oak or tropical deciduous forests, 1000–1100 m; flowers July to August. **I**: Hannon (2002: 250); Barba-Gonzalez & al. (2012: 124); Castro-Castro & al. (2015: 145); Hochstätter (2016: II: 15); Castro-Castro & al. (2016: 239); all as *Polianthes*.

≡ *Polianthes howardii* Verhoek-Williams (1976).

[3b2] Plants herbaceous, glabrous, corm and bulb fleshy, erect, 3 × 0.9 cm, with dry leaf bases 3.5–4 cm long; **R** fleshy near the corm, becoming wiry distally; **L** 5–6, in a basal rosette from a fibrous-coated bulb, erect-spreading, broadly channelled, narrowly oblanceolate to linear, tip acute or mucronate, glabrous, 22–27 (–36) × (1–) 1.5–2.5 cm, glossy green, lower face sometimes flecked with magenta, margins entire; **Inf** 0.6–1.1 m, ‘spicate’, peduncle with ±7 **Bra**, these gradually smaller than the leaves, sometimes flecked with magenta at the base, fertile **Inf** part elongate, open, 20–70 cm, with 13–30 widely spaced solitary flowers, lowest ±3–5 (–10) cm apart; **Ped** erect, 17–29 (–50) mm,

slender, becoming thicker at fruiting time; **Fl** tubular, semipendent, deflected ±30° from the horizontal; **Tep** glaucous, outer face coral-red at the base, grading to green in the distal  $\frac{1}{3}$ , irregularly streaked with yellow, inner face greenish-yellow, often with maroon stripes in the tube, tube nearly straight, at a slight angle with the ovary and constricted just above the ovary, 18–21 × 3–5 mm, throat slightly oblique, 3–5 mm Ø, lobes rounded, slightly flaring, apical hair tuft inconspicuous, 1.5–3 × 2 mm; **St** included or anthers exerted for 2 mm, **Anth** ±5 mm, yellow; **Fil** inserted near the tube base, the upper slightly longer than the lower; **Ov** 3–4 × 2.5–3 mm; **Sty** longer than the stamens, white; **Sti** white, papillate, 3-lobed, lobes reflexed at maturity; **Fr** globose, 8–10 mm Ø; **Se** unknown. — **Cytology**: 2n = 60 (Tapia-Campos & al. 2013).

Distinctive in Sect. *Polianthes* because only it and *A. confertiflora* have solitary flowers and only in *A. confertiflora* and *A. neonelsonii* is the throat of the tube as asymmetrical. Despite these similarities, *A. howardii* has closer affinities with Ser. *Bravoa* on account of its coral-red flowers and the insertion of the stamens at the base of the tube (Verhoek-Williams 1976: as *Polianthes*).

**A. hurteri** Trelease (Trans. Acad. Sci. St. Louis 23(3): 136, tt. 8–10, 1915). **Type** [syn]: Guatemala (*Trelease* 3 [ILL]). — **Lit**: Standley & Steyermark (1952: 112–113); Gentry (1982: 482–485, with ill.); Lott & García-Mendoza (1994: online version with ill.); Smith & Steyn (2004: with ill.); Véliz Pérez (2013: 238–239, 478, 485, with ill.). **Distr**: NW Guatemala (Sierra de los Cuchumatanes, Quetzaltenango); mountains in the pine-oak forest zone, 1800–3300 m; flowers December to January and March to April. **I**: Schindhelm (2006); Richter (2011: 123); Pilbeam (2013: 110).

**Incl.** *Agave samalana* Trelease (1915).

[2o] Stems none or short and thick; **Ros** rather open with outcurving leaves to compact with ascending leaves, 1–1.8 × (1.2–) 2–3 m, solitary; **L** numerous, (broadly) lanceolate, ascending to spreading, rarely reflexed, broadest at or above

the middle, acuminate, thick-fleshy, thickly rounded below, flat to slightly guttered above, slightly rough above, more asperous below, mostly 70–130 × 13–22 cm, rarely narrower, light glaucous to pale green and yellow-green, margins ± straight or repand; **marginal teeth** straight to curved, larger teeth (2–) 6–12 mm (middle of the lamina), dark brown, 10–25 (–55) mm apart, on broad bases, rarely smaller and closer or margins quite toothless, with small intermittent teeth, brown or grey; **terminal Sp** subulate or conical, broad at the base, openly grooved above, scabrous, 30–60 (–75) mm, dark brown to greyish-brown, decurrent for more than 2× its length; **Inf** (2–) 5–8 m, paniculate, peduncle short, with deltoid to lanceolate **Bra** 15–18 cm long, fertile part stout, narrow, part-**Inf** rounded, 20–45 in the upper 2/3 of the inflorescence, 15–30 cm, freely bulbiferous; **Ped** 12–30 mm; **Fl** 55–70 (–85) mm, distinctly and strongly fruit-scented; **Tep** greenish-yellow to yellow with purple tinge, tube funnel-shaped to angulate-cylindrical, thick-walled, grooved, 7–15 × 15–20 mm, lobes linear-lanceolate or spatulate, unequal, outer 16–28 × 7 (at the base) mm, erect-ascending, rounded to obtuse, inner conduplicate-involute, with thin margins, distinctly grooved dorsally; **St** bronze, purplish or yellow; **Fil** stout to slender, flattened adaxially, 45–70 mm, inserted somewhat irregularly in the middle of the tube or below the mouth, maroon-dotted; **Anth** centric, regular, straight, 17–20 (–30) mm; **Ov** cylindrical, usually rather thick, 20–45 mm, neck short; **Sty** finally slightly longer than the filaments, maroon-dotted; **Sti** capitate; **Fr** oblong, 20–50 × 15–20 mm, not or slightly beaked, stipitate or not; **Se** D-shaped, 7–8 × 5 mm.

A variable complex, usually distinguishable from other members of Sect. *Guatemalenses* (as Group *Hiemiflorae*) with rounded part-inflorescences by its larger many-leaved rosettes and consistently longer stalked part-inflorescences in the short-peduncled panicles (Gentry 1982). Standley & Steyermark (1952) placed *A. pachycentra* in the synonymy, but this was not followed by other authors. Smith & Steyn (2004) provide an amplified description and illustrations. The “type” at ILL consists of 5 sheets which are not cross-labelled thus representing syntypes (Smith & Figueiredo

2014e: 236). The species is used for fences, esp. on rock walls (Steinberg & Taylor 2008: 256, 261). To be considered as “Endangered” in the IUCN Red List categories (Véliz Pérez 2013).

**A. ×hybrida** J. Verschaffelt *pro sp.* (Nursery Cat. (Jean Verschaffelt) 12: 2, 1868). **Type:** not typified. — **Lit:** Baker (1877a: 527–528, with ills., as *A. perbella*, *A. hybrida*, *A. xylacantha vittata*); André (1903: 227, as *A. armata*); Berger (1915: 98, as *A. armata*; 114, as *A. simonii*); Trelease (1920: 237, as *A. ×hybrida*, *A. ×perbella*); Thiede & al. (2019b). **Distr:** Cultivated only.

**Incl.** *Agave xylonacantha* [?] *vittata* Hort. Belg. ex Ellemeet (1871) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave perbella* Baker (1877); **incl.** *Agave ×armata* hort. ex Thuysbaert *pro sp.* (1903) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave simonii* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[1g × 1g] This is apparently the first-ever artificial *Agave* hybrid, *A. lophantha* (as *A. univittata*) × *A. xylonacantha*, cross-pollinated in summer 1865 by Gustave-Philippe de Kerchove d’Ousselghem near Ghent, Belgium. Kerchove apparently gave seeds to J. Verschaffelt who offered material, as far as known without description, in his catalogue of 1865 (not seen) (Thiede & al. 2019b). Berger (1915: 114) later described a leaf of the hybrid. Apparently lost from cultivation.

**A. impressa** Gentry (Agaves Cont. North Amer., 146–149, ills., 1982). **Type:** Mexico, Sinaloa (*Gentry* 23366 [US, ARIZ, ASU, CAS, DES, MEXU, MICH]). — **Lit:** McVaugh (1989); García-Mendoza (2003: with ill.); Vázquez-García & al. (2007b: 41–42, t. N); González-Elizondo & al. (2009: 88–89, with ills.); Etter & Kristen (2011: with ills.). **Distr:** Mexico (S Sinaloa, Nayarit); in tropical semideciduous forests on volcanic rocks in the hot lowlands, 150–700 m; flowers January to March. **I:** Etter & Kristen (2002: fig. 3 + front cover); Heller (2006: 98); Richter (2011: 108); Pilbeam (2013: 111); Hochstätter (2015: IX: 35); Moore (2016: 259). – Fig. 29.

[1g] Subcaulescent; **Ros** openly spreading, 0.5–0.85 × to 1.6 m, solitary; **L** linear to lanceolate, rigidly spreading, thickly fleshy with



**Fig. 29** *Agave impressa*

(Etter & Kristen 3070:  
Mexico; Sinaloa, ± 30 km  
E of El Rosario, 240 m).  
(Copyright: J. Etter &  
M. Kristen)



viscid adhesive sap and few fibres, convex below, flat to guttered above, 40–60 × 5–9 cm, pale yellowish-green, with conspicuous white imprints from the central bud on the upper face, margins horny, continuous, straight to sinuous between the teeth, 2–3 mm wide, light to dark grey; **marginal teeth** straight or slightly curved, flattened, regular, blunt, mostly 3–5 mm, grey like the leaf margin, 10–15 mm apart; **terminal Sp** subulate, stout, rounded below and sometimes protruding from the base into the leaf tissue, flat and broad at the base above, rarely channelled, sharp to blunt at the tip, 30–50 mm; **Inf** erect, 2–3 m, ‘spicate’, flowering from near the closely bracteate base, part-**Inf** with 2–3 flowers; **Ped** slender, 20–25 mm; **Fl** 35–40 mm; **Tep** yellow, green in bud, tube short, spreading, 1.5–2 × 7 (at the mouth) mm, lobes linear-elliptic, thin, ascending, partially recurved, apex rounded, apiculate, equal, 17–18 × 4–5 mm, outer flat, inner wider, involute, with broad low keel; **Fil** very slender, flattened, 35–40 mm, white, inserted 1–2 mm above the tube base; **Anth** regular, centric, 15–16 mm, yellow; **Ov** slender, fusiform, slightly angled, 17–20 × 4 mm, neck smooth, not constricted; **Fr** 15–18 × 8–10 mm, sharply beaked, fruit valves curved outwards; **Se** 2–3 × 2–3 mm, shiny.

A distinctive species without close relatives. The symmetrical rosettes with spreading, white-marked, light green leaves with blunt teeth and spines are quite unlike any other *Agave* species.

Its placement in Sect. *Heteracanthae* (as Group *Marginatae*) is for convenience only, and it might also be close to *A. attenuata* ssp. *dentata* (as *A. pedunculifera*) of Sect. *Inermes* (as Group *Amolae*) (Gentry 1982). Molecular data (Gil-Vega & al. 2007) place it among Sect. *Heteracanthae* and apart from Sect. *Inermes*.

Known to Gentry (1982) only from its type locality SE of Escuinapa (Sinaloa; Etter & Kristen (2002)) where the vernacular name “masparillo” is used. Etter & Kristen (2011) report further localities near Escuinapa. In Sinaloa, *A. impressa* also occurs near La Guásima NNE of Concordia (González-Elizondo & al. 2009; Van Devender & al. 2007-126 [ARIZ, DES]). Gentry (1982) was informed that an *Agave* named “masparillo” would occur towards Bolaños in the “Sierra de los Huicholes” in Jalisco, but *A. impressa* was not found there (Hernández-Vera & al. 2007a: 500). Probably, vernacular names were confused, since “masparillo” is also used for *A. maximiliana* which is abundant in the Sierra de los Huicholes (Hernández-Vera & al. 2007a). Etter & Kristen (2011) finally found *A. impressa* on the W side of the Sierra de los Huicholes in Nayarit 50 km SW of Mesa del Nayar, and also at Presa Aguamilpa near Tepic (Nayarit), where the species was collected earlier by Charles Glass. Based on sterile specimens, Cházaro Basáñez & Valencia (2003) reported the species from the Barranca de Colimilla in Jalisco, but flowering plants proved to be different and were later described as a



new species *A. arcedianoensis* (Vázquez-García & al. 2007b; see also there). — ‘Green Giant’ is a cultivar with longer leaves and larger rosettes.

**A. inaequidens** K. Koch (Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 3: 28, 1860). **Type** [neo]: Mexico, México (Gentry & al. 19612 [US, ARIZ [2 sheets], MEXU [2 sheets]]). — **Lit**: Gentry (1982: 340–344, with ills.). **Dist**: C Mexico.

The neotype at US designated by Gentry (1982: 341) consists of two specimens (US 2601951 & 2601952) which were apparently cross-labelled afterwards.

**A. inaequidens** ssp. **barrancensis** Gentry (Agaves Cont. North Amer., 342–344, ills., 1982). **Type**: Mexico, Durango (Gentry & Arguelles 22282 [US †, syn: ARIZ [2 sheets], DES, MEXU [3 sheets], MICH [2 sheets]]). — **Lit**: González-Elizondo & al. (2009: 90–93, with ills.). **Dist**: Mexico (E-C Sinaloa, Durango); mountainous slopes of deep barrancas in the pine-oak forest and woodland region, 1800–2400 m; flowers September and December. **I**: Pilbeam (2013: 112).

[2d] Differs from ssp. *inaequidens*: **Ros** 1.5–2 × 3–3.5 m; **L** mostly longer and narrower, 100–170 (–200) × 10–17 (–24) cm, margins nearly straight to undulate; terminal **Sp** subulate-acicular and longer, 40–60 mm; **Inf** broader and shorter, part-**Inf** 20–30, broadly spreading.

Looking like a larger *A. jaiboli*, but its relations are with *A. inaequidens* (Gentry 1982). Known to Gentry (1982) only from along the Durango—Mazatlán road, but González-Elizondo & al. (2009) provide new records from NW and W-C Durango. The gathering *A. C. Sanders & al.* 4430 (ARIZ 249820, UCR 33674, UTEP 24614, WIS 0352581!) is a new state record just across the border in E-C Sinaloa.

The holotype, cited for US in the protologue, appears to be missing, leaving 8 syntypes as cited above. Most probably, Gentry intended the most complete specimens (ARIZ 266209 & 266210) both bearing his stamp “Gentry Herbarium” and his handwriting “Type Collection” to be sent to US as “holotype”. The 2 sheets at MICH were apparently cross-labelled later.

**A. inaequidens** ssp. **inaequidens** — **Lit**: Berger (1915: 165); Gentry (1982: 340–342); McVaugh (1989: 138); Vázquez-García & al. (2007b: 57–58, t. N); Greulich (2014a: with ills.); Greulich (2015: with ills.). **Dist**: Mexico (Nayarit, Jalisco, Michoacán, México, D.F., Morelos, Guerrero); rocky slopes in pine-oak forests, mostly 1850–3100 m; flowers October to April, and August. **I**: Etter & Kristen (2012: 81–82); Pilbeam (2013: 112).

**Incl.** *Agave amoena* Lemaire ex Jacobi (1865); **incl.** *Agave mescal* K. Koch (1865); **incl.** *Agave crenata* Jacobi (1866); **incl.** *Agave fenziiana* Jacobi (1866); **incl.** *Agave megalacantha* Hemsley (1880); **incl.** *Agave hookeri* Baker (1881) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave reginae* hort. ex A. Berger (1912); **incl.** *Agave heterodon* hort. ex A. Berger (1915); **incl.** *Agave bourgaei* Trelease (1920).

[2d] Stems short; **Ros** openly spreading, 1.5–3.5 m Ø, solitary; **L** variable, broadly or narrowly lanceolate or oblanceolate, ascending to outcurving, thickly fleshy (esp. towards the rounded base), concave above, esp. towards the rounded base, mostly 75–150 × 11–21 cm, light green to yellow-green, rarely faintly glaucous, margins undulate to repand and crenate; **marginal teeth** dimorphic, straight or variously curved, the flattened bases longer than the height of the teeth, commonly 8–10 mm long, chestnut-brown to dark brown, 25–40 mm apart, with few smaller intermittent teeth, larger teeth on broad prominences; **terminal Sp** stout, broadly deeply channelled above, 25–55 mm, dark brown, protruding into the leaf tissue below, sharply decurrent to the uppermost teeth; **Inf** 5–8 m, paniculate, peduncle short, fertile part narrow in outline, part-**Inf** compact, 30–50 in the upper ½ of the inflorescence; **Fl** 60–90 mm; **Tep** yellow, buds reddish-purple, tube deeply grooved, 5–12 (–15) mm, thick-walled, bulging at the filament insertions, lobes linear, erect, narrow, conduplicate, involute, strongly cucullate and papillate within at the tip, unequal, 25–30 (–34) mm, reddish; **Fil** stout, ovate in cross section, 50–60 mm, inserted above mid-tube; **Anth** centric to excentric, 26–34 mm; **Ov** cylindrical, trigonous, 30–40 mm, neck short, furrowed; **Sty** slightly longer than the tepals; **Sti**

capitate; **Fr** oblong, 40–45 × 20 mm, rounded to apiculate at the apex, without beak, stipitate, brown; **Se** semicircular, 6–7.5 × 4.5–5.5 mm, shiny black, finely punctate, the marginal wing half-curved or straight, hilar notch broad.

*A. inaequidens* is the predominant *Agave* in the Trans-Mexican mountains from Morelos through Michoacán to Jalisco. Fernández Nava & al. (1998) and the collections Soto N. & Martínez S. 5004 (MEXU 384410!) and Martínez S. & Soto N. 3677 (MEXU 843995!) provide a new record for Guerrero (Balsas Basin). Gutiérrez G. & al. 77 (MEXU 1213265! & 1213428!), a new record for Guanajuato, is filed as ssp. *barrancensis*, but may belong here according to its leaf size. Vázquez-García & al. (2007b: 57) list the species for Hidalgo and Nayarit, but no specimens could be located. Madrigal-Sanchez & Diaz-Barriga (1991) describe a fasciated inflorescence.

Best distinguished from the closely related *A. hookeri* from the same region by its bright yellowish-green leaves with teeth all along the margin (vs. glaucous light grey with teeth lacking 15–20 cm below the terminal spine; Gentry (1982)). Morphometric studies showed that *A. hookeri* is similar to cultivated *A. inaequidens*, supporting the hypothesis that it could represent the extreme of a domestication gradient *A. inaequidens* wild → *A. inaequidens* cultivated → *A. hookeri* cultivated only (Figueredo & al. 2014). Figueredo & al. (2015) found little genetic structuring of wild, silviculturally managed and cultivated populations and conclude that domestication (for mescal production) is still in its early stages.

**A. inaguensis** Trelease (Mem. Nation. Acad. Sci. 11: 47, tt. 103–105, 1913). **Type** [syn]: Bahamas, Little Inagua (Nash & Taylor 342 etc. [MO]). — **Lit**: Berger (1915: 269); Britton & Millspaugh (1920: 76); Correll & Correll (1982: 312); Jestrow & al. (2014: 234, 238, with ill.). **Distr**: Bahamas (Great Inagua, Little Inagua), Turks & Caicos Islands (South Caicos); open sandy flats and rocky dwarf coastal coppices; flowers mostly June to August. **I**: Hochstätter (2015: VII: 97).

[2t] Acaulescent; **Ros** caespitose, freely suckering; **L** oblong or lanceolate, stiffly erect, hard,

straight, narrow, rather abruptly acute and flat, sometimes conduplicate, tip sometimes sigmoidally upcurved, 40–100 × 6–9 cm, typically white-glaucous; **marginal teeth** more recurved and less uniform than in *A. nashii*, slender, very narrowly triangular, 1–2 mm, almost continuously joined by a narrow blackish border, 2–9 mm apart; **terminal Sp** 20–30 mm, dark brown; **Inf** 4–5 m, paniculate, part-**Inf** few, on slender outcurved **Br** in the upper ¼ of the inflorescence; **Ped** 5–10 mm; **Fl** ±50 mm; **Tep** yellow, tube open, ±5 mm, lobes 15–17 × 5 mm; **Fil** 35 mm, inserted almost in the tube throat; **Ov** subfusiform, 25–30 mm; **Sty** longer than the filaments; **Sti** capitate; **Fr** oblong-ellipsoid, 30–40 mm, beaked, broadly and shortly stipitate; **Se** ±6 mm.

From the 6 collections cited as “type” in the protologue (“Nash and Taylor, 342, 1215, 21832; 329, 1202, 21833, Nov. 1904”; = syntypes), none is available electronically; however, 3 specimens of the collection Nash & Taylor 1389, 1. Nov. 1904, not cited in the protologue, are at NY. According to the protologue with the habit of *A. nashii*, the second species of Sect. *Inaguenses*. *A. nashii* differs by having gradually tapering, deeply guttered leaves with a rather slender terminal spine and deltoid to broad-based marginal teeth. Originally published from Little Inagua and South Caicos, but later also collected on Great Inagua where *A. nashii* also occurs (Howard & Dunbar 1964: 12).

**A. indagatorum** Trelease (Mem. Nation. Acad. Sci. 11: 42, t. 92, 1913). **Type**: Bahamas, Watling Island (Britton & Millspaugh 6155 [MO 2056579 & 2056580 [photo & letter], F [2 sheets], NY [2 sheets]]). — **Lit**: Berger (1915: 205); Britton & Millspaugh (1920: 76); Correll & Correll (1982). **Distr**: Bahamas (Long Island, San Salvador [Watling] Island); rocky soil in coastal coppices, to 450 m; flowers mostly March to June. **I**: Hochstätter (2015: VII: 84).

[2r] Acaulescent; **Ros** solitary; **L** very narrowly lanceolate or almost oblong, fleshy, outcurved-ascending to upcurved towards the tip, gradually acute, lower face flattened or convex, upper face concave, 150–250 × 20–25 mm, dark green, somewhat greyish and at first very

glaucous beneath, almost silvery towards the base, glossy on the upper face, margins between the teeth straight, somewhat membranous, at first slightly pink; **marginal teeth** straight or slightly recurved, narrowly triangular, not lenticular at the base,  $\pm 1$  mm, 3–12 mm apart, at first slightly pink, somewhat membranous; **terminal Sp** conical, nearly straight, slender, involutely grooved to the middle, smooth,  $\pm 12$  mm, chestnut-brown or red-brown, rather glossy, decurrent for about its own length; **Inf** to  $\pm 9$  m, paniculate, reportedly bulbiferous; **Ped** 15–20 mm; **Fl**  $\pm 55$  mm; **Tep** yellow, tube rather open,  $\pm 6$  mm, lobes  $\pm 20 \times 2$  mm; **Fil**  $\pm 35$  mm, inserted in the tube throat; **Ov** ellipsoid, 20–25 mm, extended as a neck into the flower tube; **Fr** narrowly oblong, thickly stipitate, 35–60  $\times$  17–20 mm, acuminate pointed; **Se** 7–8  $\times$  5 mm.

In the key of Trelease (1913: 39) closest to *A. acklinicola*, which differs in its teeth often with lenticular bases and a stout terminal spine. See also the note under *A. bahamana*. — The species is “named in commemoration of the explorers who are reputed to have sighted this island [Guanahani, Watling or San Salvador Island] first in the New World” (Trelease 1913: 42).

**A. intermixta** Trelease (Mem. Nation. Acad. Sci. 11: 32, t. 64, 1913). **Type:** Hispaniola, Haiti (Parry 1871 [MO 2056581, US 125674]). — **Lit:** Berger (1915: 206–207); Howard (1961: 133). **Distr:** Haiti (near Santiago de los Caballeros); stream bank, on steep hills; flowers in February. **I:** Hochstätter (2015: VII: 71, identity uncertain).

[2p] **L** 100  $\times$  12 cm or more; **marginal teeth** rather broadly triangular, nearly straight, on somewhat rounded or lenticular bases, 4–5 mm, 15–25 mm apart, intervening margin nearly straight; **Inf** not known to be bulbiferous; **Ped** slender, 15–25 mm; **Fl**  $\pm 65$  mm, congested at the ends of the part-**Inf**; **Tep**  $\pm 35$  mm, yellow (?), tube narrowly conical, 8–10 mm, lobes 20  $\times$  3–4 mm; **Fil** 30 mm, inserted almost at the throat of the tube; **Ov** elongated-fusiform, 35  $\times$  5 mm; **Fr** rather broadly pear-shaped and oblong, 40  $\times$  20 mm, stipitate and beaked, somewhat rugose, light brown; **Se** somewhat glossy, narrowly winged, 7–8  $\times$  5 mm.

The herbarium specimens of *A. intermixta* are “hopelessly” intermixed with material of *A. antillarum* (Trelease, unpubl. manuscript). The protologue is a much abbreviated description as a footnote only, based on fruiting part-inflorescences with disassociated flowers, but without data on rosette, leaves, and inflorescence. Trelease had prepared a complete description of *A. intermixta* and a discussion of its affinities, but this was never published and is kept at MO (Howard 1961: 133); detail data from it are added here. The type at MO (Parry 1871) is stated to be from “Santo Domingo”, but was actually collected on the bank of a stream near Santiago de los Caballeros, according to the original field notes (Howard 1961: 133). The leaf margin in t. 43.1 of Trelease (1913) may be that of *A. intermixta* (Howard 1961: 133). According to the unpublished manuscript of Trelease at MO, *A. intermixta* differs from *A. antillarum* in its long-pedicelled elongated flowers with deep tube and filaments scarcely  $\frac{1}{2}$  longer than the perianth segments and, apparently, in leaf and fruit characters. According to Álvarez de Zayas (1995: 41) it is possibly conspecific with *A. antillarum* (see there). — Aqueous extracts are used in traditional medicine and have anti-inflammatory, cytotoxic and antibacterial effects (e.g. Quílez & al. (2004); identity doubtful).

**A. involuta** (McVaugh) Thiede & Egli (Kakt. and. Sukk. 50(5): 110, 1999). **Type:** Mexico, Jalisco (Bauml & Voss 1466 [RSA, MICH]). — **Lit:** McVaugh (1989: 231–232); Rodríguez & al. (2008: with ill.); Castillejos-Cruz (2009: [169]–[174], with ill.); all as *Manfreda*. **Distr:** Mexico (S Zacatecas, S Nayarit, N, W & C Jalisco); grassy openings and hillsides in dry oak or pine-oak forests and grasslands, 740–2000 m; flowers March to July. **I:** Rodríguez & Castro-Castro (2006: 625); Rodríguez & Castro-Castro (2007: 9); Hochstätter (2016: I: 23); Castro-Castro (2017: 136); Castro-Castro & al. (2017: 62); Castro-Castro & al. (2018: 499); all as *Manfreda*.  $\equiv$  *Manfreda involuta* McVaugh (1989).

[3a3] Plants herbaceous; corm 2.5  $\times$  1–2 cm, erect, cylindrical, bulb 3.5–5.5  $\times$  1–2.3 cm, cylindrical, completely covered with dry leaf bases 5–8 cm long, these membranous at the base and

fibrous above for 2–3 cm; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, often absent during flowering, 6–11, linear, canaliculate or in the middle involute, then nearly tubular and only 2–3 mm  $\varnothing$ , lower face papillate on the veins, upper face glabrous, 18–80  $\times$  0.2–0.9 cm, light green, margins entire to papillose, with a hyaline band; **Inf** 60–180 cm, ‘spicate’, erect to slightly arching, green-reddish and somewhat glaucous; **Bra** 6–9, rather distant; fertile **Inf** part 10–20 (–35) cm, lax, with 3–18 flowers; floral **Bra** 0.4–1  $\times$  0.2–0.4 cm; **Fl** 20–28 mm, solitary, sessile, ascending, funnel-shaped; **Tep** green with purplish tinge mainly on the inner face, tube 12–15  $\times$  5–7 mm, constricted at the mouth, lobes oblong, erect, 7–8  $\times$  3–5 mm, tip cucullate, with a bundle of short white trichomes; **Fil** 12–18 mm, erect at anthesis, exceeding the tube for 3–9 mm, inserted at mid-tube all on the same level, reddish to purplish; **Anth** 7–8.5 mm, yellow with purple tinge; **Ov** ellipsoid, 10  $\times$  2.5 mm, greenish with purple tinge, constricted above; **Sty** 28–33 mm, dark purplish; **Sti** 3-lobed; **Fr** globose to subglobose, 13–15  $\times$  11–13 mm, glaucous, sometimes with short apex, tepals persisting; **Se** deltoid, 4.8–6  $\times$  4.5 mm, shiny black.

According to the protologue (McVaugh 1989: 231–232) known from 2 collections in Jalisco only and of uncertain affinities due to its apparently unique combination of a very early flowering

season, very narrow involute leaves, and slender tepal tubes longer than the lobes. With its papillate leaf margins, the ovary protruding into the tube and the cylindrical tube not narrowed above the ovary, the taxon fits well into Ser. *Guttatae* of Sect. *Herbaceae*, however. Rodríguez & al. (2008) and Castillejos-Cruz (2009) cite additional collections from Zacatecas and Nayarit, and provide additional morphological data.

**A. isthmensis** García-Mendoza & F. Palma (Sida 15(4): 565–568, ills., 1993). **Type:** Mexico, Chiapas (*García-Mendoza & al.* 4177 [BRIT/SMU  $\dagger$ ?, DES  $\dagger$ ?, ENCB, MEXU]). — **Lit:** Starr (2012: 115–119, 312–313). **Distr:** Mexico (E Oaxaca, W Chiapas: near the Isthmus of Tehuantepec); sandstone or soils of calcareous origin, in tropical deciduous and oak forests, 50–980 m; flowers January. **I:** Smith (2002: 221); Forster (2006: 179–181); Heller (2006: 99); Richter (2011: 84, 113); Pilbeam (2013: 113–115). — Fig. 30.

[2o] **Ros** compact, 17–32  $\times$  25–36 cm, young plants with numerous rhizomatous offsets, adult plants with axillary offsets, forming dense clonal colonies; **L** 84–132, ovate, narrowed towards the base, apex truncate, concave, scabrous below, 8–10  $\times$  5–8 cm, mostly grey-glaucous to white-glaucous, sometimes green, margins deeply crenate; **marginal teeth** deltoid, (2–) 3–4 mm, brown-reddish,

**Fig. 30** *Agave isthmensis* (Beisel s.n.: Mexico; Oaxaca, near Salinas Cruz). (Copyright: U. Eggli)





on distinct prominences, <10 mm apart; **terminal Sp** sinuous, slightly applanate, 12–15 mm, brown-reddish, decurrent for 6–10 mm; **Inf** 1.7–2.2 m, paniculate, peduncle with deltoid papyraceous **Bra** 3.4–3.8 cm long, fertile part oblong, with (6–) 20–25 part-**Inf**, these 9–16 cm, in the upper  $\frac{3}{4}$  of the inflorescence; **Ped** 3–4 mm, elongating to 10 mm at fruiting time; **Fl** succulent, 38–46 mm; **Tep** yellow, tube funnel-shaped, trisulcate, 4–5 mm, lobes oblong, subequal, 19–21 × 4 mm; **Fil** 27–33 mm, yellowish, inserted at the tepal base; **Anth** 14–17 mm, yellowish; **Ov** 16–21 mm; **Sty** as long as the filaments; **Sti** capitate, 3-lobate; **Fr** ovoid, 16–22 × 10–18 mm, rostrate; **Se** applanate, 2–4 × 1–2 mm, black.

According to the protologue closest to *A. potatorum* and *A. seemanniana* (as *A. pygmaea*) and distinct by its compact, small, many-leaved rosettes with small, glaucous leaves with scabrous lower face and the rhizomatous as well as axillary offsetting. Variegated cultivars are ‘Ohi Raijin Fukurin Nishiki’ with cream-coloured leaf margins, ‘Rum Runner’ (ISI 2014-11) with broad golden-yellow midstripe (Trager 2014), and ‘Ohi Raijin Shiro Nakafu’ with broad white central stripe (Starr 2014: 222–223).

**A. jaiboli** Gentry (US Dept. Agric. Handb. 399: 89–94, ills., 1972). **Type**: Mexico, Sonora (Gentry 21177 [US, ARIZ, ASU, MEXU, MICH, US]). — **Lit**: Gentry (1982: 344–346, with ills.); Martin & al. (1998: 469). **Distr**: Mexico (S Sonora); open grassy slopes and volcanic cliffs in short-tree forest and oak woodlands, 300–1400 m; flowers in May. **I**: Pilbeam (2013: 116); Greulich (2014a: 55); Hochstätter (2015: IV: 26).

[2d] **Ros** usually open, 0.6–1 × 1.4–2 m, solitary; **L** linear to lanceolate, usually straightly ascending to spreading, sometimes incurved, widest at or above the middle, gradually narrowed below, long-acuminate, flat to guttered, 60–100 × 8–12 cm, green to yellowish-green, margins not corneous; **marginal teeth** curved down- or upwards, 5–8 mm, reddish-brown, larger teeth ±20–30 mm apart, on small regular prominences, smaller intermittent teeth 1 to several, 1–4 mm; **terminal Sp** subulate, terete, openly or narrowly

grooved in the lower  $\frac{1}{2}$  to  $\frac{2}{3}$ , smooth, 30–40 mm, reddish-brown, shiny, narrowly horny decurrent for less than its length; **Inf** 6–8 m, paniculate, peduncle with narrow scarious **Bra**, fertile part with 12–15 ascending, rather sigmoid, small, diffuse, 4-flowered part-**Inf** in the upper  $\frac{1}{2}$ – $\frac{1}{3}$  of the inflorescence; **Ped** short; **Fl** ±60 mm; **Tep** yellow tinged ferruginous, tube funnel-shaped, deeply grooved, 9–11 × 15 mm, bulging at the filament insertions, lobes unequal, rather thin, conduplicate and involute; **OTep** 22–23 × 4–5 mm, ascending, incurved, linear-lanceolate, acute, slightly guttered; **ITep** with broad keel; **Fil** somewhat flattened, 45 mm, pink, inserted above mid-tube; **Anth** nearly centric, 23–24 mm; **Ov** angular-fusiform, shortly tapered at the base, 25–30 mm incl. the 3–4 mm long neck, green; **Sty** stout, longer than the anthers at the end of anthesis; **Sti** capitate, 3-lobate; **Fr** 40–50 × 18–20 mm, shortly beaked, long-stipitate, brown; **Se** rugose, very finely punctate, 7 × 5 mm, prominently winged, shiny black.

The flower structure and the dimorphic teeth on the soft, fleshy, crenate leaves place the species in Sect. *Crenatae*. Here it is distinguished by its narrow, almost ensiform leaves. Its Sonoran relative *A. bovicornuta* is further distinguished by its broader leaves much narrowed towards the base (Gentry 1982). The Wariho ethnic group esteem the species for its sweet edible qualities (young flowering shoots and the stems are cooked and eaten), in contrast to the unpalatable *A. bovicornuta* (Gentry 1982). The holotype at US consists of 2 sheets (US 2549714 & 2549715) which were apparently cross-labelled later.

**A. jaliscana** (Rose) A. Berger (Agaven, 38, 1915). **Type** [lecto]: Mexico, Jalisco (*Pringle* 1850 [US, BM, BR, F, G, GH, LE, M, NDG, NY, P, S, VT]). — **Lit**: Rose (1903c: 22); Gentry (1972: 152–153); Verhoek-Williams (1975: 291–294); Piña Luján (1986: 15–16); McVaugh (1989: 232); Castillejos-Cruz (2009: [175]–[180], with ills.); all as *Manfreda*. **Distr**: Mexico (Sonora, Sinaloa, Durango, Nayarit, Jalisco, Michoacán); loose black loam or rocks, in oak, pine-oak or tropical deciduous forests and on



grassy slopes, (100–) 500–2500 m; flowers October to April. **I:** Hochstätter (2016: I: 24); Castro-Castro (2017: 136); Castro-Castro & al. (2017: 62); all as *Manfreda*.

≡ *Manfreda jaliscana* Rose (1903) ≡ *Polianthes jaliscana* (Rose) Shinnars (1966).

[3a2] Plants herbaceous; corm 6–10 × 3–4 cm, cylindrical, bulb 2–3.5 × 2–3 cm, ovoid to sub-cylindrical, completely covered with dried leaf bases 4–7.5 cm long, these membranous at the base and fibrous above; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, 5–10, prostrate or semi-erect, linear-lanceolate, slightly canaliculate, papillose on the veins on both faces, apex acute, 38–78 (–90) × 0.6–1.4 (–2.6) cm, light green, margins entire, with a hyaline band, and with scattered papillae throughout its length; **Inf** 90–180 cm, ‘spicate’, erect, light green to yellowish-green, with purplish tinge, **Bra** 6–9, fertile part 10–40 cm, lax, with 25–40 flowers; floral **Bra** 0.8–1.1 × 0.3–0.5 cm; **Fl** 19–26 mm, solitary, sessile, appressed to ascending; **Tep** greenish-yellow, semisucculent, campanulate, tube 7–9 × 4–5 mm, lobes narrowly elliptic to oblong, extended, 7–12 × 4–6 mm, tip cucullate, with a bundle of short white trichomes; **Fil** sparsely glandular-pilose, 40–75 (–85) mm, erect at anthesis, exceeding the tube for 4–5 mm, inserted at mid-tube at the same level, green-yellowish with reddish dots; **Anth** 7–10 mm, yellow; **Ov** cylindrical, (4–) 8–11 × 3–4 (–5) mm, greenish, not prolonging into the tube, slightly constricted above; **Sty** 60–90 mm; **Sti** 3-lobed, yellowish-green; **Fr** cylindrical to ellipsoid, 13–27 × 12–17 mm, apex apiculate, with persisting tepals; **Se** deltoid, plane-concave, with narrow black shiny margin, 5–6 × 4–5 mm.

Easy to recognize in flower by its long-exserted stamens, the short tepal tube and long lobes. The very long narrow leaves with papillose margins are also characteristic (McVaugh 1989). Similar to *A. chamelensis*, *A. fusca* and *A. debilis*, which together form a group characterized by tepal tubes <25 mm long, and filaments inserted at mid-tube (Castillejos-Cruz 2009).

**A. jarucoensis** A. Álvarez (Revista Jard. Bot. Nac. Univ. Habana 1(1): 5–11, ills., 1981). **Type:**

Cuba (Álvarez 41680 [HAJB]). — **Lit:** Álvarez de Zayas (1985: 12–15, with ills.). **Distr:** W Cuba; limestone rocks and cliffs, 200–290 m; flowers in November. **I:** Hochstätter (2015: VII: 91).

[2q] Stems short; **Ros** semiglobular, solitary, not rhizomatous; **L** many, lanceolate, weak, slightly curved to flexuous, fleshy, coriaceous, narrowed below the middle, slightly concave in the lower  $\frac{2}{3}$ , 90–120 × 12–16 cm, green to greyish, slightly dull, margins straight or lobed; **marginal teeth** triangular, straight or weakly retrorse, slightly lenticular at the base, 1–5 × 0.1–0.4 mm, larger at mid-leaf, castaneous-red-dish, base reddish, 4–15 mm apart; **terminal Sp** acicular, straight, pungent, flattened at the base, narrowly canaliculate up to the middle, 15–22 × 3–4 mm, slightly lustrous, chestnut-brown to grey, not decurrent; **Inf** 2–4 m, paniculate, fertile part in the upper  $\frac{2}{3}$  to  $\frac{3}{4}$ , part-**Inf** ±14–23, tripartite, ascending, 35–45 cm; **Ped** 5–15 mm; **Fl** 35–60 mm; **Tep** yellowish-green, tube open, narrow, 5–7 mm, lobes narrowly ovate to lanceolate, 13–16 mm, apex cucullate, yellow, inner with broad margin, outer dorsally keeled, all constricted and furrowed at the base; **Fil** 26–32 mm, yellow, inserted near the tube throat; **Anth** 17–20 mm, golden-yellow; **Ov** subcylindrical or fusiform, narrowly angulate, constricted at the base, apically furrowed, 18–24 mm, greenish; **Sty** slightly shorter than the filaments; **Sti** capitate; **Fr** oblong to nearly rounded, shortly apiculate, 22–40 × 15–20 mm, walls thick; **Se** subtriangular, 5–6 mm, shiny.

According to the protologue and Álvarez de Zayas (1985) similar to *A. papyrocarpa*, but differing in its more robust habit, ascending part-inflorescences, larger flowers, and thick fruit walls, and from *A. tubulata* in its larger, relatively shorter tepal lobes. It occurs at least sometimes in regions with a predominance of ophiolitic soils (López Almira 2013). Hochstätter (2015) published the first photograph of the species.

**A. jimeno**i Cházaro & A. Vázquez (Phytotaxa 134(1): 55–57, ills., 2013). **Type:** Mexico, Veracruz (*Jimeno & al.* 702 [XAL, IBUG, MEXU]). — **Lit:** Cházaro Basáñez & Narave-Flores (2015: with ills.). **Distr:** Mexico (C Veracruz: Tlapacoyan

region); cliff dweller in lowland tropical sub-perennial forests,  $\pm 150$  m; flowers April to June; only known from 2 localities. **I:** Hochstätter (2015: IX: 12).

[1f] Caulescent, to 60 cm, not surculose, according to the protologue polycarpic; stems 34–90  $\times$  5.1–6 (at the base) cm, pendent, bifurcate, each branch with a terminal **Ros** that turns upright; **L** 16–20, oblanceolate, flexible, concave above when young, 39–42  $\times$  8.4–8.5 cm, green-glaucous, marginal denticles concolourous with the lamina, absent from the uppermost 6 cm; **terminal Sp** flexible, 5–13 mm, dark brown; **Inf** erect, lateral according to the protologue, but actually likely terminal on rudimentary lateral rosettes, 1.32–1.4 m, ‘spicate’, peduncle with lanceolate narrow **Bra** (0.22–) 1–16  $\times$  0.22–1.2 cm, acuminate, fertile part in the upper  $\frac{1}{2}$  of the inflorescence; **Ped** 3–5.8 mm; **Fl** geminate, 28–30 mm (excl. stamens);  **Tep** yellowish, tube 7  $\times$  5 mm, lobes lanceolate, 10.5–13  $\times$  5–6.5 mm; **St** 41–44 mm; **Anth**  $\pm 15$  mm, reddish to yellow; **Ov** 13  $\times$  4–4.5 mm, without neck; **Sty**  $\pm 47$  mm,  $\pm$  as long as the filaments; **Sti** slightly thickened; **Fr** ellipsoid, 15.8–18.8  $\times$  12–13 mm; **Se** 2–3.3  $\times$  3.4–4.8 mm, black.

Compared with *A. gomezpompae* in the protologue, which is also from lowland habitats in C Veracruz in tropical semideciduous forests. Both have a long bifurcate stem, oblanceolate, flexible leaves, and erect inflorescences with flowers in their upper  $\frac{1}{2}$ . *A. jimenoii* differs in having shorter and pendent stems, smaller glaucous-green leaves with the marginal denticles lacking below the terminal spine, and shorter inflorescences. *A. jimenoii* is distantly related to *A. pendula*.

**A. justosierrana** (García-Mendoza) Thiede (Haseltonia 17: 94, 2012). **Type:** Mexico, Guerrero (*García-Mendoza & al.* 6739 [MEXU [2 sheets]]). — **Lit:** García-Mendoza (2011b: with ills., as *Manfreda*). **Distr:** Mexico (Guerrero); open, sunny spots in brownish sandy soil, in pine-oak or montane cloud forests, 1930–2400 m; flowers November to December. **I:** Hochstätter (2016: I: 25, as *Manfreda*).

$\equiv$  *Manfreda justosierrana* García-Mendoza (2011).

[3a2] Plants herbaceous; corm 3–5  $\times$  3–4.5 cm, cylindrical, bulb 4–8  $\times$  3–4.5 cm, covered with fibrous dried leaf bases; **R** filiform, contractile roots fleshy; **L** drought-deciduous, 3–11, coriaceous, recurved, broadly oblong to elliptic, narrowed at the base to 0.8–1.3 cm, apex hardened, not pungent, (25–) 40–50  $\times$  (4–) 6–9 cm, light green with large reddish dots which may fuse to irregular blotches, asperous, surface papillose, esp. on the veins, margins papillose on a hyaline band, often undulate; **Inf** erect, ‘spicate’, 1.6–2.4 m, peduncle 1.6–1.9 m, reddish, with 8–10 **Bra**; fertile part 25–50 cm, with 25–35 laxly arranged flowers; floral **Bra** 1–1.7  $\times$  0.1–0.2 cm; **Fl** (38–) 45–52 mm, solitary, sessile, ascending to diffuse; **Tep** forming a tube 22–25 (–30)  $\times$  5–10 mm, greenish-yellow, lobes oblong, revolute, 10–15  $\times$  2–4 mm, yellowish; **Fil** 30–45 mm, light green to whitish, inserted at  $\frac{3}{4}$  of the tube length; **Anth** 15–20 mm, yellow, with discontinuous reddish lines; **Ov** cylindrical, 10–15  $\times$  2–3 mm, green; **Sty** 45–65 mm, light green to whitish; **Sti** 3-lobate, papillose; **Fr** ovoid to ellipsoid, 15–25  $\times$  10–20 mm, with persistent tepals; **Se** crescent-shaped, with inconspicuous margin, 6–7  $\times$  4–5 mm, black, shiny.

Morphologically most similar to *A. scabra* according to the protologue (as *Manfreda*), and characterized by oblong to elliptic coriaceous leaves with papillose surface, esp. on the veins, large reddish dots on the upper leaf face, an inflorescence with reddish peduncle with short bracts, and laxly arranged flowers with a long tube.

**A. karatto** Miller (Gard. Dict., Ed. 8, no. 6, 1768). **Type** [neo]: St. Kitts (*Rose* 3231 [NY, US]). — **Lit:** Trelease (1913: 23–24, tt. 14–15); Berger (1915: 214–215); Hummelinck (1936: 241–243, 249, as *A. trankeera*); Hummelinck (1938: 24–27, tt. Ia, IVb); Howard & Thompson-Mills (1979: 488–492, with ills., as several synonyms); Hummelinck (1986: as several synonyms, with ills.); Hummelinck (1987: as several synonyms, with ills.); Hummelinck (1993: with ills.); Rogers (1999: with ills., as *A. barbadensis*); Rogers (2000). **Distr:** Lesser Antilles: Leeward Islands (Anguilla, St. Martin, Saba, St. Eustatius, St. Kitts, Nevis, Barbuda, Antigua, Redonda, Montserrat, Guadeloupe, La Désirade), Windward

Islands (Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Grenada and the Grenadines); rocky places and grasslands in open exposed habitats, in well drained shallow soils; flowers from March to mid-summer. **I:** Etter & Kristen (1997: front cover, as *A. obducta*, 98, as *A. unguiculata*, 99); Richter (2011: 23, 94, 95); Pilbeam (2013: 41, as *A. barbadensis*, 50, as *A. caribaeicola*, 117); Hochstätter (2015: VII: 55, as *A. caribaeicola*, 58, 60, as *A. dussiana*).

**Incl.** *Agave americana* Dillenius (1774) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave keratto* Haworth (1819) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave keratto* Steudel (1840) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave kerrato* Salm-Dyck (1859) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave kerrato* Salm-Dyck (1859) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave martiana* K. Koch (1860); **incl.** *Agave salm-dyckii* Baker (1877); **incl.** *Agave caribaea* Baker (1888) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea tuberosa* Drummond (1907) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea gigantea* Boldingh (1909) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave barbadensis* Trelease (1913); **incl.** *Agave caribaeicola* Trelease (1913); **incl.** *Agave dussiana* Trelease (1913); **incl.** *Agave grenadina* Trelease (1913); **incl.** *Agave medioxima* Trelease (1913); **incl.** *Agave montserratensis* Trelease (1913); **incl.** *Agave nevidis* Trelease (1913); **incl.** *Agave obducta* Trelease (1913); **incl.** *Agave scheurmaniana* Trelease (1913); **incl.** *Agave trankeera* Trelease (1913); **incl.** *Agave unguiculata* Trelease (1913); **incl.** *Agave vangrolae* Trelease (1913); **incl.** *Agave ventum-versa* Trelease (1913).

[2s] **Ros** mostly solitary, sometimes with basal suckers; **L** lanceolate, straight or curved outwards, occasionally slightly twisted, 100–220 (–244) × (8–) 12–23 (–40) cm, green with light glaucescence; **marginal teeth** highly variable, deltoid to acicular, usually with ± lenticular base, antrorse to retrorse, (0.1–) 0.5–3 (–5) mm, usually dark-coloured (or reddish when fresh); **terminal Sp** comprised of hardened inrolled **L** margins, stout and sharp, recurved, or straight, or incurved, long-tapered to short and stubby, (5–) 10–30 (–45) mm, 5–10 mm Ø, blackish; **Inf** 3–8 (–10) m, paniculate, with up to 4 (–5) orders of branching, part-**Inf** spreading, in the upper 1/3 of the inflorescence,

freely bulbiferous; **Ped** 7–25 mm; **Fl** 55–105 mm, often aborting; **Tep** golden-yellow, tube conical, (2–) 4–12 (–15) mm deep, lobes (14–) 20–25 (–37) × 3–8 (–12) mm; **Ov** fusiform, (18–) 20–42 (–48) mm, constricted at the apex; **Sty** (24–) 38–65 mm; **Sti** 3-lobed; **Fr** broadly oblong, 30–60 × 20 mm, often beaked, basal stalk 2–10 mm; **Se** D-shaped or irregularly polygonal, 6.5–9 mm, black.

Trelease (1913) published 12 new *Agave* species from the Lesser Antilles in Sect. *Caribaeae* (as Group), but only some of them were accepted by later authors such as Howard & Thompson-Mills (1979), or in the first edition of this handbook. A taxonomic revision of the genus in the Lesser Antilles (Leeward and Windward Islands) by Rogers (2000), including the designation of the above-cited neotype, placed all 12 species of Trelease (1913) in the synonymy of *A. karatto*, and interpreted all of them to merely represent insular variants of a now broadly circumscribed *A. karatto*. Rogers (2000) considers *A. karatto* most similar to the mainland Mexican *A. nayaritensis* of Sect. *Marmoratae* (as Group), thus confirming Gentry (1982: 507) who stated that the Caribbean *Agaves* resemble his mainland Group *Marmoratae*. *A. karatto* is partially sterile and mainly propagates vegetatively by bulbils, which, together with minimal morphological differences, is attributed to prehistoric human selection, dispersal and cultivation activities (Rogers 2000). On the Leeward Antilles (Aruba, Curaçao, Bonaire), *A. karatto* is cultivated only as hedge-row plant (Hummelinck 1938: 24).

**A. karwinskii** Zuccarini (Flora 15: 2(Beiblatt 2): 98, 1832). **Type** [neo]: Mexico, Oaxaca (*Gentry* 12049 [US [2 sheets], ARIZ, DES †, MEXU, MICH]). — **Lit:** Berger (1915: 255); Gentry (1982: 577–579, with ills.); Palma Cruz (1991: 107–111); Arias Toledo & al. (2000: 14, with ill.); Guillot Ortiz & al. (2008: 57, 61, with ill.); García-Mendoza (2011a: 27–30); León Vázquez & al. (2013). **Distr:** Mexico (S Puebla, N & C Oaxaca); limestone hills or sandy sediments in arid regions, in thorn forests, desert scrub and tropical deciduous forests, 700–2000 m; flowers September to October. **I:** Heller (2006: 153);

Richter (2011: 34); Pilbeam (2013: 118 [ill. on p. 119 is *Yucca* sp.]); Phillips (2013: 141); Mahr (2015: 8).

**Incl.** *Agave laxa* Salm-Dyck (1834); **incl.** *Agave karwinskiana* Herbert (1837); **incl.** *Agave corderoyi* Baker (1877); **incl.** *Agave bakeri* Ross (1894).

[2g] Arborescent, stems 0.3–0.7 m (to 3 m in cultivation), forming clonal colonies with spreading rhizomes; **Ros** dense, 0.6–1 × 1–1.5 m, extending down the stem from the stem tip with leaves reflexing along the stems with age; **L** 80–100, linear to linear-lanceolate, rigid, fibrous, ascending to radiately spreading or erect, narrowed and thickened towards the base, acuminate, involute at the tip towards the base of the terminal spine, convex below, guttered or concave above, (33–) 40–65 (–80) × 2–7 (–8) cm, dark to yellowish-green, margins straight; **marginal teeth** delicate, nearly straight or antrorse to cuspidate and flexuous, pyramidal with broad base, 2–4 (–6) mm (at mid-leaf), blackish, dark brown or reddish, (10–) 20–40 (–70) mm apart; **terminal Sp** variable, subulate or conical with thickened base, narrowly to broadly grooved above, 15–30 (–45) mm, blackish or dark brown to greyish and corroding at the base, decurrent or not; **Inf** 3–4 (–6) m, paniculate, peduncle green, with chartaceous triangular **Bra** 4–11 cm long, fertile part openly diffuse, oval to oblong, part-**Inf** lax, 10–15 in the upper 1/2–1/4, 15–30 cm; **Ped** 2 mm, **Fl** 40–50 (–57) mm; **Tep** greenish to pale yellow, tube bulging

between the grooves, rather thin-walled, 10–11 × 8–11 mm, lobes linear-spatulate to oblong, erect, involute, incurving before anther dehiscence, quickly wilting, unequal, 11–19 × 2–3 mm, with ferruginous tinge; **Fil** 35–40 mm, inserted irregularly at mid-tube or slightly above, greenish, dotted reddish; **Anth** regular, centric, 15–22 mm, yellow(ish); **Ov** angularly cylindrical, 20–30 × 7–9 mm, neck 1–2 mm, slightly 6-grooved; **Sty** 45 mm, dotted reddish; **Fr** oblong or obpyriform to subglobose, 35–50 × 25–30 mm; **Se** 7–10 × 6–10 mm, winged for <1 mm. — **Cytology:** 2n = 60 (Flores-Maya & al. 2010).

Easily recognized not only within Sect. *Rigidiae* (as Group) by the stem-forming tall habit with relatively small leaves and small flowers (Gentry 1982). León Vázquez & al. (2013) describe morphological and habitat characteristics. Cultivated forms have stems up to 3 m tall and have more leaves which remain persistently green all along the stem also when dry, and have a longer flowering period from August to February (García-Mendoza 2011a). Naturalized in Spain (Guillot Ortiz & al. 2008). Gentry's "neotype" at US consists of 2 sheets which appear to have been cross-labelled later. See also under *A. schneideriana*.

**A. kavandivi** García-Mendoza & Chávez-Rendón (Revista Mex. Biodivers. 84: 1071–1072, ills., 2013). **Type:** Mexico, Oaxaca (*García-Mendoza & al.* 10184 [MEXU, ENCB, IEB, MO, OAX]). — **Lit:** Ullrich (1990f); Polka (2006),

**Fig. 31** *Agave kavandivi*  
(Etter & Kristen 3912:  
Mexico; Oaxaca, S of  
Yosondua, 1850 m).  
(Copyright: J. Etter &  
M. Kristen)





both with ills., as *A. dasyliroides*; Thiede (2014b). **Distr:** Mexico (Oaxaca: Mixteca Alta); steep limestone slopes in rosette scrub and ecotones to pine-oak forests, 1300–2300 m; flowers October to November. **I:** Brand (2012: as *A. dasyliroides*); Hochstätter (2015: VIII: 13). – Fig. 31.

[1a] Stems decumbent, to 50 cm; **Ros** compact, hemispherical, 30–50 (–60) × 40–60 (–70) cm, surculose; **L** 60–80 (–100), narrowly elliptic, erect or somewhat incurved, flat, rigid, leathery, base 2–2.5 × 2–3 cm, whitish, deltoid, fleshy, with scattered papillae on some veins, lamina 25–35 (–42) × (1.2–) 1.5–2 (in the middle) cm, 1.2–1.8 cm wide at the base, glaucous or glaucous-yellow, striate, margins straight, finely denticulate, scabrous, yellowish; **terminal Sp** conical-subulate, upper face flat near the base, 6–8 (–15) × 1–2 mm, reddish-brown; **Inf** 0.6–1.5 (–2.5) m, ‘spicate’, inclined or arching, peduncle reddish, with **Bra** (6–) 11–15 × 0.2–0.5 (–1.2) (at the base) cm, linear above the deltoid base, red to purple, decreasing in size upwards, densely flowered in the upper 1/3–1/2; floral **Bra** (2.5–) 3–6.5 × (0.1–) 0.3–0.5 mm, linear above a deltoid base, the upper shorter; **Ped** ±1 mm; **Fl** (22–) 25–33 mm, campanulate, geminate; **Tep** purple, tube (5–) 8–15 × 9–12 (at the mouth) mm, somewhat sulcate, lobes 10–14 × 4–7 mm, outer slightly broader than the inner, inner ovate, erect, slightly incurved at the apex, with a triangular rib 4–4.5 mm wide; **Fil** (25–) 30–47 mm, purple, inserted in the middle of the tube; **Anth** (7–) 10–15 × 1–2 mm, purple; **Ov** (6–) 10–14 × 3–5 mm, straight, without neck, apex projecting slightly into the tepal tube, green or reddish-green; **Sty** 30–45 mm; **Sti** hardly thickened; **Fr** ellipsoid to 3-lobed, 10–18 × 7–12 mm, transversally striated, with a ring at the apex, beaked, reddish-green, with persisting tepal remains; **Se** 2–3 (–3.8) × 2–2.4 mm, black, thickened and ornamented with transversal ribs on the convex distal face.

First collected by A. B. Lau in 1988, and illustrated by Ullrich (1990f) (sterile) and Polka (2006) and Brand (2012) (flowering) under the name *A. dasyliroides*. The new species is compared with *A. stricta*, *A. rzedowskiana* and esp. *A. dasyliroides* in the protologue. It shares the

arching inflorescences with the latter, but differs in its branched habit (vs. solitary), and the characteristic reddish peduncles, and purple bracts and flowers. Commercially offered clump-forming, green-leaved plants from N of Santiago Lachiguiri (Oaxaca) might represent a related, undescribed species.

**A. kerchovei** Lemaire (Ill. Hort. 11: 64, 1864).

**Type:** [neo — icono]: US [drawing by A. Berger]. — **Lit:** Berger (1915: 110–111, with ill.); Gentry (1982: 149–153, with ills.); Arias Toledo & al. (2000: 15, with ill.); García-Mendoza (2011a: 29–31). **Distr:** Mexico (S Puebla, N & C Oaxaca), on soils of limestone origin in desert scrub, 975–1600 m; flowers January to May. **I:** Heller (2006: 100); Richter (2011: 68); Pilbeam (2013: 120).

≡ *Agave poselgeri* var. *kerchovei* (Lemaire) A. Terracciano (1885); **incl.** *Agave kerchovei* var. *diplocantha* Lemaire (1864); **incl.** *Agave kerchovei* var. *distans* Lemaire (1864); **incl.** *Agave kerchovei* var. *macrodonga* Lemaire (1864); **incl.** *Agave beaucarnei* Lemaire (1869) ≡ *Agave kerchovei* var. *beaucarnei* (Lemaire) Trelease (1914); **incl.** *Agave kerchovei* var. *pectinata* Baker (1877); **incl.** *Agave horrida* Hort. A. Berger (1898) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave expatriata* Rose (1900); **incl.** *Agave noli-tangere* A. Berger (1915); **incl.** *Agave kerchovei* var. *brevifolia* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave kerchovei* var. *glaucua* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave kerchovei* var. *miniata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave kerchovei* var. *variegata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave inopinabilis* Trelease (1920).

[1g] Acaulescent; **Ros** lax, 0.9–1.5 × 1–1.5 m, solitary; **L** 15–40 (–50), long triangular, erect, rigid, coriaceous, fibrous, base broadened, tip long acuminate, convex below, guttered above, smooth, (70–) 100–150 × 5–10 cm (at the base), green to dark green, margins horny, straight, whitish; **marginal teeth** triangular, straight to variously curved, 8–15 (–20) × 6–13 mm, remote,



(40–) 60–85 (–100) mm apart at mid-leaf, with small intermittent teeth, white-greyish, generally toothless 15–22 (–50) cm below the terminal spine; **terminal Sp** conical, deeply channelled above, (25–) 35–60 × 3–6 (–8) mm, brown to white-greyish, decurrent on the lower leaf face for (3–) 8–10 cm; **Inf** 3–5 m, ‘spicate’, erect, peduncle greenish, with linear chartaceous deciduous brown entire **Bra** 19–20 cm long, fertile part in the upper  $\frac{1}{2}$ – $\frac{2}{3}$  of the inflorescence; **Ped** 3–5 mm (fruiting 7–8 mm); **Fl** campanulate, (30–) 34–40 mm; **Tep** greenish outside, dark reddish inside, tube (2–) 4–5 × (7–) 9–10 (above) mm, lobes elliptic, subequal, 15–17 × 3–5 (–8) mm, **OTep** succulent, **ITep** keeled; **Fil** 30–35 (–40) mm, inserted at the mouth of the tube, yellowish with reddish dots; **Anth** 10–15 mm, reddish; **Ov** cylindrical, (15–) 18–21 × 4–7 mm, green, neck 20–40 mm, constricted; **Sty** 30–35 mm, yellowish; **Fr** ellipsoid, 22–30 (–35) × 8–10 (–12) mm; **Se** 3–4 (–4.5) × 2–3 mm, wing <1 mm. — **Cytology**: 2n = 120 (Palomino & al. 2007, Simpson & al. 2011).

One of the more robust species of Sect. *Heteracanthae* (as Group *Marginatae*), typically easily distinguishable by the long triangular leaves prominently armed with large, variable, remotely spaced teeth which generally lack for a long distance below the apex (Gentry 1982, García-Mendoza 2011a). Gentry’s concept included *A. convallis*, which is here recognized as a species of its own. *A. kerchovei* is closely related to *A. ghiesbreghtii*, which is sympatric over much of S Puebla and Oaxaca and differs esp. by its smaller rosettes with more and smaller deltoid leaves with less remote teeth, its longer filaments, and its much smaller, obovoid fruits (Gentry 1982, García-Mendoza 2011a). The record from Hidalgo (Barranca de Metztlán; Gentry & Sánchez-Mejorada 23383, DES; Gentry (1982: 190)) is not confirmed by later authors (García-Mendoza 2011a) and might represent a misidentification with *A. xylonacantha*, which is common there (Eguiarte & Scheinvar 2008). — The drawing selected as “lectotype” by Gentry (1982: 151, ill. on p. 150) is in fact a neotype. The species is most certainly named after Gustave-Philippe de Kerchove d’Ousselghem (1802–1881) who had one of the

most important *Agave* collections in Europe in the mid-1800s near Ghent, Belgium (Thiede & al. 2019b).

The species (vernacular name: “Maguey de ixtle”) is baked for the extraction of fibres; flower buds (vernacular names: “cacayas” (buds) and “rabo de león” (plants)) are used locally in Puebla and Oaxaca as food for humans and livestock (García-Mendoza 2011a, Brena-Bustamante & al. 2013). Aqueous suspensions of the dry powder have molluscicidal properties (Shoeb & al. 1990). In the Zapotitlán Valley, the species often hosts coccids whose honey-dew is foraged by ants and further insects (Diptera, Hymenoptera); the surplus is used as substrate by sooty moulds. Most insect visitors are predators or parasites which are attracted by a large quantity of possible prey or hosts (Cautle & al. 1998, Cautle & al. 1999). *A. kerchovei* forms part of the diet of the white-tailed deer (*Odocoileus virginianus*) in Oaxaca (Villarreal-Espino & al. 2011). The flowers are bat-pollinated (Arias Toledo & al. 2000).

**A. kewensis** Jacobi (Hamburg. Gart.- & Blumenzeit. 22: 218–219, 1866). **Type**: K 000524824 [neo, ex cult. RBG Kew]. — **Lit**: Gentry (1982: 624–626, with ills.); Ullrich (1990d: with ills., as *A. grijalvensis*); Lott & García-Mendoza (1994: online version with ills.); García-Mendoza (2003). **Distr**: Mexico (W-C Chiapas); cliff edges in calcareous soil, in tropical deciduous forests, 400–1100 m; flowers January to February. **I**: Curtis’s Bot. Mag. 123: t. 7532, 1897; García-Mendoza (2002: 181, as *A. grijalvensis*); Pilbeam (2013: 98, as *A. grijalvensis*); Hochstätter (2015: VI: 29, as *A. grijalvensis*); Berthold (2017: 52, as *A. grijalvensis*).

**Incl.** *Agave grijalvensis* B. Ullrich (1990).

[2c] Acaulescent (or with stem to 15 cm in cult.); **Ros** open, large, solitary; **L** 30–60, (narrowly) lanceolate, arching or sprawling, thickly succulent, arcuate, pliable, guttered, narrowed gradually towards the broadened base, scabrous above, 120–200 × 12–16 cm, yellowish-green, margins straight or nearly so; **marginal teeth** straight, small, deltoid, larger teeth 1–3 (–4) mm (in the upper  $\frac{1}{3}$  of the lamina), 10–40 mm apart, much reduced below or lacking on the lower  $\frac{1}{3}$  of

**Fig. 32** *Agave kristenii*

(Etter & Kristen 1293:  
Mexico; Michoacán, ±  
70 km SE of San Juan de  
Alima, 110 m). (Copyright:  
J. Etter & M. Kristen)



the lamina, brown; **terminal Sp** acicular, weak, scarcely pungent, narrowly grooved above, 30–50 mm, not decurrent; **Inf** 3–6 m, paniculate, peduncle usually short, fertile part lax, part-**Inf** 3-branched, 12–20 in the upper ½ of the inflorescence, bulbiferous; **Ped** 5–8 mm, sparsely bracteolate; **Fl** slender, 40–50 (–60 (–74)) mm; **Te**p brilliant yellow, tube funnel-shaped, 12–15 mm, grooved from the open lobe sinuses, lobes lanceolate, ascending, falcate, unequal, 18–20 × 5–6 mm, outer longer and with dark glandular apex; **Fil** 46–52 mm, inserted above mid-tube; **Anth** excentric, 26–27 mm; **Ov** slender, cylindrical, (20–) 30–40 mm, neck slightly constricted; **Sty** longer than the anthers; **Sti** capitate; **Fr** obovate or oblong, 30–35 mm, stipitate, shortly beaked; **Se** 4 × 3 mm, not further described.

Described by Jacobi 1866 from a sterile living plant cultivated at Kew (and named accordingly), which flowered not until 1895 and was then figured in Curtis’s Bot. Mag. (1897). A specimen prepared in 1895 from the flowering plant was designated as neotype (as “type”) by Gentry (1982) who identified plants from C Chiapas as *A. kewensis*. Ullrich (1990d) questioned this identification, considered *A. kewensis* as of Caribbean origin, and published the plant from Chiapas as a new species *A. grijalvensis*. The *A. kewensis* plant figured in Curtis’s Bot. Mag. was obviously cultivated under lush conditions, and deviating measurements between *A. kewensis* from Jacobi and

later sources and Gentry’s plant from Chiapas disappear with the character expressions presently known (e.g.; ovary 25 mm (Curtis’s Bot. Mag.) vs. 30–40 mm (Gentry 1982), but (20–) 30–40 mm according to Lott & García-Mendoza (1994)) Field-collected specimens (*Breedlove* 23290, MO 2602957 barcode MO-206100!) are a good match for the neotype. Gentry (1982: 630) assumed that *A. kewensis* may be one of the parents of *A. sisalana*.

Ullrich (1990d: as *A. grijalvensis*) provisionally placed the species in Sect. *Marmoratae* (as Group), based on vegetative features (rather than in Sect. *Sisalanae* (as Group) as suggested by Gentry (1982)) The molecular AFLP data of Gil-Vega & al. (2007: as *A. grijalvensis*) place *A. kewensis* widely separate from *A. marmorata* and closest to *A. sisalana* and thus confirm its placement in Sect. *Sisalanae*. — For the in vitro propagation and seed germination, see Sanchez-Urbina & al. (2008) and Santíz & al. (2012). Previously known only from rock cliffs along the Río Grijalva ravine (Gentry 1982, Ullrich 1990d: as *A. grijalvensis*, García-Mendoza 2003, Sarmiento & Ramos 2013: with ill., as *A. grijalvensis*), the species has recently also been found in the understorey of tropical deciduous forests near Tuxtla Gutiérrez (Espinosa-Jiménez & al. 2014), on rock cliffs W of Ocozocoautla at El Aguacero (Martínez-Meléndez & al. 2008, Berthold 2017), and at Villa Allende (Pérez-Farrera & al. 2016: 67–68).

**A. kristenii** A. Vázquez & M. Cházaro (Syst. Bot. 38(2): 326–328, ills., 2013). **Type:** Mexico, Michoacán (*Vázquez-García* 9076 [IBUG, MEXU, MICH, MO, WIS]). — **Distr:** Mexico (W Michoacán); seaward facing slopes of limestone outcrops, thorn forests, 50–130 m; flowers February to March. **I:** Vázquez-García & al. (2007b: Fig. M2, M9, M10, as *A. gypsophila*). — Fig. 32.

[2n] Acaulescent; **Ros** 0.4–0.5 × 1.4 m, surculose; **L** 7–10, linear to narrowly triangular or narrowly lanceolate, generally arched and wavy, firm, rigid, thick throughout, rough, convex below, guttered, 30–79 × 5–6.2 cm, to 5.5 cm wide and to 5.1 cm thick at the base, green to grey, or reddish-brown, glaucously cross-zoned on both faces, margins straight to slightly repand, involute, with prominences 4–5 × 4–5 mm; **marginal teeth** closely set basally and apically, firm, flattened, mostly curved toward the base, mostly 1–2.9 mm, basally 1–2 mm wide, 15–30 mm apart, dark brown intermittent denticles few or none; **terminal Sp** usually short and conical, firm, 5–6 mm, dark brown, not decurrent; **Inf** 3–3.6 m, paniculate, peduncle with triangular **Bra** to 14 cm long at the base, fertile part open, oblong, part-**Inf** 15–18, in the upper  $\frac{2}{3}$  of the inflorescence, with 80–87 flowers; **Fl** 32–36 mm; **Tep** orange, tube somewhat funnellform, 3–4 × 7–10 mm, lobes triangular, erect, fleshy, 10–14 × 4–5 mm, orange and galeate at the apex; **Fil** firm, 21–29 mm, inserted 1–1.5 mm above the tube base, orange; **Ov** 14–20 × 4–5 mm, neck constricted, 2.5–5 mm, green; **Sty** ± as long as the filaments; **Fr** oblongoid, slender, 30–32 × 14–15 mm, stipitate, apiculate; **Se** semicircular, flat, membranous, 4–4.5 × 3–4.5 mm, black.

The recent study of the *A. gypsophila*-complex by Vázquez-García & al. (2013) resulted in a narrower re-circumscription of *A. gypsophila* (see there for further comments). No material of *A. kristenii* was known to Gentry, and the species is narrowly endemic in coastal W Michoacán. It differs from most other members of Sect. *Marmoratae* in its surculose habit and orange rather than bright yellow flowers, and is related to *A. gypsophila* s.s., with which it shares brittle leaves with few fibres, restriction to limestone

outcrops, and similar purported medicinal properties. The plant depicted as *A. kristenii* by Guillot Ortiz & Meer (2016c: 28, fig. 1) has no cross-zoned leaves; it might belong to *A. pablocarrilloi*.

**A. lagunae** Trelease (Trans. Acad. Sci. St. Louis 23(3): 143, t. 21, 1915). **Type** [syn]: Guatemala (*Trelease* 10 [ILL 00009776 & 00009777]). — **Lit:** Standley & Steyermark (1952: 113–114); Gentry (1982: 485); Lott & García-Mendoza (1994); Véliz Pérez (2013: 241, 242, 244, 489, with ill.). **Distr:** Guatemala (regions of Escuintla/Amatitán); on gravel, talus and shady cliffs in mesophytic lowland mountains with pine-oak forests or cloud forests, 700–1600 m; flowers November; only known from the region of the type locality. **I:** Etter & Kristen (1997+).

[2o] Acaulescent; **Ros** openly spreading, to 1.4 m Ø, sparingly suckering; **L** few, linear to lanceolate, acuminate, spreading, flat to concave, finely asperous on the lower face, (30–) 60–75 × 8–15 cm, glaucous-green, margins nearly straight; **marginal teeth** straight or curved, slender, bases slightly elevated, larger teeth 4–10 mm (at mid-leaf), dark brown, 10–30 mm apart; **terminal Sp** subulate, groove above openly channelled to narrow, 30–40 mm, dark brown; **Inf** 3–4 m, paniculate, fertile part rather open, part-**Inf** rather small, 15–20 in the upper  $\frac{1}{2}$ ; **Fl** slender, 60–70 mm; **Tep** yellow, tube funnel-shaped, 5–10 mm, lobes thin, lanceolate, faintly striate, 15–21 × 5 mm, **OTep** involute towards the apex, apiculate, **ITep** with flattened keel; **Fil** somewhat flattened, 45–50 mm, inserted ± at mid-tube; **Anth** regular, centric, 10–15 (–21) mm, yellow; **Ov** slender, cylindrical, 39–45 mm, neck grooved, long, slender, constricted; **Sty** exerted after anthesis, longer than the filaments; **Sti** clavate, 3-lobate; **Fr** and **Se** unknown.

A poorly known species, classified as “Vulnerable” according to IUCN Red List categories (Véliz Pérez 2013: 489). The filaments are inserted unusually low for Sect. *Guatemalenses* (as Group *Hiemiflorae*) (Gentry 1982). The plant depicted as “*Agave lagunae*” by Hochstätter (2015: VI: 9) has much broader leaves and appears to be misidentified. Trelease’s “holotype” consists of 2 specimens which are not cross-



labelled and thus represent syntypes (Smith & Figueiredo 2014e: 237).

**A. lechuguilla** Torrey (in Emory, Rep. US Mex. Bound. 213, 1858). **Type** [lecto]: USA, Texas (*Wright* 682 [US 125459, GH, K, NY]). — **Lit:** Gentry (1982: 154–157, with ills.); Reveal & Hodgson (2002); González-Elizondo & al. (2009: 94–96, with ills.); Greulich (2016a: with ills.); Scheinvar & al. (2016: diversification). **Distr:** USA (S New Mexico, W & SW Texas), Mexico (Chihuahua, Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosí, Guanajuato, Querétaro, Hidalgo, México, D.F.); gravelly to rocky calcareous places in desert scrub, Chihuahuan Desert, 500–2500 m; flowers May to August; locally naturalized in Spain. **I:** Irish & Irish (2000: t. 21); Heller (2006: 101); Richter (2011: 115, 117); Pilbeam (2013: 121); Meer & al. (2014); Hochstätter (2015: IX: 37). — **Fig.** 33.

**Incl.** *Agave poselgeri* Salm-Dyck (1859) ≡ *Agave lophantha* var. *poselgeri* (Salm-Dyck) A. Berger (1915); **incl.** *Agave multilineata* Baker (1888); **incl.** *Agave lophantha* var. *tamaulipasana* A. Berger (1915) ≡ *Agave univittata* var. *tamaulipasana* (A. Berger) H. Jacobsen (1973); **incl.** *Agave univittata* var. *foliis striatis* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave univittata* var. *recurvispinis* Hort. Besaucèle ex A. Berger

(1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave univittata* var. *viridis* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave univittata* var. *zonata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[1g] Acaulescent; **Ros** rather open, mostly 30–50 × 40–60 cm, openly caespitose, freely suckering; **L** few, linear-lanceolate, mostly ascending to erect, sometimes falcately spreading, thick, stiff, deeply convex below, deeply guttered above, (25–) 30–50 × 2–4 (–5.2) cm, light green to yellowish-green, sometimes marked with darker green, margins straight and continuous, light brown to grey, easily separable from dry leaves; **marginal teeth** typically deflected, weak and friable, regular in size, 2–6 mm, brown or mostly light grey, mostly (10–) 15–40 mm apart, 8–20 on each leaf margin, rarely absent; **terminal Sp** conical to subulate, strong, the short groove above open or closed at the base, 15–45 mm, greyish; **Inf** (2–) 2.5–3.5 m, ‘spicate’, peduncle generally glaucous, with caducous linear **Bra** 1–3 cm long, fertile part in the upper ½, part-**Inf** mainly with 2–3 flowers (Gentry: rarely ascending with longer stalks (2–15 cm) and several- to many-flowered; = hybrids with Subgen. *Agave*?); **Fl** (24–) 30–45 mm; **Tep** yellow or frequently tinged with red or purple, tube open, campanulate, shallow, 1.5–4 × 6–12 mm, lobes linear, ascending, subequal, 11–20 mm, outer widely overlapping the inner at the base, thickly

**Fig. 33** *Agave lechuguilla*. (USA; Texas, Big Bend National Park, Lajitas). (Copyright: U. Eggli)



hooded, involute around the filaments; **Fil** spreading, 25–42 mm, yellow to reddish, inserted on the tube rim; **Anth** (11–) 15–20 mm, pale yellow; **Ov** fusiform, roundly angled, (8–) 15–22 mm, neck constricted, (2–) 4–8.5 mm; **Sty** somewhat longer than the tepals; **Sti** slightly thickened; **Fr** oblong to pyriform, rounded, apex short-beaked, 18–25 (–30) × 11–18 mm, glaucous, abruptly very shortly pedicellate or sessile; **Se** with small hilar notch and low fluted wing around the curved side, 4.5–6 × 3.5–4.5 mm. — **Cytology**:  $2n = 120$  (Granick 1944, Cave 1964, Bennett & Leitch 1995, Zonneveld 2003, Simpson & al. 2011).

Usually easily recognizable by its widely suckering habit and narrow leaves with down-slanted teeth on straight margins. This is the dominant *Agave* species in the Chihuahuan Desert, and a characteristic component of several desert communities. It has one of the most extensive ranges of all agaves, and the number of individuals probably exceeds those of all other native agaves (Gentry 1982). It hybridizes with *A. havardiana*, *A. lophantha*, *A. (parryi* ssp.) *neomexicana*, *A. nickelsiae*, *A. victoriae-reginae*, *A. ×glomeruliflora*, and *A. ×gracilipes* (Gentry 1982, Reveal & Hodgson 2002, Richter 2011: 86 Greulich 2016a) and *A. scabra* (Pinkava P-13603 [ASU0000634!]). Zamudio & Galván Villanueva (2011) provide a new record for Guanajuato.

The protologue designated *Wright* 682 and *Wright* 1907 as syntypes. The designation of *Wright* 682 (US 125459) as “type” by Gentry (1982: 154) represents a lectotypification.

*A. lechuguilla* is poisonous to cattle, goats, and sheep (Gentry 1982). In former times, it was an important source of hard fibres known as “istle”, “ixtle” or “Tampico fibre” (García-Moya & Ayala-Sosa 2007), and there is a recent revived interest in this natural resource (Castillo Quiroz & al. 2011). The ethnobotany in the fibre-harvesting “zona ixtlera” is reviewed by Sheldon (1980). It appears that the extraction of fibres from natural populations does not affect the population density, but increases the growth of the central bud on short terms (Pando-Moreno & al. 2008). Leaf growth depends mainly on water status, with nearly all leaf-unfolding occurring during the wet period (Nobel & Quero 1986). Molecular data (Scheinvar & al. 2016) reveal pleistocene area contractions and expansions concomitant with glacial-interglacial events which are consistent with biogeographical regions in the Chihuahuan Desert.

The peduncles may grow as rapidly as 20 cm/day and reach full height in 3–4 weeks. The energy for flowering is stored almost entirely in the leaves (Freeman & Reid 1985). A study along the whole range of the species in the Chihuahuan Desert found a latitudinal pattern in flower shape and colour and flower visitors: Flowers tended to be shorter, more open, and

**Fig. 34** *Agave* × *leopoldii*. (Copyright: U. Eggli)





colourful in the N part of the range, and the number of flower visits by all potential pollinators decreased significantly with increasing latitude, as did fruit set. Main pollinators are nocturnal hawk moths and esp. 2 species of diurnal large bees; bats were not observed (Silva-Montellano & Eguiarte 2003a). The overall genetic variation as revealed by allozymes is high, but without geographic pattern. The differentiation among populations is low, with S populations having the lowest levels suggesting high levels of gene flow, and N populations with greater levels, suggesting low gene flow, in consistence with floral traits and pollinator visitation rates across the species' range (Silva-Montellano & Eguiarte 2003b).

Aymerich & Gustamante (2016) and Aymerich (2016) report the taxon as locally naturalized in Spain.

**A. ×leopoldii** W. Watson (Gard. & Forest 6: 394, 1893). **Nom. illeg.**, ICN Art. 53.1. **Type:** [neo — icono]: Curtis's Bot. Mag. t. 8451, 1912, as *A. disceptata*. — **Lit:** Drummond (1912: with ill., as *A. disceptata*); Watson (1912: 414, as *A. leopoldii*); Anonymous (1913: 10–11, with ill., as *A. leopoldii*); Berger (1915: 76, as *A. leopoldii*); Smith & Figueiredo (2014d: with ills.); Walker (2018: with ill.). **Distr:** Cultivated only. **I:** Gard. Chron. ser. 3, 53: 10–11, 1913; Richter (2011: 87); Pilbeam (2013: 123). — Fig. 34.

**Incl.** *Agave ×disceptata* J. R. Drummond (1912).

[1d × 1d] According to the protologue, this is the garden hybrid *A. filifera* × *A. schidigera* (see also Berger (1915: 76)) raised around 1870 by W. B. Kellock, UK, characterised by narrow leaves with filiferous margins. The earlier name *A. leopoldii* Rafarin 1874 refers to a completely different plant with large marginal teeth and was described to be “of the Verschaffelti type” (Anonymous 1874). *A. ×leopoldii* W. Watson is therefore an illegitimate homonym, and a conservation proposal to avoid a name change was published by Figueiredo & Smith (2013a), which was recommended by the relevant committee (Applequist 2014: 1366). — The plant is not uncommon in cultivation.

**A. littoralis** (García-Mendoza & al.) Thiede & Egli (Kakt. and. Sukk. 52(6): 166, 2001). **Type:** Mexico, Guerrero (*García-Mendoza & al.* 6900 [MEXU, MO]). — **Lit:** García-Mendoza & al. (2000); Castillejos-Cruz (2009: [181]–[186]); both with ills. and as *Manfreda*. **Distr:** Mexico (Guerrero, Oaxaca); tropical (sub-) deciduous forests, rocky sites, in small soil pockets, 20–260 m; flowers August to December. **I:** Hochstätter (2016: I: 26, as *Manfreda*).

≡ *Manfreda littoralis* García-Mendoza & al. (2000).

[3a3] Plants herbaceous; corm 3–5 × 2.5–3 (at the base) cm, conical-truncate, stoloniferous, bulb 1.8–2.5 × 1.5–2.2 cm, subcylindrical, covered with dried membranous leaf bases 1.5–2.5 (–3.5) cm long; **R** fleshy, with filiform ramifications; **L** drought-deciduous, 4–6, flat, prostrate or semi-erect, semisucculent, elliptical to elliptical-lanceolate, narrowing to a canaliculate pseudo-petiole 0.5–1 cm wide, apex apiculate or acuminate, glabrous on both faces, 9–20 (–27) × 2–5 (–6) cm, greenish-yellow with purplish or dark-green dots, margins entire to the touch, microscopically finely papillose in some sections, on a narrow hyaline band; **Inf** 60–70 (–80) cm, erect to slightly arched, ‘spicate’, reddish at the base and glaucous-green above, **Bra** 9–12 (–15), fertile part 3.5–4.5 (–6.5) cm, dense, with 11–14 (–24) flowers; floral **Bra** 0.3–0.5 × 0.3–0.4 cm; **Fl** 15–20 (–25) mm, solitary, sessile, sometimes the lower with <1 mm long pedicels, erect; **Tep** greenish-yellow, campanulate, tube 1–2 (–2.8) × 2–3 mm, lobes oblong, erect or reflexed, 9–10 (–11) × 1.5–2 (–3.5) mm, tip cucullate; **Fil** (13–) 17–21 mm, erect at anthesis, exceeding the tube for (10–) 14–18 mm, inserted at the end of the tube on the same level, whitish; **Anth** 7–8 (–9) mm, whitish; **Ov** cylindrical, 3–5 (–6) × 1.5–2.5 (–4) mm, greenish, extending for <1 mm into the tube, not constricted above; **Sty** 18–22 mm; **Sti** 3-lobed, whitish; **Fr** subglobose, triquetrous, 9–10 × 8–10 mm, with inconspicuous scar at the apex, tepals persisting; **Se** plane-concave, blackish, opaque, 3–4 × 3 mm.

Placed in Ser. *Guttatae* (as *Manfreda guttata*-group) and closest to *A. guttata* and *A. planifolia* according to the protologue, but also similar to *A. bulbifera* and *A. pratensis* (Castillejos-Cruz

& Solano 2008) (as *Manfreda* & *M. rubescens*). The tropical lowland habitat is atypical and apparently not known for Subgen. *Manfreda* except *A. chamelensis*, *A. petskinil* and *A. paniculata*.

**A. longibracteata** (Verhoek-Williams) Thiede & Eggl (Kakt. and. Sukk. 50(5): 110, 1999). **Type:** Mexico, Michoacán (*Verhoek-Williams & al.* 613 [US, BH, MEXU]). — **Lit:** Verhoek-Williams (1978a: with ills.); Piña Luján (1986: 13–14); Castillejos-Cruz (2009: [187]–[192], with ills.); all as *Manfreda*. **Distr:** Mexico (W Jalisco, Colima, N Michoacán); open spots among rocks, in oak forests, grasslands, and scrub, 1120–2070 m; flowers July to September. **I:** Rodríguez & Castro-Castro (2006: 624); Rodríguez & Castro-Castro (2007: 9); Hochstätter (2016: I: 27); Castro-Castro & al. (2017: 62); all as *Manfreda*.

≡ *Manfreda longibracteata* Verhoek-Williams (1978).

[3a2] Plants herbaceous; corm 5–7 cm Ø, globose to subglobose, with stoloniferous vegetative shoots, bulb 1.5–2 × 1.2–1.8 cm, cylindrical, only at the apex covered with dried fibrous leaf bases 6–8 cm long; **R** fibrous; **L** drought-deciduous, 8–14, erect and extended, linear-lanceolate to lanceolate, narrowed towards the base, apex obtuse, apiculate, broadly canaliculate, sometimes wavy, glabrous on both faces, 21–39 × 1.5–3.5 (–4.3) cm, shiny green, sometimes with purple dots near the base, margins entire, with a hyaline band, slightly revolute; **Inf** 120–140 (–160) cm, erect, ‘spicate’, green-glaucous, **Bra** 8–10, rather distant, fertile part 10–15 (–25) cm, lax, with 15–20 flowers; floral **Bra** 1.7–4 × 1.5–2.3 cm; **Fl** 30–35 mm, solitary, sessile, ascending; **Tep** glaucous-green with reddish dots at the base, inner face greenish-yellow, forming a funnel-shaped tube 15–20 × 4–5 mm, slightly recurved, lobes oblong, extended to recurved, 12–15 × 6–7 mm, tip cucullate, with soft tip and a bundle of short white trichomes; **Fil** 34–39 mm, erect at anthesis, somewhat flattened, abruptly narrowing below the anthers, exceeding the tube for 22–24 mm, inserted at ¼ above the base of the tube and all on the same level, yellowish-green with purple dots; **Anth** (10–) 13–14 mm,

greenish-yellow; **Ov** oblong, 12–15 × 4–5 mm, greenish, prolonging slightly into the tube, not constricted above; **Sty** 44–47 (–54) mm; **Sti** 3-lobed, greenish-yellow; **Fr** ellipsoid, 20–26 × 10–14 mm, apiculate, tepals persisting; **Se** deltoid, plane-concave, 3–4 × 3–4.5 mm, opaque.

According to the protologue vegetatively most noticeable for the crisp bright green leaves with a broad round channel, and in bud or flower recognizable by the long floral bracts (see above-cited ills. by Rodríguez & Castro-Castro and Castro-Castro & al.). It appears to be closest to *A. scabra* (Verhoek-Williams 1978a: as *Manfreda*), but differs in its globose rhizome, delicate leaves, larger floral bracts, smaller filaments and styles, and its strong citronella-scent (Castillejos-Cruz 2009).

**A. longiflora** (Rose) G. D. Rowley (Repert. Pl. Succ. 26: 4, 1977). **Type:** USA, Texas (*Runyon* 10 [US, ILL, K, NY]). — **Lit:** Rose (1922: with ills., as *Runyonia*); Verhoek-Williams (1975: 222–226); Piña Luján (1985: 63–64); Reveal & Hodgson (2002); García-Mendoza (2003); Castillejos-Cruz (2009: [193]–[197], with ills.); all as *Manfreda* except Rose. **Distr:** USA (Texas), Mexico (N Tamaulipas); clay slopes, dry gravelly hills and prairies in sandy loam overlying caliche, in desert scrub, thorn forests or grasslands, always in the shade of other plants, 0–100 m; flowers end of August to September. **I:** Hannon (2002: 248, 249); Richardson & King (2011: 18); both as *Manfreda*.

≡ *Runyonia longiflora* Rose (1922) ≡ *Manfreda longiflora* (Rose) Verhoek-Williams (1975); **incl.** *Runyonia tenuiflora* Rose in sched. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Runyonia tubiflora* Rose in sched. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Polianthes runyonii* Shinnery (1966).

[3a1] Herbaceous, medium-sized (for Subgen. *Manfreda*), corm cylindrical, succulent, 2.5–6.5 × 0.8–2 cm, bulb 2.5–4 × 1–2 cm, covered with dry membranous leaf bases (2–) 5–9 cm long; **R** fleshy-fusiform, contractile, with filiform ramifications; **L** evergreen, succulent, 3–7 (–15), forming a rosette, linear-lanceolate to narrowly lanceolate, erect to semi-erect, recurved to undulate, channelled, fleshy, tip acute, with a soft

medium-sized point, 10–27 × 1.2–1.8 (–2 in cultivation) cm, light green to glaucous, with purple, brown or darker green spots over the whole surface above, margins with coarse, distantly-spaced, cartilaginous, deltoid to truncate, occasionally retrorse teeth 3–10 mm apart, intervening margin hyaline; **Inf** 20–50 (–62) (–96 in cultivation) cm, ‘spicate’, reddish to green with purple tinge, peduncle with 3–4 truncate **Bra**, fertile part 8–20 (–35 in cultivation) cm, with (7–) 10–21 densely or laxly arranged flowers; **Fl** 45–55 mm, sessile, erect, fragrant; **Tep** semisucculent, tube straight, narrowly funnel-shaped, 23–36 × 3–4 mm, lobes oblong, revolute, tip obtuse, with a small tuft of hairs, 8–15 (–19) × 3–4 mm, whitish-pink to reddish-pink with age; **St** very short; **Fil** 5–6 mm, exceeding the tube for 5–6 mm, inserted at the throat of the tube, whitish; **Ov** ellipsoid, 4–6 × 3–4 mm, not prolonging into the tube; **Sty** 35–40 mm, included or slightly exerted; **Sti** 3-lobed, papillate, greenish-yellow; **Fr** globose to ovoid, triquetrous, 9–12 × 10–13 mm, apiculate; **Se** deltoid, plane-concave, with narrow margin, 3–4 × 3–4 mm, shiny. — **Cytology**: 2n = 60 (Granick 1944).

Reddish flowers with a long tube and sessile anthers were not known from *Manfreda* when Rose (1922) described the taxon, which prompted him to erect the separate genus *Runyonia*. The species is characterized by flowers with a long, narrow tube, stamens inserted at the mouth of the tube, stamens and style included or only shortly

exserted, and a small, globose fruit (Castillejos-Cruz 2009). It is closely related to *A. maculosa* with which it shares the consistency, colour and type of the leaf margin and flower colour (Castillejos-Cruz 2009: as *Manfreda*) and is distinguished by the longer narrow tepal tube, almost sessile anthers, and included styles, and smaller and more flattened fruits (Verhoek-Williams 1975: 224, as *Manfreda*). The plant depicted by Hochstätter (2016: I: 28) is misidentified.

**A. longipes** Trelease (Mem. Nation. Acad. Sci. 11: 36, t. 63, 1913). **Type** [syn]: Jamaica (*Maxon* 1624 [US 247915 & 247916]). — **Lit**: Berger (1915: 211); Hummelinck (1927: with ill.); Adams (1972: 81). **Dist**: Jamaica (St. Andrews); local on well-drained conglomerate or igneous rocky slopes, 840–1200 m; flowers March to April. **I**: Hochstätter (2015: VII: 73).

[2p] **L** as in the broader-leaved forms of *A. sobolifera*, curved, tip outcurved, margins straight; **marginal teeth** narrowly triangular, often appressed-recurved, 2–4 mm, on broad lenticular bases, 15–30 mm apart, intervening margin straight; **terminal Sp** sometimes much compressed and conical, more strongly and persistently flattened on the upper face and less involute, 25–50 mm, often grey; **Inf** ‘paniculate’, fertile part oblong, part-**Inf** slightly ascending, ±40–45, rather flat and broad, in the upper ⅓ of the inflorescence, not known to be bulbiferous; **Ped** 20 mm; **Fl** larger, 60–70 mm; **Tep** yellow, tube openly conical,

**Fig. 35** *Agave lophantha*. (cult.: USA; Arizona, Desert Botanical Garden Phoenix). (Copyright: J. Thiede)



6–8 mm, lobes 20–25 × 5–6 mm; **Fil** 50–60 mm; **Ov** oblong-fusiform, 28–40 × 6–8 mm; **Fr** ±40 × 15 mm, slightly beaked; **Se** unknown.

Similar to *A. sobolifera*, but with larger flowers and longer filaments (Adams 1972). For differences from *A. harrisii*, see there.

**A. lophantha** Schiede (Linnaea 4: 581–582, 1829). **Type:** not typified. — **Lit:** Berger (1915: 91–94); Gentry (1982: 157–161, with ill.); Reveal & Hodgson (2002: as *A. univittata*). **Distr:** USA (Texas), Mexico (Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, Veracruz, Puebla, Chiapas); cliffs and rocky outcrops, frequent on limestone, 30–1500 m; flowers irregularly, in February, April, June, August, and October; locally naturalized in Spain. **I:** Refug. Bot. 3: t. 215, 1870, as *A. univittata*; Curtis's Bot. Mag. 108: t. 6655, 1882, as *A. univittata*; Irish & Irish (2000: t. 22); Heller (2006: 102, 103); Richter (2011: 34); Pilbeam (2013: 124); Beutelspacher & García-Martínez (2017). — Fig. 35.

≡ *Agave univittata* var. *lophantha* (Schiede) Maire & Weiller (1960) (*incorrect name*, ICN Art. 11.4, 25.1); **incl.** *Agave mezortillo* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave univittata* Haworth (1831) ≡ *Agave heteracantha* var. *univittata* (Haworth) A. Terracciano (1885) (*nom. illeg.*, ICN Art. 52.2, 25.1) ≡ *Agave lophantha* var. *univittata* (Haworth) Trelease (1914); **incl.** *Agave heteracantha* Zuccarini (1832) ≡ *Agave univittata* var. *heteracantha* (Zuccarini) Breitung (1959); **incl.** *Agave vittata* Regel (1858) ≡ *Agave heteracantha* var. *vittata* (Regel) Regel (1858); **incl.** *Agave caerulescens* Salm-Dyck ex Jacobi (1864) ≡ *Agave lophantha* var. *caerulescens* (Salm-Dyck ex Jacobi) Jacobi (1866) ≡ *Agave lophantha* f. *caerulescens* (Salm-Dyck ex Jacobi) Voss (1895) ≡ *Agave univittata* var. *caerulescens* (Salm-Dyck) H. Jacobsen (1973) ≡ *Agave lechuguilla* var. *caerulescens* (Salm-Dyck) P. Van der Meer & al. (2014) (*nom. inval.*, ICN Art. 41.5); **incl.** *Agave lophantha* var. *brevifolia* Jacobi (1866) ≡ *Agave univittata* var. *brevifolia* (Jacobi) H. Jacobsen (1973); **incl.** *Agave lophantha* var. *gracilior* Jacobi (1866) ≡ *Agave univittata* var. *gracilior* (Jacobi) H. Jacobsen (1973); **incl.** *Agave lophantha* var. *subcanescens* Jacobi (1866)

≡ *Agave univittata* var. *subcanescens* (Jacobi) H. Jacobsen (1973); **incl.** *Agave lophantha* var. *angustifolia* A. Berger (1915) ≡ *Agave univittata* var. *angustifolia* (A. Berger) H. Jacobsen (1973); **incl.** *Agave lophantha* var. *pallida* A. Berger (1915).

[1g] Stems sometimes visible on old rosettes; **Ros** 0.3–0.6 × 0.5–1 m, solitary or surculose; **L** numerous, linear to lanceolate, radiating, patulous, rather thin, pliable, somewhat thickened towards the base and rounded below, flat to concave above, generally 30–70 × 3–5 cm, light green to yellow-green, with or without pale mid-stripe, margins horny, repand to crenate; **marginal teeth** straight or mildly curved, slender, single or occasionally double, mostly 4–8 mm, 10–20 mm apart, on broad low prominences; **terminal Sp** subulate, flattened above at the base, small, 10–20 mm, ferruginous to grey; **Inf** 3–4.5 m, slender, ‘spicate’, **Fl** in the upper ½, part-**Inf** with 1–2 or also with 3–7 flowers, on short stalks; **Ped** 5–10 mm; **Fl** 35–47 mm; **Tep** light grey-glaucous-green to yellow, tube campanulate, short, open, 2–4 × 8–10 mm, lobes erect to slightly spreading, subequal, 14–20 mm, persisting erect around the filaments; **St** long-exserted; **Fil** spreading, 30–45 mm, greenish or lavender, inserted on the tube rim; **Anth** 15–20 mm, pale yellow; **Ov** fusiform, 18–22 mm, neck short or long (5–7 mm) and constricted; **Sty** thick, longer than the tepals; **Sti** slightly thickened; **Fr** oblong and 18–24 × 10–12 mm or globose and 15–20 × 12–18 mm, sessile or with short (2–3 mm) pedicel; **Se** crescent-shaped, faces with wavy ridges, edges with raised margins, 5–6 × 3–4 mm. — **Cytology:** 2n = 60 (Simpson & al. 2011: as *A. univittata*).

Often confused with the closely related *A. lechuguilla*, and distinguished by flatter leaves with sinuous to repand firm borders, prominences usually with at least one double set of teeth (frequently more), and by teeth that are more slender and closely set. Some *A. lophantha* forms with broad leaves and crenate margins with large prominences look very much like *A. xylonacantha*, and may be inseparable (Gentry 1982). *A. heteracantha* Zucc. is commonly placed in the synonymy here, but Alsemgeest & al. (2007b) suggest



that it is probably the hybrid *A. lophantha* × *A. xylonacantha*. Beutelspacher & García-Martínez (2017) provide a new record for Chiapas.

The name *A. lophantha* was first mentioned by Schiede as cited above with a short description considered as inadequate by some authors, so that the valid publication of the name is commonly ascribed to Kunth (in Enum. Pl. 5: 838, 1850) (Reveal & Hodgson 2002). The latter is antedated by *A. univittata* Haworth (Philos. Mag. Ann. Chem. 10: 415, 1831). Both names are not typified nor is any authentic material known. Gentry (1982) treated *A. lophantha* as validly published by Schiede, and this was widely followed. Breitung (1959) was the first to adopt the name *A. univittata*, and he was recently followed by Reveal & Hodgson (2002) and Govaerts (2014+). In order to clarify the matter, a formal request for a binding decision whether the descriptive statement of Schiede (1829) is adequate for valid publication was submitted by Smith & al. (2018a) and the widely established name *A. lophantha* is retained here.

Reported as local neophyte from Spain (Aymerich 2015: 100, as *A. univittata*, Gómez-Bellver & al. 2019: 24–25). Cultivars cultivated in Spain are presented by Guillot Ortiz & Meer (2012). ‘Quadricolor’ (Guillot Ortiz & Meer 2012, Puche 2014, Starr 2014: 223) is a variegated cultivar widely offered commercially.

**A. lurida** Aiton (Hort. Kew. 1: 472, 1789). **Type** [neo]: Ex cult. (*Masters* s.n. [K]). — **Lit**: Drummond (1910); Berger (1915: 244–245); Gentry (1982: 292–294, with ills.); García-Mendoza (2003); Guillot Ortiz & Meer (2008b: 25–26, with ill.); Guillot Ortiz & al. (2008: 64–65, with ill.); García-Mendoza (2011a: 32, 36); López-Pujol & al. (2015a: 55–57, with ills.). **Dist**: Mexico (NW Oaxaca); volcanic slopes in semi-arid tropical forests, ±1830 m; flowers July to August. **I**: Curtis’s Bot. Mag. 37–38: t. 1522, 1813; Refug. Bot. 5: t. 307, 1871; Heller (2006: 103); Richter (2011: 21).

**Incl.** *Agave vera-cruz* Miller (1768); **incl.** *Agave mexicana* Lamarck (1783); **incl.** *Agave verae-crucis* Haworth (1812); **incl.** *Agave magni* Desfontaines (1815); **incl.** *Agave mangui*

Desfontaines (1815) (*nom. inval.*, ICN Art. 61.1?); **incl.** *Agave lepida* D. Dietrich (1840); **incl.** *Agave haworthiana* M. Roemer (1847); **incl.** *Agave polyphylla* K. Koch (1860); **incl.** *Agave cyanophylla* Jacobi (1866); **incl.** *Agave verna* A. Berger (1915); **incl.** *Agave breviscapa* A. Berger ex Roster (1916).

[2a] Stems short; **Ros** lax, 1.2–1.8 × 2–3.4 m, solitary or only rarely surculose; **L** 60–80, linear-lanceolate, stiffly ascending to outcurving, concave to guttered and narrowed towards the base, 110–150 × 12–18 cm, dull green to glaucous-grey, margins nearly straight; **marginal teeth** straight, very regular, larger teeth (at mid-leaf) 4–6 mm, (7–) 10–15 (–20) mm apart, smaller and closer together towards the leaf base, with low black lenticular bases, on low prominences, tips usually deltoid-flattened, straight or curved, dark blackish to brown or greyish; **terminal Sp** conically subulate, shallowly grooved above, 30–45 × 6–8 (at the base) mm, greyish-brown, decurrent for several to 30 cm; **Inf** 6–8 m, paniculate, peduncle glaucous-green, with deltoid chartaceous **Bra** 30 cm long, fertile part rhomboidal, lax, with 18–25 ascending part-**Inf** 1–1.5 m long, these diffusely spreading, several times compound, open, in the upper 1/3–1/2 of the inflorescence; **Ped** slender, 5–9 mm, minutely bracteolate; **Fl** campanulate, 50–55 (–65) mm; **Te** greenish-yellow, tube funnel-shaped, grooved, 8–10 (–13) × 7–9 (–15) mm, lobes oblong, erect, incurved at the tip and hooded, slightly unequal, 18–24 × 2–3 (–6) mm (**ITe** slightly shorter), wilting after anthesis, inner with narrow thin margins; **Fil** 40–45 (–60) mm, inserted above mid-tube or towards the top; **Anth** 15–22 mm, (bright) yellow; **Ov** cylindrical to fusiform, 25–30 (–34) × 5–8 mm, neck 4–6 mm, constricted, grooved; **Fr** oblong, 55–80 × 25–40 mm, stipitate; **Se** 8–11 × 6–8 mm, winged for ±2 mm, shiny black. — **Cytology**: 2n = 90, 100, 108, 114, 120 (Simpson & al. 2011).

Characterized by glaucous linear-lanceolate leaves with closely set small teeth with broad base, large rhomboidal inflorescences with diffuse part-inflorescences, and small, soon withered flowers with short tube. It is rare in nature and threatened by extinction (García-Mendoza 2011a).



Frequently mentioned in the older literature, and for long only known from cultivation in Europe, until Gentry rediscovered material assignable to this taxon after  $\pm 200$  years in one spot in Oaxaca (Gentry 1982). The taxon is without close relatives. Ullrich (1991f) regards the neotypification of Gentry and the correlation of the re-collected material with the name *A. lurida* as doubtful. Gentry cited the prioritable name *A. vera-cruz* Miller (Gard. Dict. ed. 8: *Agave* n. 7, 1768) as a synonym, although with a question mark. Here the established name is retained pending a formal proposal to conserve it against the older competitor.

Locally naturalized in Spain (Guillot Ortiz & Meer 2008b, Guillot Ortiz & al. 2008, López-Pujol & al. 2015a, Verloove & al. 2018: 34, all with ills.).

**A. iyobaa** García-Mendoza & S. Franco (Acta Bot. Mex. 126: e1461: 2–3, ills. (pp. 4, 15), 2019). **Type:** Mexico, Oaxaca (*García-Mendoza & Martínez Aguirre* 11091 [MEXU, ENCB, MEXU, MO, OAX]). — **Distr:** Mexico (S Puebla, C Oaxaca); flat or slightly inclined sites, on limestone rocks, xerophytic scrub and ecotone with oak forests, also grown as ornamental or for mescal production, 1550–1900 m; flowers August to October.

[2h] Acaulescent; rarely stems to 80 cm; **Ros** lax to subcompact, 0.5–0.8  $\times$  0.8–1.3 m, solitary; **L** 20–50 (–100), lanceolate, erect, thickened at the base, flattened, concave towards the apex, apex

acuminate or acute, 30–50  $\times$  6–9.5 cm, 4–6  $\times$  longer than broad, greenish-yellow or dark-green, margins straight or occasionally wavy; **marginal teeth** antrorse or straight, 4–6  $\times$  4–6 mm at mid-leaf, 15–30 mm apart at mid-leaf, greyish or dark-brown, sometimes on small mamilliform bases; **terminal Sp** straight, broadly grooved to flat, 30–55  $\times$  5–7 mm, greyish or dark-brown, decurrent for 10–20 mm; **Inf** (3–) 5–7 m, paniculate, peduncle green, waxy, with triangular chartaceous **Bra** 10–15 cm long, fertile part 1.5–3 m, lax, ellipsoid, **part-Inf** (slightly) ascending, 15–25 in the upper  $\frac{1}{2}$  of the inflorescence, 20–50 cm, 2.-order branches 4–9 cm, 3.-order branches 2–4.5 cm; **Fl** (40–) 45–55 mm; **Tep** green or yellowish-green, tube tubular or urceolate, 8–15  $\times$  8–12 (at the mouth) mm, lobes erect, oblong, 10–15  $\times$  3–4 mm, dimorphic, **OTep** 1–2 mm longer than the keeled **ITep**, margins all involute, apex callose, cucullate, inner face with a tiny orange-coloured dot in bud; **Fil** erect, inserted at 2 levels at mid-tube, (30–) 35–45 mm, yellowish to purple; **Anth** 15 mm, yellowish; **Ov** cylindrical, 25–30  $\times$  3–5 mm, neck 3–5 mm; **Sty** 50–55 mm, yellowish to purple; **Sti** clavate, 3-lobate; **Fr** ellipsoid, 40–60  $\times$  25–35 mm; **Se** semicircular, unwinged, 6–9  $\times$  6–8 mm, black.

In the protologue placed in Sect. *Ditepalae* (as Group) where it is the S-most species. It is compared with *A. palmeri*, from which it differs in its smaller leaves with more remote marginal

**Fig. 36** *Agave macroacantha* (Lau s.n.: Mexico; Oaxaca, Cañón de Tomellín). (Copyright: U. Eggli)



teeth and an acuminate or acute apex, inflorescences with the fertile part in its upper  $\frac{1}{2}$ , flowers with a tube shorter than or equal to the tepals, tepals with a reddish-brown to violet tinge in bud and with an orange dot, filaments inserted at mid-tube, and ellipsoid fruits. — Vernacular names: “shtob bnijh” (Zapotec), “magüey del duende”, “magüey coyote”. The epithet is derived from the Zapotec “Lyobaa”, the name for the pre-Hispanic city of Mitla, which translates to “place of tombs” or “place of rest”; plants cultivated at the Mitla archaeological site are assumed to have originated from the surrounding mountains. The species is classified in the IUCN Red List Category “Endangered”.

**A. macroacantha** Zuccarini (Flora 15: 2 (Beiblatt 2): 97, 1832). **Type** [neo]: Mexico, Puebla (*Gentry & al.* 20242 [US, ARIZ, MEXU [2 sheets]]). — **Lit**: Trelease (1907: 247–252, tt. 18–28); Gentry (1982: 578–580, with ills.); Arias Toledo & al. (2000: 16, with ill.); Garcia-Mendoza (2011a: 33–34); Starr (2012: 127–130, with ills.). **Distr**: Mexico (S Puebla, N Oaxaca: Tehuacan-Cuicatlán valley); dry sedimentary slopes, in desert scrub or short-tree forests, 700–1800 m; flowers May to July. **I**: Curtis’s Bot. Mag. 97: t. 5940, 1871, as *A. bessereriana*; Irish & Irish (2000: t. 23); Heller (2006: 19, 104, 105); Richter (2011: 33, 113); Pilbeam (2013: 125); Phillips (2013: 140); Hochstätter (2015: VII: 44); Moore (2016: 285). — Fig. 36.

≡ *Agave flavescens* var. *macroacantha* (Zuccarini) Jacobi (1864) (*incorrect name*, ICN Art. 11.4, 25.1); **incl.** *Agave pugioniformis* Zuccarini (1832); **incl.** *Agave flavescens* Salm-Dyck (1834); **incl.** *Agave macracantha* Herbert (1837) (*nom. inval.*, ICN Art. 61.1?) ≡ *Agave flavescens* var. *macracantha* (Herbert) Jacobi (1865); **incl.** *Agave bessereriana* de Smet ex Jacobi (1865); **incl.** *Agave bessereriana* Van Houtte (1868) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave linearis* Jacobi (1869); **incl.** *Agave subfalcata* Jacobi (1869); **incl.** *Agave bessereriana* [?] *candida* Jacobi (1870); **incl.** *Agave bessereriana* [?] *longifolia glauca* Jacobi (1870) (*nom. inval.*, ICN Art. 24.2); **incl.** *Agave bessereriana* [?] *longifolia viridis* Jacobi (1870) (*nom. inval.*, ICN

Art. 24.2); **incl.** *Agave bessereriana* [?] *glauca* T. Moore (1871); **incl.** *Agave bessereriana* [?] *hystrix* hort. ex Hooker (1871); **incl.** *Agave bessereriana* [?] *amoena* Green (1871) (*nom. inval.*, ICN Art. 38.1); **incl.** *Agave oligophylla* Baker (1877); **incl.** *Agave sudburyensis* Baker (1877); **incl.** *Agave paucifolia* Baker (1878) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave integrifolia* Baker (1888); **incl.** *Agave macroacantha* var. *integrifolia* Trelease (1907); **incl.** *Agave macroacantha* var. *latifolia* Trelease (1907); **incl.** *Agave macrantha* Trelease (1907) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave macroacantha* var. *planifolia* A. Berger (1915).

[2g] Stems none or short, to 30 cm, creeping or erect; **Ros** 20–40 × 30–50 cm, commonly caespitose and forming colonies with up to 10 rosettes; **L** (35–) 50–70, linear or oblong, rigid, erect or radiately spreading, patulous, acuminate, convex below, flat above, 15–25 (–35) × 1.5–2.5 (–3.5) cm, bluish-grey-glaucous or yellowish-glaucous, slightly canaliculate, margins straight or slightly repand; larger **marginal teeth** antrorse, larger ones (at mid-leaf) 3–5 (–7) × (at the base) 4–6 mm, blackish to dark brown, irregularly spaced (10–) 20–35 mm apart, with slender tips mostly curved from small low bases; **terminal Sp** conical, straight to sinuous, rounded below, flat above and flatly grooved, (20–) 25–35 (–45) × (at the base) 3–6 (–7) mm, blackish or dark brown to grey, decurrent, penetrating into the leaf tissue for 2–3 mm; **Inf** 2–3 (–3.5) m, paniculate, peduncle glaucous-reddish, with chartaceous triangular **Bra** 5–8 (–13) cm long, fertile part lax, slender, oblong, part **Inf** shortly spreading, 8–14 in the upper  $\frac{1}{2}$  of the inflorescence, 20–30 cm, sometimes bulbiferous, bulbils leafy; **Ped** 2–5 mm; **Fl** slightly urceolate, (45–) 50–55 (–60) mm; **Tep** glaucous-green with purple tinge, tube broadest in the middle or urceolate, grooved, 10–15 × 7–10 mm, lobes oblong, erect, ± equal, 13–20 × 2–3.5 mm, reddish or with purple tinge; **ITep** with narrow keel but soon receding, quickly wilting at anthesis; **Fil** (30–) 35–45 mm, reddish or purple, inserted at mid-tube or slightly above; **Anth** slightly excentric, spotted, 20–21 mm, yellowish; **Ov** cylindrical to angular-fusiform, 25–30 × 4–6 mm, neck 2–4 mm,

constricted, deeply grooved; **Sty** 45–50 mm; **Sti** 3-lobed; **Fr** oblong to ovoid, 40–60 × 20–30 mm, dark brown, beak prominent, constricted, stipitate; **Se** triangular, winged for ±2 mm, 6–8 × 4–7 mm, dull black. — **Cytology**: 2n = 60 (Flores-Maya & al. 2010).

Characterized by small, dense rosettes with short, glaucous leaves with few teeth (5–11), a large, black terminal spine, and a short and oblong inflorescence (García-Mendoza 2011a). Trelease (1907) gives a detailed review of the complicated taxonomic history throughout European literature and lists many synonyms and misapplications of Zuccarini's name. His treatment is followed here.

*A. macroacantha* 'Verde' is an invalidly published cultivar name for a form with light green leaves (Heller 2006: 104–105, with ill.). The cultivars 'Royal Spine' (Starr 2012: 227–229, with ill.) and 'Little Shark' (Starr 2014: 219) are hybrids with *A. victoriae-reginae*. 'Bloodspot' is a hybrid with *A. [Manfreda] maculata* (×*Mangave*; Klein (2010: as *Manfreda maculosa*)), and 'Lavender Lady' and 'Inkblot' are further ×*Mangave* hybrids with 'Bloodspot' as one parent (Trager 2018: 99). Meer & Guillot Ortiz (2015) show cultivars cultivated in Spain. Moore (2016: 285) depicts variegated specimens.

The flowers of *A. macroacantha* are visited by Hymenoptera, butterflies, and hummingbirds during the day, and by bats and moths during the night. Nectar is principally produced during the night, and only nocturnal visitors are successful pollinators (Arizaga & al. 2000a). *A. macroacantha* is extremely dependent on nocturnal pollinators, and bats are esp. important, with the seed set being different between different bat species (Arizaga & al. 2000b). Most rosettes are derived from rhizomatous offsets, and propagation by seed and bulbils is rare and possibly only occurs in rainy years and under protective nurse plants (Arizaga & Ezcurra 2002). Bulbil production is highest when flowers are abortive or pollination fails, thus acting as an insurance increasing the probability of successful reproduction (Arizaga & Ezcurra 1995).

**A. maculosa** Hooker (Curtis's Bot. Mag. 85: t. 5122 + text, 1859). **Type**: [suggested lecto —

icono]: l.c. t. 5122. — **Lit**: Mulford (1896: 70–72, t. 28); Rose (1903c: 17); Berger (1915: 30–31, with ill.); Small & Runyon (1934); Verhoek-Williams (1975: 209–221); Piña Luján (1985: 62–63); Verhoek-Williams & Hess (2002: 464); Diggs & al. (2006: 410–411, with ill.); Castillejos-Cruz (2009: [210]–[215], with ill.); the last 5 as *Manfreda maculosa*. **Distr**: USA (S Texas), Mexico (Coahuila, Nuevo León, N Tamaulipas); dry chaparral, on slopes or between rocks, and in pine or oak or tropical deciduous forests or desert scrub, 10–2000 m; flowers May to July. **I**: Howard (2001: 10); Richardson & King (2011: 18); Hochstätter (2016: II: 5); all as *Manfreda*.

≡ *Manfreda maculosa* (Hooker) Rose (1903) ≡ *Polianthes maculosa* (Hooker) Shinnars (1966); **incl.** *Agave maculata* Engelm. ex Torrey (1858) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave maculosa* var. *minor* Jacobi (1869); **incl.** *Agave maculosa* var. *brevituba* Engelm. (1875) ≡ *Agave maculata* var. *brevituba* (Engelm.) Mulford (1896).

[3a1] Plants herbaceous, medium-sized, reproducing vegetatively by buds in the axils of the leaves or from the corm; corm 3.5–5 (–6) × (0.8–) 1.5–2 cm, bulb short, 1.8–5.5 (–6.5) × 1–2 cm, covered with dried membranous leaf bases (1.8–) 3.5–7 cm long; **R** fleshy, with filiform ramifications, contractile; **L** evergreen, 4–6 (–11), erect-arching, lanceolate to narrowly elliptic, fleshy, very brittle, slightly channelled, 10–26 (–36) × 1–2.5 (–3.9 in cultivation) cm, dark green to glaucous, spotted with lighter green and brown or green, spots round to elliptic, sometimes glaucous, margins hyaline, apex acute, weak; **marginal teeth** usually present, large, cartilaginous, deltoid to truncate, bipartite, 3–7 mm apart; **Inf** (0.3–) 0.6–1.4 (–1.8 in cultivation) m, erect, 'spicate', reddish to greenish with purple tinge, fertile part (7.5–) 14–22 (–29; to 48 in cultivation) cm, lax, with 7–33 (–41) diffuse to ascending flowers; **Fl** 25–36 mm, sessile; **Te**p tube funnel-shaped, (6–) 12–21 × 4–5 mm, lobes oblong, involute, extended, tips obtuse, with a bunch of white hairs, (6–) 11–13 (–16) × 3–4 mm, greenish-white or whitish-pink to yellowish, aging to deep rose, purple or nearly brown; **Fil** erect at anthesis, 10–18 (–24) mm, exceeding the tube for 8–16 (–22) mm, inserted at the same level almost at

the mouth of the tube, yellowish-white; **Anth** 6–10 mm, yellow; **Ov** ellipsoid, 6–14 (–19) × 3–4 mm, not constricted, not extending into the tube; **Sty** 36–40 mm, to 10 mm shorter or to 4 mm longer than the lobes; **Sti** 3-lobate, yellowish-green; **Fr** globose or ellipsoid to oblong or subcylindrical, 11–20 (–25) × 10–16 mm; **Se** deltoid, plane-concave, with narrow margin, 4–5 × 3–4 mm, shiny.

Baker (1888a: 196), Mulford (1896: 70), and recently Govaerts (2014+: accessed Sept. 2018) interpreted *A. maculata* Regel 1856 as earliest name for this taxon, but Engelmann (1878: 301), Rose (1903c: 17) and Small & Runyon (1934: 49) argue that Regel described a clearly different species, esp. on account of its long-exserted stamens.

*A. maculosa* is characterized by involute perianth lobes, the funnel-shaped tube, and filaments 10–24 mm long inserted near the mouth of the tube not or hardly exceeding the lobes (Castillejos-Cruz 2009). It is closest to *A. longiflora*, with which it shares the consistency, colour and margins of the leaves, short stamens, lobed stigma, and the white to yellowish perianth ageing to rose, therewith closely approaching Sect. *Polianthes*. Both species occur in similar arid habitats and share succulent leaves with CAM photosynthesis (Verhoek-Williams 1975: 217; Castillejos-Cruz 2009; both as *Manfreda*). The lectotype suggested by Verhoek-Williams (1975: 209) was not effectively published.

The plant is sometimes used as ornamental, the corm as soap and shampoo and the chewed leaves against snakebites (Verhoek-Williams 1975: 213, Piña Luján 1985: 63, both as *Manfreda*). The species is the specific host plant for the caterpillars of the butterfly *Manfreda* Giant-Skipper (*Stallingsia maculosa*) (Quinn 2014). The cultivar ‘Silver Leopard’ has leaves with a silvery-grey hue and large, dark maroon dots, and ‘Bloodspot’ hort. Klein (2010) is a hybrid with *A. macroacantha* of Subgen. *Agave* (= ×*Mangave*).

**A. ×madrensis** Villarreal & al. (J. Bot. Res. Inst. Texas 8(2): 443–445, ills., 2014). **Type:** Mexico, Nuevo León (*Ramírez* 106 [MEXU, ANSM, CFNL, ENCB, TEX]). — **Distr:** Mexico (Nuevo León); in limestone soils on steep slopes, in oak scrubland to forests, 2500–2700 m; flowers during summer.

[1g × 2m] This is the putative natural hybrid *A. lechuguilla* (Subgen. *Littaea*) × *A. gentryi* (Subgen. *Agave*), with a ‘racemose-paniculate’ inflorescence intermediate between both subgenera. According to the protologue, it is intermediate in habit between its putative parents and morphologically similar to *A. montium-sancticaroli*, with a similar intermediate inflorescence and thus likewise strongly suggested to represent a similar intersubgeneric hybrid (see there). Only known from 4 plants and additional immature specimens believed to belong here.

**Fig. 37** *Agave manantlanicola* (Etter & Kristen 3728: Mexico; Jalisco, Sierra de Manantlán, 2800 m). (Copyright: J. Etter & M. Kristen)





**A. manantlanicola** Cuevas & Santana-Michel (Brittonia 64(3): 330–335, ills., 2012). **Type:** Mexico, Jalisco (Cuevas & al. 10065 [ZEA, IBUG, IEB, MEXU]). — **Lit:** Kristen & Etter (2014: with ills.). **Distr:** Mexico (Jalisco: Sierra de Manantlán); near-vertical rocky volcanic cliffs or occasionally peak cliffs with fog during the rainy season, in pine forests, 2640–2865 m; flowers June to August. **I:** Pilbeam (2013: 126–127); Hochstätter (2015: VII: 22). — Fig. 37.

[1b] Stems mostly prostrate with age, 50–90 × 20–25 cm, covered throughout with often dry leaves, with up to 10 suckers; **Ros** polycarpic, open, to 1 × 1.8 m; **L** 50–60, plus 30–70 recurved dry leaves, oblong, linear, often falcate, apex ascending, channelled, 45–76 × 6–13 cm, 5 cm thick at the base, glaucous or yellowish-green at the base, turning reddish at anthesis, margins horny, continuous and razor-sharp; **marginal teeth** none; **terminal Sp** canaliculate, 30–45 mm, reddish-brown, decurrent; **Inf** 3–5 m, ‘spicate’, peduncle red to reddish-brown, basal **Bra** ovate-linear, 7.8–10.7 × 1.6–3 cm, all bracts reflexed with age, fertile part confined to the upper 1/3 of the inflorescence; **Ped** 1–2 mm; **Fl** 39–48 mm, geminate; **Te** reddish outside, yellowish-green inside, tube 2–6.5 mm, lobes oblong, reflexed at anthesis, apex cucullate, galeate, blunt or sharp, 15–22 × 2.5–6.5 mm, yellow-green inside, apex reddish, inner lobes with white margins, usually 2–3 mm wider than the outer lobes; **St** 6 or sometimes 7; **Fil** inserted at the base of the lobes on the mouth of the tube, 27–45 mm, tip reddish; **Ov** cylindrical, striate, 18–22 × 5–8 mm, yellow-green, neck 2–3 mm; **Sty** cylindrical, hollow, 30–42 mm, tip reddish; **Sti** 3-lobate, barbate; **Fr** oblong, trigonous, (20–) 24–34 × (13–) 16–18 mm, shortly apiculate, stipe 3–7 mm; **Se** semicircular, sometimes ellipsoid, 5–6 × 3.3–4 mm, bright black, margin slightly winged.

Similar to other W Mexican species of Sect. *Inermes* (as Group *Amolae*) according to the protologue, including *A. attenuata*, *A. gilbertii* (as *A. bakeri*), and *A. vazquezgarciae*, as well as *A. chazaroi* which is here placed in Sect. *Inermes* (as Group *Marginatae*). It stands out for its bluish leaf colour, its thick stems, and its high-elevation habitats. *A. manantlanicola* appears most similar

to the likewise stem-forming *A. attenuata* ssp. *attenuata*, which differs in more slender stems, smooth or serrulate leaf margins, absence of a terminal spine, and yellowish-green tepals. Both are termed “polycarpic” and flower repeatedly from “lateral” inflorescences, which are actually likely terminal on rudimentary lateral rosettes. It hybridizes with *A. inaequidens* in 1 of the 3 populations (Kristen & Etter 2014).

**A. mapisaga** Trelease (Contr. US Nation. Herb. 23: 130, 1920). **Type:** Mexico, D.F. (Trelease 147 [MO 188125]). — **Lit:** Gentry (1982: 602–603, with ill.); Vázquez-García & al. (2007b: 59, t. P); García-Mendoza (2011a: 35–37). **Distr:** Mexico (Tamaulipas, Zacatecas, Jalisco, Querétaro, Hidalgo, México, Guerrero, Tlaxcala, Puebla, Oaxaca); cultivated only, 1900–2700 m; flowers April to August. **I:** Smith (2002: 226, as var. *mapisaga*); Lyons (2002: 163, as var. *lisa*); Gomez Rhine (2009: 22, as var. *lisa*); Pilbeam (2013: 128); Hochstätter (2015: II: 7; 8, as ssp. *lisa*).

**Incl.** *Agave salmiana* var. *recurvata* Jacobi (1866); **incl.** *Agave salmiana* var. *angustifolia* A. Berger (1915); **incl.** *Agave mapisaga* var. *lisa* Gentry (1982) ≡ *Agave mapisaga* ssp. *lisa* (Gentry) Hochstätter (2015).

[2b] Stems short, massive; **Ros** openly spreading, 2–2.5 × 2.5–4.8 m, surculose; **L** 30–50, linear, spreading to ascending, rigid to flexible, sometimes re- or inflexed when mature, base very thickly fleshy, long-acuminate, upwards guttered, convex below, flat above, 150–250 × 19–30 cm, green, pale glaucous, or zonate, margins mostly straight to repand; **marginal teeth** straight, small, sometimes keeled below, dark brown, 2–5 mm from low broad bases forming a continuous horny margin, 15–50 (–60) mm apart, uppermost 25–40 cm without teeth; **terminal Sp** conical-subulate, robust, narrowly grooved above, 25–50 mm, dark to greyish-brown, long decurrent; **Inf** massive, 5–9 m and more, paniculate, peduncle greenish, with closely-set large succulent deltoid reddish-brown **Bra** 15–40 cm long, fertile part lax, pyramidal, in the upper 1/3–1/2 of the inflorescence, to 1 m, with 20–25 widely spreading, massive and dense part-**Inf** several times compound; **Ped** 10–18 mm; **Fl** funnel-shaped,



80–90 (–100) mm, succulent; **Tep** yellow to yellowish-green, sometimes with reddish tinge, buds frequently reddish, tube funnel-shaped, fleshy thick-walled, deeply grooved, 14–21 × 10–15 mm, lobes linear, erect to incurving, margin involute, unequal, 20–30 × 6–8 mm; **OTep** conduplicate and narrowing to 5 mm, apex bluntly galeate; **ITep** 2–3 mm shorter, with thick fleshy keel, involute and 2-costate within; **Fil** thick but flattened, 55–80 mm, inserted at 2 levels 11–15 mm above the tube base and at mid-tube, yellow; **Anth** excentric, 25–35 mm, yellow; **Ov** cylindrical, thick, roundly 3- to 6-angled, 40–52 × 5–8 mm, green, neck 4–5 mm, not constricted; **Sty** stout, 80–95 mm and eventually longer than the stamens; **Fr** oblong, woody, 60–70 × 20–25 mm, brown, short-beaked, stipitate; **Se** drop-shaped, 7–8 × 5–6 mm, wavy-sculptured, hilar notch near apex, marginal wing very narrow, upcurving, black. — **Cytology**: 2n = 150 (= 5×) (Gómez-Pompa & al. 1971, Simpson & al. 2011).

A pentaploid cultivar cultivated for pulque for thousands of years, distinguished from the related *A. salmiana* by its longer, linear, long-acuminate leaves with straight margins, smaller and more narrowly spaced teeth and shorter terminal spine, without the sigmoid apical bend characteristic for the latter, but less often cultivated than *A. salmiana* (Gentry 1982, García-Mendoza 2011a; see also under *A. salmiana*). A detailed ordination and classification of 48 morphological characteristics from 62 populations of the *A. salmiana* group (Mora-López & al. 2011) showed a gradient of domestication in the sequence *A. salmiana* ssp. *crassispina* (wild) → *A. salmiana* ssp. *salmiana* (cultivated only) → *A. mapisaga* (cultivated only), concomitant with the increase in rosette and leaf size and the reduction of the marginal teeth and terminal spines. The highly domesticated *A. mapisaga* is derived from within *A. salmiana* and “only cultivated in highly humanized environments” such as plantations (Mora-López & al. 2011).

*A. mapisaga* var. *lisa*, apparently a clonal variety with unknown provenance, was obtained at Huntington BG from F. Schmoll of Querétaro, Mexico, as “maguey lisa” (Gentry 1982; a specimen from 1933 is filed as *A. mapisaga* ‘Lisa’

(HNT 417)). It is propagated at the Huntington by in vitro-techniques (Gomez Rhine 2009). According to Gentry (1982), it is the largest-growing *Agave*; only *A. franzosinii* and *A. atrovirens* may reach similar or even larger sizes. García-Mendoza (2011a) referred it to the synonymy of the species, which is followed here; it can be retained as cultivar ‘Lisa’.

*A. salmiana* var. *recurvata* Jacobi and *A. salmiana* var. *angustifolia* A. Berger are placed in the synonymy here following García-Mendoza (2011a) and Govaerts (2014+: accessed April 2014). Due to the long, linear leaves, both taxa fit better here than in *A. salmiana* as proposed for the latter by Gentry (1982: 609).

**A. margaritae** Brandege (Proc. Calif. Acad. Sci., ser. 2, 2: 206, t. x, 1889). **Type**: Mexico, Baja California (*Brandege* s.n. [UC 149990]). — **Lit**: Trelease (1912b: 57–58, tt. 55–56); Breitung (1963: 173–174, ills.); Gentry (1978: 48, 108, t. 1); Gentry (1982: 389); Ullrich (1989a: with ills.); Webb & Starr (2015: 82, ill.). **Dist**: Mexico (Baja California Sur: Santa Margarita and Magdalena Islands). **I**: Richter (2011: 105); Pilbeam (2013: 129); Hochstätter (2015: V: 21).

**Incl.** *Agave connochaetodon* Trelease (1912).

[2i] Acaulescent; **Ros** compact, to 0.25–0.3 × 0.5–0.75 m, prolifically caespitose; **L** 40–50, ovate to broadly lanceolate, rather openly spreading, thick, fleshy and rigid, narrowed above the base, shortly acuminate, concave above, smooth, 12–25 × 6–10 cm, yellowish-green to glaucous-blue, transversely banded, margins crenate; **marginal teeth** variously curved or flexed, weakly attached, 4–5 mm or to 8–15 mm (middle of the lamina), reddish-brown to greyish, 10–15 mm apart, sometimes on moderate to prominent prominences; **terminal Sp** subulate, shortly and shallowly grooved above, 20–30 mm, chestnut-brown becoming dull grey, shortly decurrent; **Inf** 2–4 m, paniculate, peduncle with small bracts, fertile part slender, part-**Inf** 6–12 in the upper 1/3 or less of the inflorescence; **Ped** 2–3 mm; **Fl** 45–50 mm; **Tep** light yellow, tube ±10 mm, lobes attenuate, 15 × 10 mm; **Fil** 25 mm, adnate to the base of the lobes; **Ov** fusiform, 25–30 mm; **Fr** oblong or pear-shaped, 30–50 × 15–20 mm, not stipitate but

**Fig. 38** *Agave marmorata* (Etter & Kristen 126: Mexico; Puebla, near Zapotitlán Salinas, 1520 m). (Copyright: J. Etter & M. Kristen)



somewhat beaked; **Se** 3–5 × 4 mm, smooth. — **Cytology**:  $n = 30$  (Baker & al. 2009).

An island endemic known only from Isla Magdalena and Isla Margarita, with considerable variation in the size, curvature and colour of the teeth and its prominences (Gentry 1978, Gentry 1982). It is distinguished from all other taxa from Baja California esp. by its short, broad leaves and the deep flower tube; the latter is also found in *A. vizcainoensis*, which differs, however, in its leaf characters (Gentry 1978, Gentry 1982, Webb & Starr 2015).

**A. maria-patriciae** Cházaro & Arzaba (Phytotaxa 360(3): 263–268, ills., 2018). **Type**: Mexico, Veracruz (Arzaba & al. 451 [XAL, CHAPA, MEXU]). — **Distr**: Mexico (C Veracruz); volcanic substrate in oak forests, ±650 m; flowers December to January; only known from the type locality.

[1f] Stems 0.1–0.2 m, suberect, bifurcately branching, with persistent leaf sheaths; **Ros** usually 2–3 per plant; **L** 13–18, lanceolate to oblong, fleshy, frequently inflexible, 25–29 × 3.5–6.8 cm, light green with pale and blurred yellow mid-stripe, margins straight, with continuous red colouration, **marginal teeth** mere denticles, 2–3 mm, dark brown or reddish-brown, absent 4–5 cm below the terminal spine; **terminal Sp** 5–9 mm, dark brown; **Inf** 1.05 m, from the main rosette, ‘spicate’, peduncle with narrowly triangular **Bra** 3–9.6 × 2–3 cm, fertile part in the upper ½ of the

inflorescence, apex recurved; **Ped** ±1 mm; **Fl** geminate, 24–26 mm; **Tep** pale green, tube funnel-shaped, 7–8 × 8 mm, lobes lanceolate, fleshy, reflexed, apex obtuse, scarcely cucullate, dimorphic; **OTep** 12 × 4 mm, green-brownish inside, pale green outside; **ITep** 11 × 5 mm, membranous, with a conspicuous brownish keel on the back; **St** exserted; **Fil** flattened, tapered, 18 mm, pale greenish-yellow with reddish dots at the apex, inserted shortly below the rim of the tube; **Anth** centric, 10–13 × 2 mm, brown; **Ov** fusiform, 13 × 6 mm, smooth, green, neck slightly constricted, 2–3 × 3–4 mm; **Sty** 27–30 mm, pale greenish-yellow with reddish dots at the apex; **Sti** capitate; **Fr** trigonous, 15–18 × 5 mm, shortly beaked, brown (unripe yellow-green); **Se** crescent-shaped to auriculate, 3–4 × 2–3 mm, shiny.

According to the protologue most similar to *A. pendula*, with which it shares lanceolate to oblong leaves with a yellow mid-stripe, but differing in its shorter leaves, shorter stems and shorter inflorescences, leaves with reddish margins, longer denticles and a thicker terminal spine, its smaller and succulent flowers with reflexed and not broadly cucullate tepals, and subsessile capsules.

**A. marmorata** Roez (Gartenflora 23: 76, 1874). **Type**: [neo — icon]: Curtis’s Bot. Mag., 138: t. 8442, 1912. — **Lit**: Berger (1915: 270–271, with ills.); Gentry (1982: 512–514, with ills.); Ullrich (1992a: with ills.); Arias Toledo & al. (2000: 17, with ill.); García-Mendoza (2011a:

37–39); Hernández López & al. (2017: with ills.). **Distr:** Mexico (S Puebla [esp. around Tehuacán], Oaxaca); gravelly hillsides, volcanics and sedimentaries, in arid scrub and tropical deciduous forests and ecotones of both with oak forests, 680–1830 m; flowers March to April, also in August. **I:** García-Mendoza (2002: 180, 185); Heller (2006: 105); Forster (2006: 176); Etter & Kristen (2007b: 178); Richter (2011: 45, 82); Pilbeam (2013: 130); Mahr (2015: 8); Hochstätter (2015: VI: 21); Moore (2016: 239). – Fig. 38.

**Incl.** *Agave todaroi* Baker (1888).

[2n] Acaulescent; **Ros** openly spreading, 1–2 × 1.5–2.5 m, solitary, rarely surculose; **L** 16–20 (–50), broadly lanceolate, frequently repand, thick at the base, infolding along the middle of the lamina, involute at the tip at the spine base, convex below, flat above, generally roughly scabrous-papillose, (60–) 100–135 (–170) × 20–30 (–40) cm, yellowish- or light green to glaucous-grey, sometimes glaucously zonate, margins crenate, with fleshy prominences 1–2.5 cm tall; **marginal teeth** straight, flattened, with very broad bases, 6–10 (–15) × 7–10 (–15) (at the base) mm, light to dark brown or blackish, 15–30 (–60) mm apart, often with intermittent teeth; **terminal Sp** shortly conical, sinuous, strong, papillose, laterally flattened, grooved, 15–20 (–40) mm, brown or greyish, rarely shortly decurrent; **Inf** 5–7 (–10) m, paniculate, peduncle green, stout, with chartaceous triangular **Bra** 15–20 (–27) cm long, fertile part lax, oblong, with 20–40 (–50) part-**Inf** several times diffusively compound, in the upper ½–⅓ of the inflorescence, 30–50 cm; **Ped** 5–8 mm; **Fl** campanulate, small, 30–40 (–50) mm; **Tep** brilliant yellow, tube shallowly funnel-shaped, grooved, the sinuses soon spreading, (3–) 4–6 × (7–) 10–12 mm, lobes linear to oblong, fleshy, erect, involute, apex galeate, equal, 12–17 (–20) × 2–3 (–5) mm, dark-coloured; **Fil** slender, 30–37 mm, yellow, inserted at mid-tube or at the base of the lobes; **Anth** centric, 10–13 (–18) mm, yellow; **Ov** cylindrical, (17–) 20–25 × 3–5 mm, light green, neck 1–3 mm, not constricted, scarcely grooved; **Sty** ±30 mm; **Sti** capitate; **Fr** oblong, 25–35 (–40) × 15–20 (–25) mm, short-beaked, slenderly stipitate, brown; **Se** winged for ±1 mm, 5–7 × 3–5 mm. — **Cytology:** 2n = 60 (Flores-Maya & al. 2015).

Introduced 1872–1873 by Benedict Roezl and published the following year. Distinguished by its lax rosettes of coarsely rough leaves with strong prominences and a strong, shortly conical terminal spine, and small golden-yellow flowers in large, lax panicles (Gentry 1982, García-Mendoza 2011a). The above-cited neotype was designated by Gentry (1982: 512).

It is used for the production of pulque and aguamiel, the stems and young inflorescences are eaten, and the flowers are used as Easter decoration (García-Mendoza 2011a). The flowers are visited nocturnally by bats, which are not pollinating, and during the day by 6 species of hummingbirds acting as nectar robbers and 9 species of perching birds, of which Orioles are the most possible pollinators (Ornelas & al. 2002). The harvesting practices in sylviculturally managed populations in Puebla have negative effects on the population dynamics because harvesting for mescal decreased individual survival and growth (Jiménez-Valdés & al. 2010). The germination in habitat may be enhanced on biological soil crusts (Godínez-Alvarez & al. 2012).

**A. ×massiliensis** A. Berger *pro sp.* (Agaven, 167, 1915). **Type:** not typified. — **Lit:** Berger (1912: 361); Trelease (1914: 235, 236); both as *A. massiliensis*. **Distr:** Cultivated only.

[1f × 2a] This is the garden hybrid *A. americana* × *A. mitis* [var. *mitis*] (as *A. densiflora*). It was distributed by the nursery Haage & Schmidt (Erfurt, Germany) in 1901 (Berger 1912). The name was first mentioned by Berger (1912), and is attributed to “Trelease in L. H. Bailey 1914” by Govaerts (2014+) but the first description was given by Berger (1915). — Apparently lost from cultivation.

**A. maximiliana** Baker (Gard. Chron., ser. nov. 8: 201, 1877). **Nom. illeg.**, ICN Art. 52.1. **Type** [neo]: Cult. Kew (*Brown* s.n. [K 000543880]). — **Lit:** Gentry (1982: 325, 348–351, with ills.). **Distr:** Mexico (Sinaloa, Durango, Zacatecas, Nayarit, Jalisco, Colima).

See Smith (2017a) for the typification.

**A. maximiliana** var. **katherineae** (A. Berger) Gentry (Agaves Cont. North Amer., 350, ill. (p.

351), 1982). **Nom. inval.**, ICN Art. 35.1. **Type** [lecto]: Ex cult. BG La Mórtoia (*Berger* s.n. [US 1023783]). — **Lit:** *Berger* (1915: 197–198, as *A. katherinae*); *Gentry* (1982: 350–351, with ill.); *McVaugh* (1989: 139); *Vázquez-García & al.* (2007b: 60); *González-Elizondo & al.* (2009: 98, 101, with ill.). **Distr:** Mexico (E-C Sinaloa, W-C Duango, Nayarit, W & C Jalisco, Colima); rocky slopes in pine-oak or oak forests and ecotones with oak woodlands and tropical deciduous forests, 900–2350 m; flowers December to July.

≡ *Agave katherineae* A. *Berger* (1915).

[2d] Differs from var. *maximiliana*: **Ros** larger; **L** larger, 60–90 cm, greener, margins more crenate-repand, with numerous interstitial teeth; **Tep** tube longer, 12 × 12 mm, lobes longer, 22–23 mm; **Fil** inserted 9–10 mm above the tube bottom near its throat.

This is a variant esp. with larger rosettes and greener leaves (*Gentry* 1982). It was included in the synonymy of the species by *McVaugh* (1989), but upheld by *Vázquez-García & al.* (2007b), *González-Elizondo & al.* (2009) and *Govaerts* (2014+), which is followed here. — *Berger* (1915) named the taxon after Lady Katherine Hanbury but incorrectly gave the epithet as ‘katharinae’, which is here corrected. The incorrect spelling ‘katherinae’ is also sometimes encountered.

The type at US consists of 2 sheets prepared by *Berger* (s.n.) in 1914 (US 1023758 & 1023783) which are not cross-labelled and thus represent syntypes. The designation by *Gentry* (1982: 350) that the “Type” “consists of leaf margin, a peduncular bract, and leaf cross section” refers to US 1023783 and represents a cryptic lectotypification.

**A. maximiliana** var. **maximiliana** — **Lit:** *Berger* (1915: 195); *Gentry* (1982: 346–350, with ills.); *McVaugh* (1989: 139); *Vázquez-García & al.* (2007b: 59–60, t. Q); *González-Elizondo & al.* (2009: 97–101, with ills.). **Distr:** Mexico (C Sinaloa, C-W Durango, S Zacatecas, Nayarit, W Jalisco, Colima); dry rocky mountain slopes in the oak- and pine-forest zone, in rather dry calcareous or igneous rocky soils, 930–2000 (–2700) m; flowers December to August. **I:** *Richter* (2011: 73, 108, 110); *Etter & Kristen* (2012: 86);

*Pilbeam* (2013: 131, as *A. maximiliana*); *Greulich* (2014a: 56, 61); *Hochstätter* (2015: IV: 27).

**Incl.** *Agave gustaviana* J. N. *Haage & E. Schmidt* (1874); **incl.** *Agave gustaviana* *Baker* (1877) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave crenata* A. *Berger* (1911) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave conjuncta* A. *Berger* (1915).

[2d] Acaulescent to short-stemmed; **Ros** to 1.6 m Ø, solitary; **L** usually broadly (ob-) lanceolate, curved, straight or slightly recurved, softly fleshy, generally 40–80 × 10–20 cm, mostly pale glaucous-pruinose over yellow-green to green, or bluish-glaucous, margins variously repand to crenate, with strong prominences; **marginal teeth** dimorphic, the larger teeth variously curved, compressed, 6–10 mm (at mid-leaf), 15–30 mm apart, tips slender from elongate low (sometimes confluent) bases, on strong prominences, intermittent teeth much smaller, numerous, variable; **terminal Sp** slenderly conical, straight, openly grooved above, rounded below and shortly protruding at the base, smooth, 25–40 mm, brown or chestnut-brown to grey, shortly decurrent; **Inf** 5–8 m, paniculate, fertile part narrow, **part-Inf** small, rather rounded, 15–25 (–30) in the upper 1/3–1/2 of the inflorescence; **Fil** slender, 52–65 mm; **Tep** greenish-yellow, frequently tinged with brown-red, tube openly funnel-shaped, grooved, 5–9 (–12) × 12–14 mm, lobes linear, narrow, ascending to incurved, conduplicate, roundly cucullate, subequal, 15–22 × 4–6 (–7) mm, inner with high or low keel, involute; **Fil** 28–35 mm, sometimes pink, inserted above mid-tube; **Anth** mostly centric, regular, 18–24 mm, yellow; **Ov** angular-cylindrical to fusiform, 28–35 (–38) mm, neck short or long, furrowed; **Sty** slightly longer than the filaments; **Sti** capitate; **Fr** shortly oblong, tip rounded, 35–50 × 17–20 mm, stipitate; **Se** with wavy testa, 5.5–6 × 4.5–5 mm, finely punctate, marginal wing abruptly raised.

The most common wild upland *Agave* in W-C Mexico (Nueva Galicia), replaced more E-wards by the similar but larger *A. inaequidens* (*McVaugh* 1989). *González-Elizondo & al.* (2009) describe and depict a “possibly undescribed variant” with narrow, shorter leaves (27.5–36 × 10.5–14.3 cm)



**Fig. 39** *Agave mckelveyana*. (cult.: USA; Arizona, Arizona-Sonora Desert Museum Tucson). (Copyright: J. Thiede)



from the Sierra de los Huicholes (Nayarit, Zacatecas, Durango and Jalisco).

The prioritable name *A. gustaviana* J. N. Haage & E. Schmidt (Pflanzen-Verzeichnis 1874: 1, 1874) was validated by a diagnosis in the nursery catalogue (Reveal 2012, Smith & Figueiredo 2014d: 68). Smith (2015) regarded the descriptive statement as inadequate for valid publication, but it was subsequently “recommended to treat as validly published” (Applequist 2016). To avoid a name change, Smith (2017b) proposed to conserve *A. maximiliana* against *A. gustaviana*. — Vernacular names: “maguey de la sierra”, “lechuguilla”, “masparillo”, “a’hl mai” (= maguey chico) (Vázquez-García & al. 2007b). The flowers are used in a stew with eggs and butter called “Bayusa” (Etter & Kristen 2003b, ill. in Etter & Kristen 2012: 86).

**A. mckelveyana** Gentry (Cact. Succ. J. (US) 42: 225–228, ills., 1970). **Type:** USA, Arizona (Gentry 21979 [US, ARIZ, DES, MEXU]). — **Lit:** Gentry (1982: 390–392, with ills.); Turner & al. (1995: 55–56); Hodgson (1999a: 6–7); Reveal & Hodgson (2002); Hawker (2016: 60–64, ills.); Parker (2017: 256, 261, with ills.). **Distr:** USA (W-C Arizona); open sandy, gravelly or rocky places in upper desert scrub, chaparral and pinyon-juniper woodlands, 800–2200 m; flowers May to July. **I:** Heller (2006: 106, 107); Richter (2011: 81); Pilbeam (2013: 132); Hochstätter (2015: V: 12). — Fig. 39.

**Incl.** *Agave aquariensis* Trelease ex Gentry (1970) (*nom. inval.*, ICN Art. 39.1, 40.1).

[2i] Acaulescent; **Ros** 20–45 cm, solitary or suckering; **L** rather few, linear or lanceolate, rigid, firm, spreading, tip ascending, broadest in the middle, acuminate, thickish and deeply concave towards the base, guttered towards the apex, 17.5–40 × 2.8–5 cm, light glaucous-green or yellowish- to dark green, usually lightly cross-zoned, margins nearly straight or repand; **marginal teeth** upcurved or recurved, rather friable, small to medium-sized, larger teeth in the middle of the lamina, 4–8 mm, greyish with reddish tips, sometimes with a brown ring at the base, mostly 10–30 mm apart, on low tubercle-like prominences; **terminal Sp** subulate, rounded except for a shallow groove above at the base, 15–40 mm, chestnut-brown to grey, decurrent to the 1. or 2. tooth; **Inf** 2–5 m, paniculate, peduncle slender, green, with persistent triangular **Bra** 0.5–2 cm long, fertile part narrow, part-**Inf** small, compact, ascending, 10–19 in the upper 1/3–1/2 of the inflorescence, with 6–12 flowers, > 10 cm; **Ped** shortly bracteolate; **Fl** 30–40 mm; **Tep** openly spreading, light yellow, tube shallow, broadly campanulate, 2–4.5 × 8–10.5 (–18) mm, light green to light yellow, lobes linear-conduplicate, spreading, thin, with open sinuses, equal or subequal, 11–13 × 2.5–4 mm, outer longer and narrower than the round-keeled inner, both abruptly hooded at the tip, wilting soon after anthesis; **St** long-exserted; **Fil** flattened towards the base, 25–33 mm, inserted



near or at the top of the tube, light yellow; **Anth** (7–) 9–16 mm, yellow; **Ov** fusiform or cylindrical, faintly grooved below the tepal sinuses, 16–22 mm incl. the slightly constricted neck 1–2.5 mm, light green to grey; **Sty** 25–38 mm; **Sti** capitate, 3-lobate; **Fr** linear to (narrowly) oblong, obtuse to apiculate, striate, 30–45 × 10–14 mm, beaked, shortly stipitate; **Se** obovate or crescent-shaped, 5–6.5 × 4–4.5 mm, rugose, margin with a complete low wing. — **Cytology**:  $n = 30$  (Baker & al. 2009).

Ecologically separated by its more humid and cooler mountain habitat from its close relative *A. deserti* ssp. *simplex*, which is confined to lower elevations in the Sonoran Desert (Gentry 1982). It hybridizes with *A. deserti* ssp. *simplex*, *A. utahensis* ssp. *utahensis* and *A. chrysantha* (Hodgson 1999a, Reveal & Hodgson 2002: as var., Parker 2017). *A. mckelveyana* occurs outside the range of nectar-feeding bats and is pollinated by hummingbirds, carpenter bees, and wasps. Fruit set is low and appears to be resource- (nutrient) limited rather than pollinator- or pollen-limited (Turner & al. 1995).

**A. megalodonta** García-Mendoza & D. Sandoval (Acta Bot. Mex. 126: e1461: 11–12, ills. (pp. 13, 15), 2019). **Type**: Mexico, Oaxaca (García-Mendoza & al. 11145 [MEXU, IEB, MEXU, MO, OAX]). — **Distr**: Mexico (S Puebla, E Guerrero, W Oaxaca: upper Balsas River basin); in soils derived from limestone and gypsum, in tropical deciduous forests and xerophytic scrub, 1000–1600 m; flowers December to January.

[lg] Acaulescent; **Ros** lax, solitary, (0.8–) 1–1.4 × (1–) 1.3–1.7 m; **L** 15–40, ensiform to oblong-lanceolate, erect to recurved, fibrous, thin at the base, broadly canaliculate, smooth to the touch, apex long acuminate, (50–) 60–100 × 7–12 (–14) cm, 6–10× longer than broad, green-yellowish or dark green, with purplish dots on both faces, upper face with yellowish longitudinal mid-stripe, often with impressions of the teeth on both faces, margins straight, corneous, continuous, white or greyish, dentate; **marginal teeth** antrorse or straight, very variable in shape, hooked, (10–) 15–35 × 10–15 (–25) mm at mid-leaf, white or greyish, 20–50 (–70) mm apart at mid-leaf, sometimes with 1–2

small teeth at the base; **terminal Sp** acicular, (30–) 45–70 (–90) × (5–) 10–25 mm, greyish; **Inf** erect, (3–) 5–6.5 m, ‘spicate’, peduncle glaucous or purplish, waxy, with long triangular chartaceous **Bra** 25–30 × 1.5–3.5 cm, fertile part dense, in the upper  $\frac{1}{3}$ – $\frac{1}{2}$  of the inflorescence; floral **Bra** 3–6 × 0.3 cm, filiform; **Ped** short; **Fl** (32–) 35–45 mm; **Tep** pale yellow or greenish-yellowish, tube campanulate, 3–6 × 4–7 mm (at the mouth), lobes elliptic or oblong, straight to diffuse, with purple dots on the margins and the adaxial face, 15–20 × 3–5 mm, **ITep** narrower, clasping the filaments after anthesis; **Fil** 35–40 (–47) mm, purple to brownish, inserted in the distal part of the tube; **Anth** 10–15 mm; **Ov** cylindrical, 14–18 (–25) × 3–4 mm, neck 3–5 mm; **Sty** 35–40 mm, with purplish dots; **Sti** 3-lobate, with purplish dots; **Fr** ovoid-ellipsoid, 15–20 × 10 mm; **Se** semicircular, unwinged, 3 × 2–2.5 mm, black.

In the protologue placed in Sect. *Heteracanthae* (as Group *Marginatae*). It is closely related to *A. xylonacantha*, which occurs ±250 km further N and differs in its longer and relatively narrower, smooth leaves with straight margins with larger teeth variable in shape, a longer terminal spine, and flowers with a longer tube and broader lobes, and smaller capsules. However, the protologue does not account for the full range of character expressions for *A. xylonacantha* given by Gentry (1982) and here; with these data, the differences in leaf size and tube length largely disappear. — Vernacular name: “maguey espumoso”. Occasionally used for mescal production. Classified in the IUCN Red List Category “Near Threatened”.

**A. microceps** (Kimmach) A. Vázquez & Cházaro (in Vázquez-García & al. (eds.), *Agaves Occid. Méx.*, 61, ills. (t. O, pp. xlii–xliii), 2007). **Type**: Mexico, Sinaloa (Kimmach 1923 [HNT, MEXU, US]). — **Lit**: Kimmach (1995: as *A. filifera* ssp., with ills.). **Distr**: Mexico (C Sinaloa, S Nayarit); rocky mountain ridge with tropical deciduous forests at 460 m (Sinaloa), and rocky cliff with mixed pine-oak-*Arbutus* forests at 2100 m (Nayarit); only known from 2 localities. **I**: Pilbeam (2013: 81, as *A. filifera* ssp.); Hochstätter (2015: VIII: 50).

≡ *Agave filifera* ssp. *microceps* Kimmach (1995); **incl.** *Agave filifera* var. *compacta* Trelease (1914).

[1d] Densely caespitose, forming cushions to  $\geq 1 \times 0.3$  m; **Ros** 20–35  $\times$  20–30 cm; **L** linear to linear-oblongate, acuminate, acute, 12–20  $\times$  1–2 (in the middle) cm, abruptly widening to 2.5–3.5 cm within 2 cm of the base, 4–10 mm thick near the base, 2–4 mm thick above, youngest leaves sometimes with 1–3 white streaks on the upper face, margins with a brownish or purplish grey band  $\pm 2$  mm wide, and every 1–3 cm with a separating, sinuous, white thread 10–40  $\times$  1–2 mm, otherwise entire; **terminal Sp** acicular, short; **Inf** 1–1.35 m, ‘spicate’, peduncle in the basal 30 cm with prominent, linear, acuminate, acute **Bra** 8–10 cm long, basal 1 cm of the bracts at right angles to the axis, remaining part parallel to the axis, upper **Bra** smaller, yellowish-pink, fertile part of the inflorescence 80 cm; **Fl** geminate, 5–10 mm apart on a peduncle  $\pm 2$ –4 mm long; **Ped**  $\pm 2$  mm; **Fl** 50–55 mm, at right angles to the axis; **Tep** greenish-yellow, tube longitudinally grooved, 8–10  $\times$   $\pm 4$  (at the base) mm, gradually widening to 6 mm at the mouth, greenish-yellow, lobes subequal, 9–10  $\times$   $\pm 5$  (in the middle) mm, obtuse, cucullate; **OTep** ovate,  $\pm 10$  mm, tips suberect; **ITep** slightly obovate,  $\pm 9$  mm, tips abruptly recurving; **Fil** narrowing just below the anther, 22–25  $\times$   $\pm 1$  mm, pinkish-yellow; **Anth** 10–11 mm, yellow; **Ov** oblong, truncate at the base, narrowing more gradually at the top, slightly ridged, 7–8  $\times$   $\pm 5$  mm, greenish-yellow; **Sty** 39–44 mm, greenish-yellow; **Sti** truncate, 3-lobed, lobes  $< 1$  mm, papillose; **Fr** oblong-ellipsoid, 10–12  $\times$  6–8 mm, slightly apiculate, light brown; **Se** flattened, semicircular, 4–4.5  $\times$   $\pm 2.5$  mm,  $\pm 1.5$  mm thick, black.

According to the protologue (as ssp. of *A. filifera*), the rosettes are similar to those of *A. schidigera*, but are much smaller and proliferous, and the inflorescences are smaller with larger flowers. The taxon is possibly a redescription of *A. filifera* var. *compacta*, but the name has priority at species and subspecies rank. Plants were first distributed 1980 as ISI 1184. The fruits were not described in the protologue, and data is here added

from the specimen Kimmach & Sánchez-Mejorada 2260 (MEXU; digital image!). See also under *A. filifera*.

**A. millsaughii** Trelease (Mem. Nation. Acad. Sci. 11: 41, tt. 87–88, 1913). **Type:** Bahamas, Great Exuma (Britton & Millspaugh 3091 [MO 2056612, F, NY]). — **Lit:** Berger (1915: 204); Britton & Millspaugh (1920: 75); Correll & Correll (1982: 313); Álvarez de Zayas (1995: 40); Acevedo-Rodríguez & Strong (2012: 86); Freid & al. (2014: 210, 211, 218). **Distr:** Bahamas (Great Exuma); dry slopes, low coppices and scrublands; flowers mostly December to February. **I:** Hochstätter (2015: VII: 85).

[2r] Acaulescent; **Ros** solitary; **L** narrowly oblanceolate, concave, to 125  $\times$  15 cm or more, green, somewhat glossy; **marginal teeth** straight and spreading or occasionally reflexed, sometimes with upcurved tips, narrowly triangular, 3–5 mm, brown to nearly black, mostly 15–25 mm apart, scarcely lenticular at the base, intervening margins nearly straight; **terminal Sp** triquetrous, conical, straight, round-grooved to about the middle or occasionally involute, smooth, rather dull, 15–20  $\times$  3–4 mm, red-brown, decurrent for its length or more; **Inf** to  $\pm 10$  m, paniculate, oblong, peduncle with broadly triangular **Bra**, fertile part with subascending part; **Inf** in the upper  $\frac{2}{3}$  of the inflorescence; **Ped**  $\pm 10$  mm; **Fl** 45–50 mm; **Tep** yellow, tube conical,  $\pm 7$  mm, lobes 15–20  $\times$  4 mm; **Fil** scarcely 30 mm, inserted nearly in the tube throat; **Ov** fusiform, 19–25  $\times$  4–5 mm; **Fr** shortly oblong, 33–35  $\times$  18–20 mm, beaked, shortly stipitate; **Se** crescent-shaped, 7  $\times$  5 mm.

In the key provided in the protologue closest to *A. bahamana*, which differs in its dull grey leaves with rather short terminal spine. See also the note under *A. bahamana*.

**A. minor** Proctor (Contr. US Nation. Herb. 52: 118, 2005). **Type:** Puerto Rico (Proctor & al. 46978 [SJ, NY [photo], UPRRP [photo], US [photo]]). — **Lit:** Acevedo-Rodríguez & Strong (2012: 86). **Distr:** Puerto Rico (Cabo Rojo); dry scrubland, 100–200 m; known only from a single population of several individuals.

[2q] Acaulescent; **Ros** tight, clustering by means of short stolons; **L** lanceolate or narrowly elliptic, ascending to erect, 40–60 × 4.5–6 cm; **marginal teeth** ±1 mm, mostly 6–10 mm apart; **terminal Sp** needle-like, to 30 mm; **Inf** (only 1 seen) 1.2 m, ‘paniculate’, peduncle ±90 cm, **Bra** widely separated, deltate-acuminate with spinose apex, 3–4.5 cm, part-**Inf** few, short, ascending, 1.5–4 cm stalked; **Fl** densely clustered on very short branches; **Tep** (only dried withered ones seen) ±15 mm, yellow; **St** not known; **Ov** not described; **Fr** rounded-oblong, deeply grooved between the locules, ±20 × 14–16 mm; **Se** angular, rugose, ±5 mm wide.

Differing from the other two *Agave* species native in Puerto Rico (*A. missionum* of Sect. *Antillanae*; *A. eggersiana* of Sect. *Caribaeae*) in its smaller size. It is compared with *A. missionum* in the protologue, from which it differs in smaller leaves, inflorescences and fruits, but remains insufficiently known. With its small teeth, small flowers, and small seeds, the species can clearly be placed in Sect. *Antillares*, which otherwise includes 6 species from Cuba, indicating that *A. minor* is not close to the two other species from Puerto Rico.

**A. missionum** Trelease (Mem. Nation. Acad. Sci. 11: 37–38, tt. 72–75, 1913). **Type:** Virgin Islands, St. Thomas (Trelease 15 [MO]). — **Lit:** Berger (1915: 212–213); Britton & Wilson (1923: 156); Hummelinck (1986: 162–163, with ill.); Álvarez de Zayas (1995: 41); Francis (2004: 34–35, with ill.); Proctor & Acevedo-Rodríguez (2005: 118–120, figs. 27a–e, 388: fig. 61e); Acevedo-Rodríguez & Strong (2012: 86). **Distr:** Puerto Rico (incl. Culebra and Vieques), US Virgin Islands (St. Croix, St. John, St. Thomas); British Virgin Islands (Anegada, Guana, Tortola, Virgin Gorda); dry rocky mostly non-calcareous habitats over sedimentary or igneous rocks, sandy dunes, often at disturbed sites, near sea level to ±800 m; flowers around Easter. **I:** Hochstätter (2015: VII: 74).

**Incl.** *Agave vivipara* Oldendorp (1777) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave morrisii* Eggers

(1889) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave portoricensis* Trelease (1913).

[2p] Acaulescent; **Ros** solitary, large, not surculose; **L** lanceolate to broadly lanceolate, gradually acuminate to a spinose apex, fleshy, mostly 90–275 × 13–23 (–25) cm, dark glossy green or very slightly greyish, sometimes slightly glaucous when young, margins nearly straight; **marginal teeth** straight or variously recurved, conspicuously triangular, 2–5 (–8) mm, brown or blackish, mostly 7–15 (–30) mm apart, smaller teeth from often confluent lenticular bases; **terminal Sp** subulate, straight or a little upcurved, round-grooved to about the middle or occasionally involute, smooth, (10–) 15–25 mm, brown, or grey in age, somewhat glossy, decurrent at the base and dorsally intruding into the green leaf tissue; **Inf** 5–7 m, ‘paniculate’, narrowly oblong, often bulbiferous, part-**Inf** ±30–35, nearly horizontal or sometimes slightly ascending, in the upper ½–⅔ of the inflorescence, with dense cymose flower clusters; **Ped** 10–20 mm; **Fl** erect, 45–55 mm; **Tep** yellow or greenish-yellow, tube conical, 6.5–8.5 mm, lobes 15–23 × 5 mm; **St** long-exserted; **Fil** 28–40 mm; **Anth** falcate, 14–21 mm; **Ov** oblong-fusiform, 20–35 × 6–10 mm; **Sty** 40–50 mm; **Sti** 3-lobed; **Fr** broadly oblong-ellipsoid, somewhat turbinate, or subglobose, stipitate and beaked, 25–48 × 17–25 mm; **Se** only rarely produced, irregularly and obtusely triangular, flat, 5–9 × 5–6 mm.

In the first edition of this handbook, *A. eggersiana* was placed in the synonymy here, and *A. portoricensis* was recognized as a distinct species, but following Proctor & Acevedo-Rodríguez (2005), *A. eggersiana* is now recognized as distinct species, and *A. portoricensis* is treated as synonym of *A. missionum*. *A. missionum* is somewhat variable in several characters, including the size of the marginal teeth, the shape of the panicle, the texture of the capsules, and the presence or absence of bulbils (Francis 2004, Proctor & Acevedo-Rodríguez 2005). Recently, a third species from Puerto Rico was published, *A. minor* (see there). — The dried inflorescences are used by some residents as christmas tree (Colli

**Fig. 40** *Agave mitis* (Etter & Kristen 993: Mexico; San Luis Potosí, Sierra Alvarez, 2350 m). (Copyright: J. Etter & M. Kristen)



1983: 20). Vernacular names: “karata”, “corita”, “cocuiza”.

**A. mitis** Martius (Del. Sem. Hort. Bot. Monac. 1848: 4, 1848). **Type** [neo]: Mexico, Tamaulipas (Gentry 20077 [MEXU, DES, US]). — **Lit:** Berger (1915: 62–66, as *A. mitis*, *A. celsii* & *A. albicans*); Gentry (1982: 220–224, as *A. celsii* & var. *albicans*, with ills.); Smith & Steyn (2002b: as *A. celsii* var. *albicans*); Eguiarte & Scheinvar (2008: 48–50, as *A. celsii* var. *albicans*); Starr (2012: 136–139); Thiede (2016); all with ills. **Distr:** Mexico (SE Coahuila, S Nuevo León, W & SW Tamaulipas, SW & S San Luis Potosí, NE Guanajuato, N & NE Querétaro, N & C Hidalgo, N Puebla); mostly on limestone outcrops, also in stream-side thickets, in cloud forests, rarely epiphytic, 460–2440 m; flowers March to July. **I:** Curtis’s Bot. Mag. 82: t. 4934, 1856, as *A. celsii*; Curtis’s Bot. Mag. 102: t. 6248, 1876, as *A. botteri*; Curtis’s Bot. Mag. 123: t. 7527, 1897, as *A. haseloffii*; Curtis’s Bot. Mag. 123: t. 7558, 1897, as *A. bouchei*; Irish & Irish (2000: t. 9, as *A. celsii*); Heller (2006: 108, 158); Richter (2011: 75, 122); Pilbeam (2013: 133); Hochstätter (2015: IX: 7, as ssp. *albidior*). – Fig. 40.

**Incl.** *Agave mitis* var. *mitis* ≡ *Agave micracantha* var. *mitis* (Martius) A. Terracciano (1885) (*incorrect name*, ICN Art. 11.4, 25.1); **incl.** *Agave celsii* var. *celsii*; **incl.** *Agave celsii* Hooker (1856) ≡ *Agave bollii* var. *celsii* (Hooker) A. Terracciano (1885) (*incorrect name*, ICN Art. 11.4, 25.1); **incl.**

*Agave rupicola* Regel (1858); **incl.** *Agave rupicola* var. *brevifolia* Regel (1858); **incl.** *Agave rupicola* var. *longifolia* Regel (1858); **incl.** *Agave rupicola* var. *rubridentata* Regel (1858); **incl.** *Agave micracantha* Salm-Dyck (1859); **incl.** *Agave micracantha* var. *albidior* (Salm-Dyck) Ullrich (1993) (*nom. inval.*, ICN Art. 41.5) ≡ *Agave mitis* ssp. *albidior* (Salm-Dyck) Hochstätter (2015); **incl.** *Agave celsiana* Cels (1861); **incl.** *Agave oblongata* Hort. Tonel ex K. Koch (1862) ≡ *Agave sartorii* var. *oblongata* (Hort. Tonel ex K. Koch) A. Terracciano (1885); **incl.** *Agave concinna* Hort. Tonel ex K. Koch (1862) (*nom. illeg.*, ICN Art. 53.1) ≡ *Agave macroacantha* var. *concinna* (Hort. Tonel ex K. Koch) A. Terracciano (1885); **incl.** *Agave densiflora* Regel (1863) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave albicans* Jacobi (1865) ≡ *Agave micracantha* var. *albicans* (Jacobi) A. Terracciano (1885) ≡ *Agave celsii* var. *albicans* (Jacobi) Gentry (1982); **incl.** *Agave bouchei* Jacobi (1865) ≡ *Agave rupicola* var. *bouchei* (Jacobi) A. Terracciano (1885); **incl.** *Agave ehrenbergii* Jacobi (1865); **incl.** *Agave celsiana* Jacobi (1865) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave goeppertiana* Jacobi (1866); **incl.** *Agave haseloffii* Jacobi (1866); **incl.** *Agave ousselghemiana* Jacobi (1869); **incl.** *Agave celsiana* [?] *albida* hort. (1871) (*nom. inval.*, ICN Art. 38.1); **incl.** *Agave micracantha* var. *picta* J. Croucher ex R. Hogg (1874); **incl.** *Agave botteri* Baker (1876); **incl.**



*Agave concinna* Hort. Angl. ex Baker (1877) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave micracantha* [?] *variegata* Peacock (1878) (*nom. inval.*, ICN Art. 38.1); **incl.** *Agave macrantha* Todaro (1879) ≡ *Agave macroacantha* var. *macrantha* (Todaro) A. Terracciano (1885); **incl.** *Agave macrantha* var. *concinna* A. Terracciano (1885); **incl.** *Agave bollii* A. Terracciano (1885) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Agave ousselghemiana* [?] *albo-picta* hort. (1885) (*nom. inval.*, ICN Art. 38.1); **incl.** *Agave albicans* var. *variegata* Münzer (1893) (*nom. inval.*, ICN Art. 38.1); **incl.** *Agave ousselghemiana* [?] *picta* hort. (1905); **incl.** *Agave celsiana* [?] *nana* Anonymous (1906) (*nom. inval.*, ICN Art. 38.1); **incl.** *Agave albicans* var. *ctenophora* Trelease (1914); **incl.** *Agave albicans* var. *mediopicta* Trelease (1914).

[1f] **Ros** branching axillary, forming large, long-lived, dense clumps; **L** ovate, oblong, or spatulate, ascending to outcurving, thickly soft-fleshy, short-acuminate, sometimes undulate, convex below, guttered or concave above, 30–60 (–70) × 7–13 cm, green to light grey-glaucous, margins straight to sometimes ± wavy; **marginal teeth** small, frequently 2-tipped, sometimes with ciliate crests, 1–3 mm, whitish to reddish-brown, closely spaced; **terminal Sp** acicular, weak, 10–20 mm, brownish, decurrent along the leaf tip for 1–6 cm and more; **Inf** 1.5–2.5 m, ‘spicate’, (always?) “lateral” but likely terminal on rudimentary lateral rosettes, peduncle with dense, chartaceous, deltoid, long-caudate, persistent **Bra** 1.5–7 cm long, fertile part dense, becoming lax at fruiting time, part-**Inf** with geminate flowers; **Fl** fleshy, 40–60 mm; **Tep** green outside, yellow to reddish or lavender to purplish within, tube funnel-shaped, thick-walled, 3-angled, 6-furrowed, 10–17 × 10–12 (at the apex) mm, lobes linear-lanceolate, thick-fleshy, ascending to recurving, shortly acuminate, cucullate, glandular-floccose at the tip, unequal, 12–18 × 5–8 mm, inner with a broad fleshy keel; **Fil** 40–60 mm, whitish with fine pale purple stripes, yellowish, brownish, or brownish-purple, inserted at the tube apex; **Anth** mostly excentric, 17–22 mm, yellow, green(ish), red or brown, before dehiscence yellowish, brown, purplish-brown or dark purple; **Ov** 3-angled, cylindrical, 6-grooved, truncate at base and apex,

13–20 mm, without neck; **Sty** stout, shorter, as long as or longer than the filaments, whitish-green, light greenish-cream, rose, (pale) purple or brown, sometimes dotted with purple or reddening towards the tip; **Sti** weakly 3-lobate; **Fr** angularly ovoid, thick-walled, 18–25 × 9–12 mm, rough, dark brown, beaked; **Se** semicircular, 3–4 × 2–3 mm, with well-developed complete marginal wing. — **Cytology**: 2n = 60 (Cave 1964, Simpson & al. 2011).

Distinguished by its small compact rosettes, broad, delicately denticulate leaves with mostly 2-tipped teeth, and dense, clavate inflorescences (Gentry 1982: 222). Gentry wrongly used the name *A. celsii* for this taxon, and the nomenclature, including the designation of a neotype as cited above, was finally clarified by Ullrich (1993a) and reviewed by Thiede (2016). *A. ehrenbergii* Jacobi (1865) should be placed in the synonymy here (Thiede 2016; see note under *A. legrelliana*).

The plates in Curtis’s Botanical Magazine cited above finely illustrate the considerable variability of the species. This variability in the colouring of tepals, filaments, anthers and styles is remarkable and may occur within the same population from plant to plant (Gentry 1982: 223). Plants with pale glaucous to nearly whitish leaves (var. *albidior*/var. *albicans*) were introduced into cultivation before 1859 (Thiede 2016). A small colony along the eastern rim of the N and C Barranca de Metztlán was assigned to this variety by Gentry (1982) (map in Eguiarte & Scheinvar (2008)). The deviating leaf colouration is bridged by intermediates to typical green-leaved plants, and the differences in the length of the lobes given by Gentry are not supported by early authors, so that this variety can not be upheld (Thiede 2016). — ‘Multicolor’ is a variegated cultivar (Starr 2012: 140).

The probability that a flower develops into a fruit is 43.9%, and that at least one ovule of a flower develops into a seed is 35%. On average, each inflorescence develops only 51 fruits with 49 viable seeds each. Main floral visitors are bats and also bees, bumblebees, sphingids, and hummingbirds (Eguiarte & Scheinvar 2008). The genetic variation is high and mostly found within populations. The populations are moderately differentiated from each other, suggesting a



relatively low gene flow among them, with more distant populations being genetically more different (Eguiarte & Scheinvar 2008).

**A. montana** Villarreal (Sida 17(1): 191–195, ills., 1996). **Type:** Mexico, Nuevo León (*Villarreal & al.* 8120 [MEXU, ANSM, ASU, DES, ENCB, IBUG, XAL]). — **Lit:** Greulich (2012c); Starr (2012: 141–147, 325–327); Alsemgeest & Roosbroeck (2012?); all with ills. **Distr:** Mexico (S Nuevo León, W Tamaulipas, NE Querétaro); rocky limestone slopes in mountain regions, in open pine-oak forests or above the timberline, 2300–3400 m; flowers May to July. **I:** Spracklin (2007: 146); Pilbeam (2013: 135); Grieco (2013); Hochstätter (2015: III: 4); Greulich (2016b).

[2m] Acaulescent; **Ros** semiglobose, compact, 0.75–1.25 × 1.25–1.65 m, solitary; **L** 84–112, regular in 12–16 rows, shortly elliptic, base broadened, apex acuminate, slightly guttered to nearly flat, 30–50 × 15–18 cm, yellowish-green, margins straight, near the tip bordered brown-purple; **marginal teeth** antrorse, retrorse or nearly straight, broadly triangular from a lenticular base, 3–10 × 5–15 mm, longest in the upper 1/2, much shorter below, greyish, 6–20 (–35) mm apart, 16–18 per leaf margin; **terminal Sp** acicular, narrowly triangular, 30–50 mm, greyish, decurrent for 4–12 cm as broad margin confluent with the upper marginal teeth; **Inf** 3.5–4.5 m, paniculate, peduncle thick, with elliptical succulent **Bra** 18–25 × 8–12 cm, reddish-brown, completely covering the peduncle, fertile part ovoid, part-**Inf** 20–30 in the upper 2/3 of the inflorescence, 25–30 cm; **Ped** 10–15 mm; **Fl** 60–70 mm; **Tep** yellow, reddish in bud, tube 20 × 12–14 mm, lobes lanceolate, 20 × 3–4 mm; **Fil** flattened, 50–60 × 3 mm, inserted at the base of the lobes; **Anth** 19–20 mm, yellow; **Ov** 30 mm, neck slightly constricted; **Sty** shorter than the filaments; **Fr** oblong, 50–60 × 15–20 mm, coffee-brown; **Se** drop-shaped, 5–6 × 3–4 mm, shiny black.

According to the protologue related to *A. parrasana* of Sect. *Parryanae* (as Group) and esp. to *A. gentryi* (= *A. macroculmis sensu* Gentry p.p.) in which it was formerly erroneously included despite being clearly distinct in many features. The descriptions of both Gentry (1982) and Ullrich

(1990i) for *A. gentryi* combine characters of both species (see there).

According to the protologue, *A. montana* differs from the partially sympatric *A. gentryi* by larger, non-offsetting rosettes with more and smaller leaves with curved marginal teeth, and inflorescences with dentate bracts, the fertile part ovate in outline with 20–30 part-inflorescences and smaller flowers. First only known from the type locality, further localities have been discovered subsequently. It shows possible intergrades (hybrids?) with *A. gentryi* where they are sympatric (Starr 2012: 99, Greulich 2012c: 49–52); the cultivar ‘Baccarat’ is such an intermediate of wild origin (Starr 2014: 219, with ill.). Alsemgeest & Roosbroeck (2012?) even suggest a separate Group *Parrasanae* (*nom. inval.*) for the three species *A. gentryi*, *A. montana* and *A. parrasana*. Hochstätter (2015: I: 31) published his Sect. *Hibernicae* for *A. montana* and *A. gentryi* which is accepted here, also including *A. parrasana*. The species is somewhat frost-hardy under garden conditions, see Grieco (2013).

**A. montium-sancticaroli** García-Mendoza & al. (J. Bot. Res. Inst. Texas 1(1): 79–81, ills., 2007). **Type:** Mexico, Tamaulipas (*García-Mendoza & al.* 7605 [MEXU, ENCB, TEX, UAT]). — **Distr:** Mexico (Tamaulipas); on plains and plateaus over calcareous rocks and sandy soils, in submontane scrub or its transitions to oak forests, 150–800 m. **I:** Hochstätter (2015: IX: 40).

[1g × 2g?] **Ros** compact, 1.5–2 × 2–2.5 m, surculose; **L** 50–80 (–100), erect, lanceolate, rigid, 100–120 × 9–12 cm, yellowish-green, glaucescent towards the base, sometimes with transversal glaucous bands, margins with thin horny band; **marginal teeth** straight to retrorse, 4–6 × 1.5–3 (at the base) mm, 10–30 (–45) mm apart, more narrowly set near the leaf base, with 1 or several small denticles between the teeth, greyish; **terminal Sp** dorsally channelled, 25–35 mm, decurrent for 12–16 cm; **Inf** 5.5–7 m, ‘racemose-paniculate’, ± fusiform, peduncle 3–4 m, with deltoid chartaceous **Bra** 11–16 × 2.5–5.5 cm, part-**Inf** (60–) 80–140, the lower 8–13 cm, diminishing to 2–4 cm towards the tip; **Ped** (0.5–) 1–1.5 mm, elongating to 20 mm in ripe fruits; **Fl** 45–50 (–55)

mm, in groups of 10–20 per ‘umbel’; **Tep** yellowish-green, tube 5–6 (–8) × 7–10 (–12) (at the apex) mm, lobes 15–22 × 3–4 (–7) mm, apex cucullate; **Fil** 35–40 (–55) mm, green with purple tinge, inserted at the tube apex; **Anth** 13–15 (–20) mm, yellow; **Ov** cylindrical, 20–25 (–30) × 4–6 mm, neck constricted; **Sty** 50–55 mm; **Sti** 3-lobed; **Fr** oblong, 35–45 × 17–20 mm; **Se** 4–6 × 3–4 mm, winged for 0.5 mm, black.

In the protologue placed in Sect. *Heteracanthae* (as Group *Marginatae*) and compared with *A. × glomeruliflora*, which is the name used for a series of natural hybrids between *A. lechuguilla* (Subgen. *Littaea*) and *A. gracilipes*, *A. havardiana* and *A. (parryi) ssp. neomexicana* (Subgen. *Agave*) with an intermediate ‘race-mose-paniculate’ inflorescence. The inflorescence of *A. montium-sancticaroli* is similarly intermediate between the subgenera, and thus likewise strongly suggests that the species is an inter-subgeneric hybrid, possibly between *A. angustifolia* (which it resembles in habit) and the sympatric *A. funkiana* or *A. lophantha*. Indeed Etter & Kristen (1997+: accessed Oct. 2018) list it as hybrid. According to the protologue, it is used for mescal production. *A. doctorensis*, likewise with an intermediate inflorescence and of putative hybrid origin, is compared with *A. montium-sancticaroli* in the protologue (see there).

**A. moranii** Gentry (Occas. Pap. Calif. Acad. Sci. 130: 58, ill. (pp. 59–61), 1978). **Type:** Mexico, Baja California (Gentry & McGill 23287 [US [syn], ARIZ, ASU, CAS, DES, MEXU, MICH, SD]). — **Lit:** Gentry (1982: 392–395, with ill.); Turner & al. (1995: 56–57); Thorne & al. (2010: 32–33); Webb & Starr (2015: 74–75, with ill.). **Distr:** Mexico (Baja California: S San Pedro Martír); rocky slopes and plains in a small desertic area, in desert scrub and ecotone with chaparral, 450–2065 m; flowers April to July. **I:** Pilbeam (2013: 136); Hochstätter (2015: V: 23).

[2j] Stems short; **Ros** symmetrically sword-leaved, 1–1.5 × 2 m, solitary; **L** triangularly long-lanceolate, straightly ascending to spreading, rigid, rounded beneath, deeply guttered, 70–120 × 8–12 cm, light to yellowish-green, sometimes glaucous, margins towards the tip white-horny;

**marginal teeth** sinuously curved, flattened, 6–12 mm (at mid-leaf and below), light grey, 20–40 mm apart, base broad or continuous with the leaf margin, teeth reduced and more remote towards the leaf tip; **terminal Sp** stout, broadly grooved above, 40–60 mm, nearly white, tip chestnut-brown, decurrent to the middle of the lamina; **Inf** 4–5 m, paniculate, peduncle frequently swollen and closely bracteate below the fertile part, part-**Inf** closely spaced, compact, large, subtended by prominent, lanceolate, reflexing, strong **Bra**, 20–30 per **Inf**; **Ped** slender, 10–30 mm, bracteolate; **Fl** 50–70 mm; **Tep** bright yellow, tube broadly funnel-shaped, 4–6 × 12–13 mm, **Nec** ridged by the decurrent filaments, lobes broadly linear, erect to ascending, acute, with papillate tufted beak, 18–24 × 6–7 mm, inner with a prominent bulbous keel and 2 costae within, slightly lobed at the base; **Fil** very slender, 35–46 mm, inserted on the nectary rim and partly on the lobe bases; **Anth** centric; **Ov** fusiform, tapered at the base, 25–40 mm, neck short, grooved, thick; **Sty** slightly longer than the filaments; **Sti** capitate; **Fr** long-oblong, 50–70 × 16–20 mm, short-beaked, stipitate, yellowish to brown; **Se** drop-shaped, 7–8 × 5–6 mm, marginal wing smooth, variable in width, shiny.

Characterized and distinguished by its large solitary rosettes with large, long, rigid, sword-like leaves with an apical white-horny margin, stout peduncles and relatively congested panicles. Gentry (1982) placed it in his Group (now Sect.) *Deserticolae* and allied it with *A. avellanidens* and *A. gigantensis*. Webb & Starr (2015) placed all three species as well as *A. turneri* in a separate Sect. *Conicae* (see also under *A. avellanidens*). The species appears to hybridize with *A. pringlei* according to Gentry (1978) and Gentry (1982: as *A. deserti* ssp.), but Webb & Starr (2015) found no evidence in the field. Gentry’s “holotype” at US consists of three sheets which thus represent syntypes; two of them were apparently cross-labelled later.

**A. × mortolensis** A. Berger *pro sp.* (Hort. Mortol. 13, 361, 1912). **Type:** not typified. — **Lit:** Berger (1915: 156); Ullrich (1993b: 25, 30); both as *A. mortolensis*. **Distr:** Cultivated only.

[2a × 2b] A garden hybrid that originated at La Mótola, possibly *A. americana* ssp. *americana* (as *A. ingens* in the protologue) × *A. salmiana* ssp. *salmiana*. Apparently lost from cultivation.

**A. multicolor** (E. Solano & Dávila) Thiede (Haseltonia 17: 95, 2012). **Type:** Mexico, Guanajuato (Solano C. & Correa D. 871 [MEXU, CHAPA, ENCB, FEZA, IEB, MO, NY, RSA, UAMIZ, US]). — **Lit:** Solano Camacho & Dávila Aranda (2003: with ills., as *Polianthes*). **Distr:** Mexico (Guanajuato); dark to brown soils with sandy texture, in pine, pine-oak and oak forests and grasslands, 2200–2490 m; flowering August. **I:** Castro-Castro & al. (2015: 145); Hochstätter (2016: II: 18); Castro-Castro & al. (2016: 721); Castro-Castro (2017: 137); all as *Polianthes*.

≡ *Polianthes multicolor* E. Solano & Dávila (2003).

[3b2] Herbaceous; corm cylindrical, ±0.8–1 × 2 cm; bulb long ovoid, (1.5–) 2.7–4 (–4.5) × 1–1.5 (–2) cm, covered with dried leaf bases; **R** contractile, thickend; **L** 2–4 (–6), linear, grass-like, (7–) 11–30 (–37) × 0.1–0.45 (–0.9) cm, papillose (“buliforme”), margins papillose; **Inf** (28–) 33–64 cm, ‘spicate’, fertile part with 3–9 (–16) floral nodes with geminate flowers, **Bra** at the base of the peduncle 4–18 (–21) × 0.14–0.43 (–0.7) cm, linear; **Ped** (3.5–) 4.4–16 mm; **Fl** geminate, fragrant, 18–28 mm, at the base with 2 bracteoles; **Tep** tube inside completely yellow,

sometimes white, nearly funnel-shaped, abruptly curved just above the ovary, 1.4–3.6 (–4.2) mm Ø at the mouth, lobes broadly ovate to broadly elliptic, perpendicularly spreading, 2–4 × 1.1–3.3 (–3.6) mm, tips obtuse to rounded, colour variable, from cream to nearly white, white-pinkish, pink, pink with white stripes, yellowish-pink, nearly red to orange-yellowish; **Fil** 10–17 mm, white to yellow, inserted 3–6 mm above the tip of the ovary; **Anth** oblong, 3.9–5.4 (–6) mm, yellow, included; **Ov** ±4 × 1–2 mm; **Sty** (11–) 12–17 mm, white or yellow; **Sti** 3-lobed; **Fr** semiglobose, 10–13 (–24) × 8–10 mm; **Se** semicircular, (2.1–) 3–3.9 × 2.2–2.9 mm, black.

According to the protologue characterized by its nearly funnel-shaped flowers with a great colour variability. It is similar to *A. coetocapnia* (as *Polianthes geminiflora*), which differs in having broader bulbs, broader leaves and bracts, and tubular, pendent and orange or coral-pink to red flowers with erect lobes. *A. multicolor* has the greatest flower colour variability of all taxa of Sect. *Polianthes*.

**A. multifilifera** Gentry (US Dept. Agric. Handb. 399: 46–50, ills., 1972). **Type:** Mexico, Chihuahua (Gentry 8167 [US 2558493 + 2558494 [syn], ARIZ, DES, MEXU, US]). — **Lit:** Bye & al. (1975: 97, 111, with ill.); Gentry (1982: 112–117, with ills.); González-Elizondo & al. (2009: 75–76, with ills., as *A. filifera* ssp.); Starr (2012: 148–153, 317–319, ills.). **Distr:** Mexico

**Fig. 41** Agave *multifilifera*. (Mexico; Chihuahua, El Divisadero) (Copyright: J. Thiede)



(SE Sonora, SW Chihuahua, N Sinaloa, N Durango); cliffs and rocky sites in pine-oak or oak forests, 1400–2200 m. **I:** Irish & Irish (2000: t. 24); Heller (2006: 109); Richter (2011: 130); Pilbeam (2013: 82, as *A. filifera* ssp.); Hochstätter (2015: VII: 41, 47, as *A. filifera* ssp.). – Fig. 41.

≡ *Agave filifera* ssp. *multifilifera* (Gentry) B. Ullrich (1992).

[1d] **Ros** ±1 × 1.5 m, solitary, not surculose, with a short trunk at maturity; **L** 200 or more, linear-lanceolate, erectly ascending to declined, broadest at the base, firm but pliable, slightly convex below, flat above, smooth, 50–80 × 1.2–3.5 cm, light green, margins with numerous long detaching fibres; **terminal Sp** long, subulate, flattened above, 10–15 mm, castaneous to aging grey; **Inf** to 5 m, ‘spicate’, fertile from just above the longest leaves, part-**Inf** with 2 (–3) flowers; floral **Bra** ±8 cm in the lowest flowers, greyish, subulate, higher up shorter; **Ped** short, thick; **Fl** 40–43 mm; **Tep** pale waxy green with pink tinge on the lobes, buds green with lavender luster, tube shortly funnel-shaped, 5 × 10 (at the apex) mm, the nectariferous tissue ± filling the tube, lobes narrowly elliptic, some erect, some recurving at anthesis, apiculate, subequal, 16–17 mm, the papillate area broad and decurrent on the inner lobes, outer lobes narrower, 5–5.5 mm wide, and also with a low keel; **Fil** long, slender, elliptic in cross section, 35–40 mm, red; **Anth** 16–17 mm, yellow; **Ov** fusiform, 20–21 mm, neck 5 mm, constricted, faintly grooved; **Sty** slender, whitish; **Sti** slightly thickened; **Fr** slenderly ovoid, 20–25 × 10–12 mm, apiculate; **Se** 3.5–4.5 × 2.5–3 mm, hilar notch abrupt, the curved margin with a wrinkled or erose winglike edge.

One of the most robust taxa in Sect. *Littaea* (as Group *Filiferae*), differing from the other species related to *A. filifera* mainly by its larger dimensions, its higher leaf number and its short and broad floral tube. See also the note for *A. schidigera*. Ullrich (1992h) reduced *A. multifilifera* and also *A. schidigera* to subspecies of *A. filifera*, but his reclassification was not followed by Vázquez-García & al. (2007b: 71), Starr (2012) and Govaerts (2014+). Gentry’s two “holotype” sheets at US are not cross-labelled thus representing syntypes.

The leaves are an important source of fibre, and the hearts and leaf bases are pit-baked and eaten or made into “mesagoli” (mescal bread) or “sugui” (alcoholic beverage) (Bye & al. 1975: 97).

**A. murpheyi** F. Gibson (Contr. Boyce Thompson Inst. Pl. Res. 7: 83, fig. 1, 1935). **Type:** USA, Arizona (Gibson s.n. [Herb. Boyce Thompson Arboretum]). — **Lit:** Gentry (1972: 99–101, with ills.); Gentry (1982: 440–443, with ills.); Nabhan (1995: with ills.); Adams & Adams (1998: with ills.); Hodgson (1999b); Reveal & Hodgson (2002); Parker & al. (2007); Klopper & al. (2010: 61–62); Parker (2018a: 22–23). **Distr:** USA (C & S Arizona), Mexico (NW Sonora); near drainage systems in desert scrub, around pre-Columbian living sites, 400–1000 m; flowers March to July. **I:** Irish & Irish (2000: tt. 25–26); Pilbeam (2013: 137); Hochstätter (2015: III: 11).

[2h] Acaulescent; **Ros** compact, 0.6–1.2 × 0.8–1.4 m, caespitose, freely suckering; **L** numerous, linear-spatulate, ascending, firm, thin, straight, thickish and convex towards the base, broadest just in the middle, short-acuminate, convex towards the base below, concave towards the apex above, 50–80 × 6–10 cm, light glaucous-green to yellowish-green, frequently lightly cross-zoned, with clearly visible impressions left by the central bud, margins repand; **marginal teeth** regular, single, mostly curved to the margin, or upcurved, small, mostly 3–4 mm, dark brown to black or grey, ±10–20 mm apart; **terminal Sp** conical, thick, very shortly grooved or flattened above, short, 12–20 mm, dark brown to pruinose-grey, decurrent for 3.5–5 cm to the uppermost teeth; **Inf** 3–4 m, paniculate, peduncle thickish, green, with persistent triangular **Bra** 10–15 cm long, fertile part narrow, part-**Inf** (slightly) ascending, compact, short, 10–16 in the upper ¼ or ⅓ of the inflorescence, with 12–21 flowers, > 10 cm, freely bulbiferous, rarely producing fruits; **Fl** thick, stout, (51–) 60–75 mm; **Tep** cream, tips purplish to brownish, tube deep, urceolate, 14–20 × (11–) 14–19 mm, lobes erect, leathery, unequal, (14–) 15–20 × 4–7 mm, outer somewhat larger, with roughened thick brownish hooded tip, all tepals slightly clasping the filaments; **St** long-exserted; **Fil** erect, (33–) 45–50 mm, yellow, inserted



unequally at or slightly above mid-tube, cream to pale yellow; **Anth** (16–) 22–26 mm, yellow; **Ov** (18–) 22–40 mm, neck slightly constricted, 0.5–3 (–6) mm; **Fr** rarely produced, obovoid to oblong or ovoid, 50–70 mm, apex short-beaked, shortly pedicellate; **Se** (7–) 9–11 × 6 mm. — **Cytology**:  $2n = 60$  (Pinkava & Baker 1985).

A cultigen derived via domestication, cultivated from ±600 to 1350 CE and used as food by the ethnic group of the Hohokam. The plants persisted as relict clones up to the present, always associated with pre-Columbian living sites of native Americans (Nabhan 1995; Parker & al. 2007). Genetic studies by Parker & al. (2007) showed that the genetic variability is lower than in purely wild species and comparable to modern agricultural crops, but the species is not derived from a single clone, and its genetic variation does not follow a geographic pattern, possibly resulting from genetic exchange by bulbils and seeds. It is of conservation concern.

Hybridization with *A. chrysantha* is known from Arizona (Gentry 1982, Reveal & Hodgson 2002). *A. murpheyi*, *A. verdensis* and *A. yavapaiensis* are the sole species among the pre-Columbian cultivar species in Arizona which (rarely) develop ripe fruits and seeds (fruits of *A. delamateri*, *A. phillipsiana* and *A. sanpedroensis* are unknown). For notes on further pre-Columbian cultivar species in Arizona, see *A. verdensis*. — ‘Rodney’ is a variegated cultivar with yellow leaf-margins (Moore 2016: 242).

**A. nanchitlensis** (Matuda) Thiede & Govaerts (Phytotaxa 306(3): 238, 2017). **Type**: Mexico, México (Matuda 37640 [MEXU, CODAGEM, UAMIZ]). — **Lit**: Matuda (1974); Piña Luján (1986: 14); Ullrich (1989b); García-Mendoza (2003); Castillejos-Cruz (2009: [216]–[220]); all with ill. and as *Manfreda*. **Distr**: Mexico (México); rocky sloping oak or pine-oak forests, 1600–2100 m; flowers October to January. **I**: Hochstätter (2016: I: 31).

≡ *Manfreda nanchitlensis* Matuda (1974).

[3a2] Plants herbaceous, small (for Subgen. *Manfreda*), daughter **Ros** arising in the axils of the current year’s rosette; corm 2.5–4.5 × 1.5–3 cm, cylindrical, bulb 1.2–6.8 × 2.5–3.2 cm,

cylindrical, completely covered with dried fibrous leaf bases 6–9 cm long; **R** fleshy and fibrous, with filiform ramifications, contractile; **L** drought-deciduous, 4–10, spreading, recurved, linear, thick, canaliculate, papillose on both faces, apex obtuse, 20–30 × 0.4–0.8 cm, shiny green, with abundant purple dots near the base, margins entire, with a hyaline band; **Inf** 40–95 (–150) cm, erect, green-glaucous, ‘spicate’, peduncle with 7–10 **Bra**, base truncate, increasingly smaller upwards, fertile part 10–20 (–25) cm, lax, with 7–10 flowers; floral **Bra** 5–8 × 1 mm; **Fl** 28–31 mm, solitary, sessile, diffuse to divaricate; **Tep** yellowish-green to reddish-green on the outer face, forming a tube (16–) 22–30 × 4–5 mm, sparsely recurved, lobes oblong, revolute, 9–14 × 3–4 mm, tip cucullate, with a bundle of short white trichomes; **Fil** 27–37 mm, somewhat flattened, erect at anthesis, exceeding the tube for 22–32 mm, inserted near the mouth of the tube all on the same level, yellowish-green with purple dots; **Anth** 10 mm, greenish-yellow; **Ov** oblong, 11–16 × 3–5 mm, green-glaucous, not extending into tube, slightly constricted above; **Sty** 54–62 mm, yellowish-green; **Sti** 3-lobed; **Fr** cylindrical to ellipsoid, 22–27 × 10–20 mm, apiculate, with persistent perianth; **Se** deltoid, plane-concave, 3–4 × 3 mm, shiny.

According to Verhoek-Williams (1975: 289), this is the most slender species in Sect. *Herbaceae* (as *Manfreda*) and thus easily recognized by its nearly grass-like leaves, its lax inflorescence, and its long narrow floral tube. Only *A. graminifolia* (not covered by Verhoek-Williams) has even narrower leaves. — The combination under *Agave* was first published invalidly by Thiede & Egli (1999) and was later validated as given above.

**A. nashii** Trelease (Mem. Nation. Acad. Sci. 11: 45–46, tt. 101–103, 1913). **Type** [syn]: Bahamas, Inagua (Nash & Taylor 517 [B, MO, NY]). — **Lit**: Berger (1915: 269); Britton & Millspaugh (1920: 76); Correll & Correll (1982: 313–314); Álvarez de Zayas (1995: 40); Acevedo-Rodríguez & Strong (2012: 86); Freid & al. (2014: 218). **Distr**: Bahamas (Great Inagua); in sandy-rocky soils on dry S exposures, in dwarf shrubs and



scrubland; flowers throughout the year. **I:** Hochstätter (2015: VII: 98).

[2t] Acaulescent; **Ros** caespitose, freely suckering; **L** attenuate-oblong, erect, hard, straight, narrow, gradually tapering, guttered, 30–50 × 4–5 cm, grey-green, sometimes purple-tinged, somewhat glaucous and transversely banded; **marginal teeth** straight or somewhat curved, acuminately triangular, sometimes nearly or quite confluent, scarcely 2 mm, usually 3–5 mm apart, intervening margin nearly straight; **terminal Sp** conical, tapered, recurved or upcurved at the tip, smooth, somewhat polished, narrowly slit-grooved to beyond the middle, 15 × 3 mm, purplish-brown, decurrent; **Inf** 3.5–4 m, ‘paniculate’, very lax, part-**Inf** ±6–8, on slender outcurved **Bra** in the upper 1/3 or more of the inflorescence; **Ped** 5–10 mm; **Fl** 35–50 mm; **Tep** yellow to light yellow, tube openly conical, 3 mm, lobes 10 × 3 mm; **Fil** 25 mm, inserted almost in the tube throat; **Ov** subfusiform, or obovoid in development, 16–20 × 5–7 mm; **Fr** oblong or oblong-pear-shaped, 20–35 × 13–20 mm, shortly stipitate, beaked; **Se** 4–5 × 4 mm.

Insufficiently known. The name is based on 3 syntypes, those not shown above are *Nash & Taylor* 1389 and *Nash & Taylor* 21855. — For differences from *A. inaguensis*, the second species of Sect. *Inaguenses*, see there.

**A. nayaritensis** Gentry (Agaves Cont. North Amer., 515–516, ills., 1982). **Type:** Mexico, Nayarit (*Gentry* 21167 [US, ARIZ, DES, MEXU, MICH]). — **Lit:** McVaugh (1989: 139–140); Etter & Kristen (2002: with ills.); Cházaro Basáñez & al. (2005a: with ills.); Etter & Kristen (2007c); Vázquez-García & al. (2007b: 61–62, tt. R2, R3, S); González-Elizondo & al. (2009: 102–103, with ill.). **Distr:** Mexico (S Sinaloa, SW Durango?, Nayarit); volcanic cliff edges in tropical deciduous forests, 350–700 m; flowers March to May. **I:** Cházaro Basáñez & al. (2005a); Richter (2011: 82); Pilbeam (2013: 138); Hochstätter (2015: VI: 22).

[2n] Acaulescent or stems rarely to 10 cm; **Ros** open, 0.7–1.1 × 1.3–1.8 (–2.2) m, solitary, rarely surculose; **L** 9–30 (–40), lanceolate, rather floppy, etiolated when growing in the shade, narrowed

towards the base to 8–10 cm, widest above the middle or at 2/3 of their length, long-acuminate, somewhat asperulous, 85–115 × 12–15 (–18) cm, light green to light yellowish-green, partly with glaucous tinge at the base, margins repand to straight; **marginal teeth** small, 1–4 mm, chestnut-brown or darker, regularly spaced, 3–20 mm apart, sometimes with scattered minute intermittent teeth; **terminal Sp** conical, with a short narrow groove above, sometimes up to the middle, 9–20 mm, dark brown, sometimes black, not decurrent; **Inf** (1.2–) 2–4 m, paniculate, peduncle short, reddish, with large, triangular-lanceolate, chartaceous **Bra**, fertile part diffuse, (long) ovate, part-**Inf** widely spreading, several times compound, 10–15 in the upper 1/2 of the inflorescence, 25–55 cm long; **Ped** short, bracteolate; **Fl** 40–45 mm; **Tep** bright yellow, tube broadly funnel-shaped, shortly grooved, 4 mm, lobes linear from spreading sinuses, erect to slightly incurved, involute, galeate at the tip, rather thin, subequal, 15–17 × 3–4 mm, inner with a small keel; **Fil** 35–37 mm, inserted near the mouth of the tube; **Anth** centric, 15–16 mm, yellow; **Ov** rounded-trigonous, 20–25 mm, neck short, slightly constricted, furrowed; **Fr** opening for the upper 2/3 only, 16–28 × 10–14 mm, dark brown; **Se** with surface pattern, 5 × 3.5 mm, dull black.

Distinguished by its slender green leaves with small marginal teeth and terminal spine, and its broad, diffuse panicle with small, bright yellow flowers with shallow, open tubes, but without close relationship to other members of Sect. *Marmoratae* (as Group) (Gentry 1982). Long known from the type locality in C Nayarit only, the species was recently found at further localities in Nayarit and S Sinaloa (Etter & Kristen 2002, Etter & Kristen 2007c), and these authors also provide additional morphological data. González-Elizondo & al. (2009) tentatively place sterile plants from SW Durango here. Gentry’s “holotype” at US consists of two sheets which were apparently cross-labelled later. — See also the note under *A. karatto*.

**A. neocernua** Thiede (Bradleya 33: 83, 2015). **Type:** Mexico, Jalisco (*Castro-Castro & al.* 2495

[IBUG, IEB, MEXU]). — **Lit:** Castro-Castro & al. (2015: as *Polianthes cernua*, with ills.). **Distr:** Mexico (W Jalisco); in deep and acid soils in open pine-, oak- and juniper-forests, 1700–2120 m; flowers in early August. **I:** Hochstätter (2016: II: 7); Castro-Castro & al. (2016: 721); Castro-Castro (2017: 145); all as *Polianthes cernua*.

≡ *Polianthes cernua* Art. Castro & al. (2015).

[3b2] Herbaceous; corm 0.6–1.9 × 1.1–1.5 cm, oblong, bulb 2–2.6 × 1.5–1.9 cm, ovoid, completely covered with dried fibrous leaf bases; **R** fleshy, thickened, contractile; **L** drought-deciduous, (2–) 3 (–4), sometimes an additional one attached a few cm above the peduncle base, prostrate or slightly elevated from the ground, oblong-obovate, widest at the middle, tapering somewhat abruptly at base and apex, glabrous, apex acute, (6–) 8–12 × 0.6–2.2 (–4.5) cm, shiny green, margins entire, with a hyaline band; **Inf** 45–80 cm, erect, ‘spicate’, greenish, peduncle with 2–3 **Bra**, linear-lanceolate, base truncate, internodes decreasing in size distally, fertile part ±35–38 cm, very lax, with (3–) 4–6 (–10) remote floral nodes; floral **Bra** 6–15 × 2–3 mm; **Ped** 11–17 mm during anthesis, 15–20 mm in fruit, strongly recurved; **Fl** geminate, unscented, 20–25 × 3–6 mm, pendent; **Tep** orange in the lower 2/3, upper 1/3 and lobes yellowish-green, forming a straight tube 16–19 × 4–6 mm at the base of the lobes, lobes broadly ovate, almost equal, erect, imbricate, 2–4 × 2.5–3 mm, margin hyaline, apex of **OTep** obtuse, apex of **ITep** truncate, apices with a bundle of short white trichomes; **Fil** filiform, 14–16 mm, included, inserted 1–1.5 mm above the ovary apex, yellow; **Anth** linear, 4–5 mm, green, at anthesis placed at the upper portion of the mouth of the tube; **Ov** fusiform, 4.5–5 × 2.5–3 mm; **Sty** filiform, 16–20 mm, greenish-orange, exerted from the tube 2–3 mm at anthesis; **Sti** 3-lobed, papillose; **Fr** globose to oblong, 8–20 × 7–11 mm, with persisting tepals; **Se** ovate-depressed, flat, 4–6 × 3–5 mm, black to dark brown, dull.

According to the protologue characterized by its oblong-ovate, prostrate leaves, recurved pedicels, tubular, not curved, bicolorous perianth with imbricate and erect lobes, and morphologically closest to *A. bicolor*, which shares bicoloured flowers, and to *A. coetocapnia* ssp. *clivicola*,

which shares pendent flowers. Hummingbirds were observed as flower visitors; this might also be the case for other red-flowering species of Sect. *Polianthes*. — Upon transfer to *Agave*, a replacement name was necessary due to the earlier name *A. cernua* A. Berger.

**A. ×neokewensis** Thiede (Haseltonia 17: 95, 2012). — **Lit:** Watson (1899a); Anonymous (1910); both as *Bravoa kewensis*. **Distr:** Cultivated only.

**Incl.** *Bravoa ×kewensis* W. Watson (1899).

[3b2] This is the garden hybrid *A. coetocapnia* (as *Bravoa geminiflora*) × *A. bulliana* (as *Bravoa (Prochnyanthes) bulliana*). It was raised at Kew in 1894 and was described as *Bravoa ×kewensis* when it flowered in 1899 (Watson 1899a, Anonymous 1910). Upon transfer to *Agave*, a replacement name was necessary due to *A. kewensis* Jacobi 1866. It is the only hybrid known that involves *A. bulliana* (the only species of the former genus *Prochnyanthes*) as parent. Apparently lost from cultivation.

**A. neonelsonii** Thiede & Egli (Kakt. and Sukk. 50(5): 112, 1999). **Type:** Mexico, Durango (Nelson 4630 [US, GH]). — **Lit:** Rose (1903a: 10); Solano & Ríos-Gómez (2014: 100–101, ill.); both as *Polianthes nelsonii*. **Distr:** Mexico (S Chihuahua, Durango, Aguascalientes); on grassy meadows, slopes or ridges in pine-oak or pine forests, 1900–2500 m; flowers June to August. **I:** Barba-Gonzalez & al. (2012: 124); Hochstätter (2016: II: 19); Castro-Castro & al. (2016: 721); all as *Polianthes nelsonii*.

≡ *Polianthes nelsonii* Rose (1903).

[3b1] Herbaceous; corm 1.2–2 × 1–1.2 cm; bulb 1–3 (–5) × 0.6–1.8 cm, oblong, completely covered with dried fibrous leaf bases; **R** fleshy, thickened, contractile; **L** drought-deciduous, (2–) 4–5 (–7), erect to semi-erect, linear, narrow and grass-like, glabrous, 12–26 (–29) × 0.1–0.7 cm, green, margins serrulate; **Inf** (20–) 25–54 (–61) cm, erect, green, ‘spicate’, peduncle with 2–4 **Bra** much reduced upwards, lowest one (3.5–) 7–20 × 0.1–0.5 cm, fertile part ± (5–) 8–9.5 cm, very lax, with (1–) 2–6 remote floral nodes; floral **Bra** ±4–7 × 2 mm; **Ped** none; **Fl** geminate,

55–63 mm, upright at the base; **Tep** white, then pink, senescent red, forming a tube 30–66 × 2–5 mm, very slender below, greenish at the base grading to whitish or pink near the middle, curved downwards near the middle, mouth strongly oblique, lobes ovate, erect, 2–5 × 1.5–4 mm, apex rounded; **Fil** filiform, 3–9 (–16) mm, included, inserted 25–50 (–60) mm from the apex of the ovary, near the mouth of the tube; **Anth** linear, 4.5–8 (–9) mm; **Ov** fusiform, ±6–8 × 3–4 mm; **Sty** filiform, 35–60 (–73) mm, exerted at anthesis; **Sti** 3-lobed, exerted; **Fr** and **Se** unknown.

For long recorded from the type and paratype collection from Durango only, but Solano & Feria (2007), who studied the geographical distribution and niche modelling of the species, list 74 records from 25 localities in Aguascalientes and esp. in Chihuahua and Durango. A similarly strongly asymmetrical mouth of the tube is found only in *A. confertiflora*. Morphologically also similar to *A. alboaustralis* (see there). The record for Guerrero by Martínez Gordillo & al. (1997: 131) is probably a misidentification for *A. coetocapnia* (= *Polianthes geminiflora*) or *A. producta* (= *P. elongata*), the sole species of Sect. *Polianthes* in that state. *A. neonelsonii* is locally used as ornamental (Barba-Gonzalez & al. 2012: 125). — Upon transfer to *Agave*, *Polianthes nelsonii* needed a new name to avoid homonymy with the earlier *A. nelsonii* Trelease 1912.

**A. nickelsiae** Roland-Gosselin (Rev. Hort. (Paris) 67: 579–580, 1895). **Type**: [neo — icono]: Cact. Succ. J. (US) 32: 36, fig. 22 left, 1960. — **Lit**: Berger (1915: 90, as *A. ferdinandi-regis*); Alsemgeest & al. (2007a: figs. 4 & 6, as *A. victoriae-reginae* fa. *ferdinandi-regis*); González-Elizondo & al. (2011: 78–81); Martínez-Palacios & Eguiarte (2011); Thiede (2011: 151–152); Starr (2012: 154–156); all with ill. except Berger. **Distr**: Mexico (SE Coahuila: only near Saltillo), conglomerate ridges with sparse soil and frequent calcareous rock fragments at the surface, in desert scrub, 1500–1690 m. **I**: Brown (1945: 108, 109, as *A. ferdinandi-regis*); Heller (2006: 14, as *A. victoriae-reginae*; 145, as *A. ferdinandi-regis*); Richter (2011: 131); Roosbroeck (2012: 162);

Pilbeam (2013: 231–232, as *A. victoriae-reginae* fa.); Hochstätter (2015: IX: 55); Walker (2017: 165).

≡ *Agave victoriae-reginae* fa. *nickelsiae* (Roland-Gosselin) Trelease (1920); **incl.** *Agave victoriae-reginae* var. *laxior* A. Berger (1912); **incl.** *Agave ferdinandi-regis* A. Berger (1915) ≡ *Agave victoriae-reginae* fa. *ferdinandi-regis* (A. Berger) Alsemgeest & al. (2007) (*nom. inval.*, ICN Art. 41.5).

[lg] Acaulescent or with short invisible stem; **Ros** to 75 × 65 cm, subcompact or open, caespitose, rarely solitary, not surculose; **L** 170–280, oblong, narrowing gradually towards the apex, not incurved, 13–23 × 5.5–8.5 cm, white bands inconspicuous at the rounded tip, turning black towards the terminal spine, dorsally keeled in the upper part, ventrally concave except towards the base, there thickened and strongly convex to keeled, greyish-green to dull green, with white bands 1 (–2) mm broad on both faces and the margins, puberulent, margins horny, white, entire, continuous over the whole length, sometimes separating in the upper part, 3–5 mm wide; **marginal teeth** none; **terminal Sp** pyramidal to lanceolate, thick, 20–28 mm, broadly channelled above and roundly keeled below, nearly black, base broad, strongly decurrent along the leaf margins, usually with 3 adjacent teeth; **Inf** erect, 4.5–6.5 m, ‘spicate’, peduncle robust, with several chartaceous deltoid **Bra**, part-**Inf** usually with 3 flowers; **Ped** short, thick; **Fl** 58–65 mm; **Tep** cream-white or greenish-white, tinged purple at the apex, tube funnel-shaped, 3–5 × 8–9 mm, lobes extended, subequal, broadly linear, 18–22 × 4–6 mm, flat towards the apex, inner somewhat keeled; **Fil** 60–66 mm, inserted above the throat of the tube, with purple tinge; **Ov** thickly fusiform, 18–21 mm, neck short; **Fr** and **Se** unknown. — **Cytology**: 2n = 60, 120, 180 (Zonneveld 2003).

A recent study of the *A. victoriae-reginae* complex by González-Elizondo & al. (2011) re-established *A. nickelsiae*, better known as *A. ferdinandi-regis*, as a separate species and published the similar, completely new *A. pintilla*. Both have open to subcompact rosettes with greyish-green to pale green or bluish-green leaves. *A. nickelsiae* differs by having 170–280



**Fig. 42** *Agave nizardensis* (Etter & Kristen 3892: Mexico; Oaxaca, near Nizanda, 190 m). (Copyright: J. Etter & M. Kristen)

grey-green to dull green, puberulent, oblong leaves with a strong, decurrent terminal spine (vs. 60–180 green to bluish-grey-green, narrowly triangular, not puberulent leaves with a not or hardly decurrent terminal spine in *A. pintilla*). Almaraz-Abarca & al. (2013c) investigated the phenol composition of these taxa and found *A. pintilla* to be well-characterized chemically, while *A. nickelsiae* is very similar to *A. victoriae-reginae*.

For the history and introduction, see Thiede (2011). The species forms natural hybrids esp. with *A. asperrima* (see *A. × saltilloensis*) and also with *A. lechuguilla*. In contrast to *A. victoriae-reginae* which mainly propagates by seeds, *A. nickelsiae* propagates mainly clonally with rhizomes, and flowers only rarely (González-Elizondo & al. 2011). The reason may be that cross-pollination between individuals in the diploid *A. victoriae-reginae* is unimpeded, but limited between di-

tetra- and hexaploid individuals of *A. nickelsiae* (Thiede 2011).

The neotypification by Gentry (1982: 185, as *A. victoriae-reginae* fa. *nickelsii*) wrongly cites the figure and page number from the collective reprint of Breitung's series of papers (Breitung 1968) (p. 26, fig. 53 [correct is 55]), rather than from Breitung (1960: 36, fig. 22 left).

**A. nizardensis** Cutak (Cact. Succ. J. (US) 23(5): 143–145, ill., 1951). **Type:** Mexico, Oaxaca (Cutak 19 [MO]). — **Lit:** Breitung (1960: 182–183, with ill.); Gentry (1982: 75); Palma Cruz (1991: 123–125); Ullrich (1991i: with ill.); García-Mendoza (2003: with ill.). **Distr:** Mexico (Oaxaca: Nizanda); steep slope in crevices and pockets of limestone rocks in tropical deciduous forests, 120–350 m. **I:** MacDougall (1960); Heller (2006: 14, 111); Richter (2011: 61); Pilbeam (2013: 140). – Fig. 42.

[1b] Acaulescent; **Ros** open, small, unarmed, surculose; **L** 8–15, linear-lanceolate, ± patent and nearly horizontally spreading, sparsely fibrous, rather brittle or pliable, ± straight, convex below, flat above, tapering gradually from the broad base to the rounded tip, 20–35 × 1–1.5 (–2.5) cm, green with distinct pale midstripe, margins finely serrulate with irregular deltoid whitish denticles; **marginal teeth** none; **terminal Sp** conical, not pungent, small, 3–8 mm, reddish; **Inf** 1–2 m, 'spicate', peduncle slender, glaucous, with numerous ascending oblong-lanceolate **Bra** 4–10 cm long, fertile part to 25 cm, in the upper ¼, sparsely flowered, part **Inf** 5–10, more remote below and few densely arranged at the tip, with 2–4 flowers; **Ped** geminate, 6–10 mm, bracteolate; **Fl** 23–33 (–40) mm; **Tep** greenish-yellow to pale yellow, tube shortly funnel-shaped, 3–4 mm, lobes narrowly elliptic to lanceolate, ascending, involute, subequal, 15–16 mm, outer more apiculate and narrower (4 mm wide) than inner; **Fil** 35–40 mm, inserted at the mouth of the tube; **Anth** centrally affixed, 13–14 mm, grass-green to yellow; **Ov** cylindrical, 7–12 (–15) mm, neck short, not constricted; **Sty** longer than the filaments; **Sti** capitate, 3-lobate; **Fr** globose, 10–19 × 12–16 mm, dark brown, thin-walled, unripe green with glaucous hue; **Se**



5–6 × 2–4 mm, crescent-shaped. — **Cytology:**  $n = 60$  (Gómez-Pompa & al. 1971; Simpson & al. 2011).

According to Gentry (1982) a very distinct species without close relatives, only known from around the type locality Nizanda and few collections ±5 km N- to E-wards. It does not fit well into any section or group but was nonetheless placed in Sect. *Inermes* (as Group *Amolae*) (Gentry 1982). This prompted Ullrich (1991i) to erect the monotypic Sect. *Nizandensae* for the species, but this is not followed here.

The taxon was discovered by MacDougal in February 1939 (MacDougal 1971: 3) and later reintroduced by him (MacDougal 1960). Molecular data (Gil-Vega & al. 2007) place the species closest to *A. spicata* (as *A. yuccaefolia*) and close to other members of Sect. *Inermes* (as Group *Amolae*). Glass (1983) depicts a hybrid of cultivated origin with *A. striata* ssp. *falcata* (as *A. falcata*).

**A. nuusaviorum** García-Mendoza (Acta Bot. Mex. 91: 78–80, ills., 2010). **Type:** Mexico, Oaxaca (García-Mendoza & al. 9204 [MEXU, ENCB, IEB, MO, OAX, US]). — **Lit:** García-Mendoza (2011a: 39–43, with ills.). **Distr:** Mexico (NW Oaxaca).

**Incl.** *Agave nussaviorum* García-Mendoza (2010) (*nom. inval.*, ICN Art. 61.1).

García-Mendoza (2011a) corrected the original spelling of the epithet ‘nussaviorum’ as shown above, since it derives from “ñuu savi” (= land of clouds), the local name for the Mixteca Alta region and its inhabitants, according to the protologue.

**A. nuusaviorum** ssp. **deltoidea** García-Mendoza (Acta Bot. Mex. 91: 83–85, ills., 2010). **Type:** Mexico, Oaxaca (García-Mendoza & Martínez 6051 [MEXU, OAX]). — **Lit:** García-Mendoza (2011a: with ills.). **Distr:** Mexico (Oaxaca); igneous rocky sites, 2400–2600 m; flowers September to October. **I:** Pilbeam (2013: 142).

[2o × 1g?] Differs from ssp. *nuusaviorum*: **L** deltoid to broadly lanceolate, 20–40 × (8–) 14–20 (at the base) cm, margins entire, straight, horny or rarely dentate; **marginal teeth** (1–) 4–5 mm, from

bases (6–) 10–13 mm broad, retrorse, appressed to the margin or rarely free and recurved, greyish, 10–20 mm apart; **terminal Sp** (40–) 60–100 × 5–8 mm, greyish, dorsally channelled, decurrent for 10–14 cm or continuous with the leaf margins.

Occurring in the same region as ssp. *nuusaviorum*, but in a different habitat with different soil and at higher altitude. The intermediate, ‘racemose’ inflorescence of ssp. *deltoidea* suggests that it might have arisen as hybrid or allopolyploid between taxa of Subgen. *Agave* and Subgen. *Littaea*. If *A. nuusaviorum* should indeed be of allopolyploid intersubgeneric hybrid origin (see under ssp. *nuusaviorum*), ssp. *deltoidea* might have arisen independently and should then be recognized at species rank.

**A. nuusaviorum** ssp. **nuusaviorum** — **Lit:** García-Mendoza (2011a). **Distr:** Mexico (Oaxaca); flats or hill slopes on soils derived from calcareous rock or sandstone, in pine or pine-oak forests or dry scrub, 1700–2500 m; flowers late August to December. **I:** Pilbeam (2013: 141); Meer (2016b: 154).

[2o × 1g?] Acaulescent; **Ros** solitary, open to compact; **L** 25–40, lanceolate, oblong to ovate, erect to recurved, flexible, somewhat concave towards the middle and apex, (12–) 20–40 × (5–) 7–11 cm, greenish-yellow, glaucous towards the base, margins crenate, prominences conspicuous towards mid-leaf, 5–10 mm, variably curved; **marginal teeth** retrorse, antrorse or straight, (5–) 8–12 × (5–) 8–10 mm, chestnut-brown to greyish, 20–35 mm apart, narrower and smaller towards the base, with broad base covering the tip of the prominences, sometimes with intermittent denticles; **terminal Sp** sinuous to straight, channelled above, 20–30 (–40) × 3–5 (–8) mm, chestnut-brown to greyish, decurrent for 1–2 cm; **Inf** (1.5–) 3–5 (–6) m, ‘racemose’, peduncle greenish to purple, with triangular, reddish-brown **Bra** 12–17 cm long, fertile part  $\frac{1}{3}$ – $\frac{1}{6}$  of the inflorescence, congested, part-**Inf** 20–40 (–60), ‘umbellate’, with 6–12 flowers, 3–5 cm apart, stalk <3 cm; **Ped** 2–5 (–10) mm; **Fl** slightly campanulate, 45–55 (–70) mm; **Tep** yellowish with purple tinge, tube slightly sulcate, 7–10 (–13) × 7–10 (at the tip) mm, lobes triangular or oblong,



thickish, 15–25 × 2–5 mm, subequal, outer slightly larger, margins involute, apex cucullate, hard, inner keeled; **Fil** (25–) 35–45 (–55) mm, inserted 2–3 mm below the lobe bases, yellowish with purple tinge; **Anth** 20–25 × 2 mm, yellowish; **Ov** cylindrical, 23–30 (–35) × 4–6 mm, green, neck 2–3 (–5) mm; **Sty** 40–60 mm; **Sti** clavate, 3-lobate; **Fr** oblong to ovoid, 40–60 × 20–25 mm, rostrate, stipitate; **Se** crescent-shaped, flat, 5–6 × 4–5 mm, with narrow wings, black.

In the protologue the species is placed in Gentry's Group *Hiemiflorae* (now Sect. *Guatemalenses*) and compared with *A. potatorum* and *A. seemanniana*. It is most similar to the former from which it differs in its much more open rosettes with fewer, greenish-yellow leaves, and esp. in its 'racemose' inflorescences. The intermediate, 'racemose' inflorescence suggests that *A. nuusaviorum* might have arisen as hybrid between species of Subgen. *Agave* and Subgen. *Littaea*, and the protologue gives *A. potatorum* (Subgen. *Agave*) and *A. convallis* or *A. angustiarum* (Subgen. *Littaea*) as possible parents. The hybrid hypothesis is unlikely, however, as the taxon has a relatively broad distribution, and the putative parents are absent at many localities. *A. nuusaviorum* could be of allopolyploid origin and would then be tetraploid, which is consistent with the observation that it propagates by seed. The hybrid hypothesis was accepted by Etter & Kristen (1997+; accessed Oct. 2018), who list the taxon as *A. ×nuusaviorum*.

**A. oaxacana** (García-Mendoza & E. Solano) Thiede (Haseltonia 17: 95, 2012). **Type:** Mexico, Oaxaca (García-Mendoza & Solano 6970 [MEXU]). — **Lit:** García-Mendoza & Solano (2007: as *Polianthes*). **Distr:** Mexico (Oaxaca); mountain slopes, in pine-oak forests, 2390–2600 m; flowering September to October. **I:** Hochstätter (2015: II: 20, as *Polianthes*).

≡ *Polianthes oaxacana* García-Mendoza & E. Solano (2007).

[3b2] Herbaceous; corm cylindrical, (1.5–) 4–5 × 1–2 cm, with leaf scars, bulb ovoid, 5–8 × 2–3 cm, covered with dried fibrous leaf bases; **R** thickened, 8–12 cm, contractile; **L** 3–4, linear, semisucculent, curved, attenuate, tip acute,

slightly thickened, (40–) 60–70 × 1–1.5 (–2) cm, green, base whitish, margins hyaline, microscopically papillose, sometimes reddish; **Inf** erect, 'spicate', 1.4–1.8 m, peduncle 1.2–1.5 m, with 6–7 **Bra** similar to the leaves, fertile part 10–30 cm, with 3–7 laxly arranged flowering nodes; **Fl** sessile, geminate, 45–52 mm, zygomorphic, unscented; **Tep** tube ascending at the base, curved in the middle, broadly dilatated distally, throat campanulate, (30–) 38–42 × 10–14 mm, lobes ovate to orbicular, subequal, 5–7 × 4–6 mm, distally rose outside, yellowish inside, with violet tinge when dry, apex cucullate, acute to apiculate, slightly thickened, papillose; **St** included; **Fil** 10–12 mm, inserted at different heights near the throat, lower (15–) 20–21 mm above the ovary, upper (20–) 25–27 mm, rose; **Anth** linear, (7–) 9–10 mm, greenish-yellow, at anthesis appressed to the upper part of the throat; **Ov** (6–) 9–13 × 4–6 mm, slightly prolongating into the tepal tube; **Sty** filiform, 35–42 mm, whitish-yellow, included; **Sti** 3-lobed; **Fr** oblong to globose, 15–20 × 13–16 mm; **Se** deltoid to semicircular, flat, 4–6 × 3.5–4 mm.

Belonging to Ser. *Bravo* of Sect. *Polianthes* according to the protologue, and characterized by sessile flowers with a tube ascending at the base, curved in the middle, and campanulate above that is rose outside and yellowish inside. This makes *A. oaxacana* intermediate between the Ser. *Polianthes* and Ser. *Bravo*, but its stamen insertion and the colour of the unscented flowers argue for a placement in the latter.

**A. obscura** Schiede (Linnaea 5: 464, 1830). **Type** [neo]: Mexico, Veracruz (Gentry & al. 20417 [US, ASU, DES, MEXU]). — **Lit:** Berger (1915: 49–50, 51–53, as *A. obscura* & *A. densiflora*); Cházaro Basáñez (1981); Gentry (1982: 230, as *A. polyacantha* & var. *xalapensis*); Ullrich (1990j); Ullrich (1992f); Alsemgeest & al. (2006b); Jimeno-Sevilla (2010: 379–380); all with ill. except Berger. **Distr:** Mexico (W-C Tamaulipas, C San Luis Potosí, N & W-C Veracruz, N & C Oaxaca); in pine and oak forests or on volcanic lava flows ('malpais') with pines, rarely epiphytic, 1000–2440 m; flowers May to July. **I:** Curtis's Bot. Mag. 83: t. 5006, 1857, as

*A. densiflora*; Heller (2006: 112); Pilbeam (2013: 143); Hochstätter (2015: IX: 8).

**Incl.** *Agave densiflora* Hooker (1857)  $\equiv$  *Agave polyacantha* var. *densiflora* (Hooker) A. Terracciano (1885); **incl.** *Agave chloracantha* Salm-Dyck (1859); **incl.** *Agave uncinata* Jacobi (1865); **incl.** *Agave xalapensis* Roezler ex Jacobi (1865)  $\equiv$  *Agave polyacantha* var. *xalapensis* (Roezler ex Jacobi) Gentry (1982); **incl.** *Agave brauniana* Jacobi (1866)  $\equiv$  *Agave chloracantha* var. *brauniana* (Jacobi) A. Terracciano (1885); **incl.** *Agave muilmannii* Jacobi (1870); **incl.** *Agave micracantha* Baker (1872) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave flaccifolia* A. Berger (1915); **incl.** *Agave densiflora* var. *angustifolia* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave densiflora* var. *foliis striatis aureis* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave hookeri* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave myriacantha* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[1f] **Ros** openly spreading, medium-sized, single or caespitose; **L** lanceolate-acuminate to oblong short-acuminate or more ovate, straightly ascending to upcurving, tissue firm, finely fibrous, lamina narrowed above the base, broadest in the middle, usually flat, 35–65  $\times$  7–12 cm, green or yellow-green, passing into glaucous, margins generally straight, not horny except for the thinly decurrent terminal spine; **marginal teeth** deltoid, sometimes curved up or down, 2–6 mm, reddish to coffee-brown or dark brown, 5–12 mm apart, occasionally with small intermittent teeth; **terminal Sp** acicular, straight, small, rounded below and above, sometimes flatly grooved above, 5–35 mm, dark or reddish brown; **Inf** 2–3 m, ‘spicate’, stout, peduncle with long-caudate deltoid **Bra**, fertile part laxly or densely flowered, in the upper  $\frac{1}{3}$ – $\frac{1}{2}$ , rarely bulbiferous; **Ped** stout, 2–3 mm; **Fl** 46–51 mm, mostly geminate; **Tep** reddish, tube funnel-shaped, scarcely grooved, smooth, glandular-thickened at the filament strands and between, 7–9  $\times$  9 mm, lobes unequal, lanceolate, ascending to outcurved, 19–23  $\times$  5 mm, **OTep** rounded on the back, **ITep** usually narrower, with large keel, keel broad at the base,

long tapering to the tip; **Fil** 50–70 mm, reddish, inserted on the rim of the tube; **Anth** nearly centric, 19–21 mm; **Ov** cylindrical, 17–20  $\times$  7 mm, green, neck short, not constricted; **Fr** obovoid, 18–24  $\times$  10 mm, constricted at the base, obtuse at the tip, dark brown; **Se** crescent-shaped, 3.5–4  $\times$  2–3 mm, dull black, hilar notch on the rounded end, marginal wing low. — **Cytology**: 2n = 60 (Gómez-Pompa & al. 1971, Simpson & al. 2011, both as *A. xalapensis*).

Schiede (1830) collected his reddish-flowered *A. obscura* on the malpais (lava flow) W of Xalapa between La Joya and Las Vigas in W-C Veracruz, which information is repeated by Cházaro Basáñez (1981), Ullrich (1990j), and Ullrich (1992f). Trelease (1920: 137), Breitung (1959: 146) and Gentry (1982: 161) misapplied the name to a plant occurring  $\pm$ 30 km SW from that region between El Limón (in W-C Veracruz) and Zacatepec (in E-C Puebla). Gentry (1982: 230) used the name *A. polyacantha* var. *xalapensis* for Schiede’s plant from between La Joya and Las Vigas, but *A. xalapensis* actually represents a later synonym of Schiede’s *A. obscura*. The plants from between El Limón and Zacatepec are closest to *A. horrida* (Cházaro Basáñez 1981) and, since they were as yet without name, were published as *A. horrida* ssp. *perotensis* by Ullrich (see under that name).

In the concept applied here (following Ullrich (1990j) and Ullrich (1992f)), *A. obscura* encompasses *A. polyacantha* and its var. *xalapensis sensu* Gentry (1982). Ullrich (1990j: 81) designated the Gentry collection from Las Vigas cited above as neotype for *A. obscura*. The neotype designated by Gentry (1982: 161) for his “*A. obscura*” is in conflict with the protologue of the species, as shown above, and was chosen by Ullrich (1990j) as holotype for his *A. horrida* ssp. *perotensis*. *A. obscura* differs from other species in Sect. *Micracanthae* (as Group *Polycephalae*) in that its leaves are firmly fleshy and not soft, and that its tepal tube and ovary are not markedly furrowed, and its ovary is not 3-angled (see key in Cházaro Basáñez & Vázquez-García (2013)).

*A. polyacantha* Haworth 1821, published with black spines and unknown inflorescence, was compared with the Caribbean *A. vivipara* of Subgen. *Agave*, cannot be applied with certainty and

**Fig. 43** *Agave ocahui* var. *ocahui* (Etter & Kristen 660: Mexico; Sonora, near Matape, 800 m). (Copyright: J. Etter & M. Kristen)



the name should be abandoned (Ullrich 1990j). For *A. engelmannii*, placed in the synonymy of *A. polyacantha* by Gentry (1982: 228), see under *A. ×engelmannii*.

**A. ocahui** Gentry (US Dept. Agric. Handb. 399: 72–76, ills., 1972). **Type:** Mexico, Sonora (Gentry & Arguelles 16637 [US [syn], ARIZ, DES, MEXU, MICH]). — **Lit:** Gentry (1982: 75–79, with ills.). **Distr:** Mexico (Sonora).

Related to other Sonoran species of Sect. *Inermes* (as Group *Amolae*) (*A. vilmoriniana*, *A. chrysoglossa*), based on the smooth narrow leaves with unarmed margins, the prolifically flowering inflorescences and the small, slender, yellow flowers with shallow tubes and tepals clasping the filaments (Gentry 1982: 78). — The “holotype” at US consists of 2 sheets, which are not cross-labelled, and thus represent syntypes.

**A. ocahui** var. **longifolia** Gentry (Agaves Cont. North Amer., 78, ills. (p. 79–80), 1982). **Type:** Mexico, Sonora (Gentry 11610 [US, ARIZ, DES, MEXU]). — **Lit:** Etter & Kristen (2001: with ills.); Starr (2012: 158). **Distr:** Mexico (E-C Sonora); scattered in the mountain region in woodland or on volcanic or limestone rocks, 460–1370 m; flowering February. **I:** Pilbeam (2013: 145); Hochstätter (2015: VII: 24, as ssp.).

≡ *Agave ocahui* ssp. *longifolia* (Gentry) Hochstätter (2015).

[1b] Differs from var. *ocahui*: Stem thick and round; **L** linear-lanceolate, straightly ascending or recurving, sometimes falcate, mature **L** 60–80 (–90) × 2–3 (near the base) cm.

These larger, more robust and longer-leaved plants maintain these features even when cultivated together with the shorter-leaved var. *ocahui*. Varietal status is appropriate since they appear not to be geographically isolated from var. *ocahui* (Gentry 1982: 78–79).

**A. ocahui** var. **ocahui** — **Lit:** Gentry (1982: 75–78); Etter & Kristen (2001); Starr (2012: 157–161); all with ills. **Distr:** Mexico (NE Sonora); cliffs and outcrops of volcanic rocks, 460–1370 m; flowering April to June. **I:** Irish & Irish (2000: t. 28); Heller (2006: 17, 113); Pilbeam (2013: 144); Hochstätter (2015: VIII: 24); Moore (2016: 71). – Fig. 43.

[1b] Stems short; **Ros** dense, green, *Yucca*-like, 0.3–0.6 (–0.9 in cultivation) × 0.3–0.6 (–0.9 in cultivation) m, solitary; **L** numerous, linear-lanceolate, erect to ascending, some older leaves declined or falcate, mostly stiff, widest at the base, flat above, surface smooth, minutely and densely punctate in fine lines, 25–50 × 1.5–2.5 cm, green, margins straight, lined with a narrow reddish-brown firm border detachable in dry leaves; **marginal teeth** none; **terminal Sp** weak, rather brittle, 10–20 mm, pruinose-grey over brown; **Inf** slender, 3–4.5 m, ‘spicate’, peduncle with numerous narrow chartaceous **Bra**, densely flowered from 1–1.5 m

above the base, part-**Inf** with geminate flowers; **Fl** 30–38 mm; **Ped** short; **Tep** yellow, tube broadly funnel-shaped, 2–4 mm, lobes oblong, subequal, tips abruptly acute, outcurving, clasping the filaments after anthesis, 14–16 × 4.5 mm; **Fil** inserted at the tepal base, 35–40 mm, pale yellow; **Anth** centric, 10–15 mm, yellow; **Ov** 15–20 mm, neck constricted; **Sty** thick, clearly longer than the tepals; **Sti** capitate; **Fr** small, ovoid, 12–15 × 7–8 mm, apiculate, tardily dehiscent, yellowish-tan to reddish; **Se** small, crescent-shaped, rather thick, 2.5 × 1.5–1.7 mm.

Young plants can be confused with *A. × arizonica* (with shorter leaves), *A. pelona* (with leaves 2× broader and turning purplish in sun, and with white margins and a much longer terminal spine), young *A. chrysoglossa* (with fewer, thicker and longer leaves), and also with young plants traded as “*A. × romani*” (see there) (with broader, more guttered and glaucous green leaves). ‘Blue Glow’ is a hybrid with *A. attenuata* (Starr 2012: 56–58, ills.).

**A. occidentalis** (Art. Castro & Aarón Rodríguez) Thiede & Gideon F. Smith (Bradleya 37: 262, 2019). **Type:** Mexico, Jalisco (*Rodríguez & al.* 5924 [IBUG, CIIDIR, IEB, MEXU, SLPM]). — **Lit:** Castro-Castro & al. (2017: with ills., as *Manfreda*). **Distr:** Mexico (S Nayarit, W Jalisco); ecotone between oak and pine forests, subdeciduous tropical forests, and savannoid vegetation, 700–1000 m; flowers in August.

≡ *Manfreda occidentalis* Art. Castro & Aarón Rodríguez (2017).

[3a3] Plants herbaceous; corm (2.9–) 4.5–5.6 (–13.5) × 1.4–2.4 (–5) cm, oblong-ovoid, bulb 2–2.6 × 1.5–1.9 cm, oblong-ovoid, completely covered with dried leaf bases ±3–6 cm long; **R** fleshy, cuneiform, 7–17 cm long, with filiform ramifications, contractile; **L** drought-deciduous (?), 4–7 (–10), erect, lanceolate to oblong-elliptic, widest in the middle and tapering at both ends, thin to leathery, canaliculate, papillate on the veins on both faces, apex acute, not pungent, formed by the involute lamina, 48–83 × 1.8–4.5 cm, dull green, margins with a hyaline band, finely denticulate-erose under magnification; **Inf** (60–) 90–190 (–220) cm, erect, greenish, ‘spicate’, peduncle with 6–10 **Bra**, 2 lower ones larger,

similar to vegetative leaves, fertile **Inf** part 7–28 cm, dense, with 15–30 flowers; floral **Bra** triangular to subulate, 7–18 × 2–6 mm, truncate, soon drying, frequently deciduous; **Fl** 18–25 mm, solitary, sessile (rarely to 0.2–0.5 mm pedicellate), ascending to diffuse; **Tep** yellowish with light purple stripes, perianth as a whole funnel-shaped, tube 3–5 × 2–4 mm, straight, lobes lanceolate, reflexed, 10–15 × 2–4 mm (measurements corrected, given too small in the protologue), tip papillate; **Fil** 14–25 mm, subulate, inserted 3–7 mm above the ovary apex, yellow; **Anth** 9–11 mm, green and red striate, helicoidal after dehiscence; **Ov** oblong-ovoid, 5–7 × 3–4 mm, greenish, protruding 1–2 mm into the tube, slightly constricted above; **Sty** filiform, 21–35 mm, yellowish, exerted 18–30 mm from the tube; **Sti** 3-lobed, papillose, clavate; **Fr** globose to ovoid, trigonous, 15–20 × 7–13 mm, apiculate, with persisting tepals; **Se** crescent-shaped to ovate, 4–6 × 3–4 mm, shiny.

According to the protologue (as *Manfreda*), the species belongs to Ser. *Guttatae* (as *Manfreda guttata*-group) and is morphologically most similar to *A. planifolia*, but differing in its oblong-ovoid corm (vs. globose to ovate), canaliculate leaves papillate on the veins on both faces (vs. flat and not papillate), shorter, funnel-shaped, yellowish flowers with light purple stripes, a shorter tube and a shorter style (vs. salver-shaped and yellow flowers).

**A. offoyana** De Smet *ex* Jacobi (Hamburg. Gart.- & Blumenzeit. 21: 214–215, 1865). **Type:** not typified. — **Lit:** Trelease (1913: 35–36, tt. 58–62); Berger (1915: 209–211, with ill.); León (1946: 316–317, with ill.); Álvarez de Zayas (1985: 3, 9); all as *A. legrelliana*; Álvarez de Zayas (1995: 41); Acevedo-Rodríguez & Strong (2012: 86, as *A. ehrenbergii*). **Distr:** W & C Cuba (Havana, Mayabeque, Matanzas, Camaguey); rocky slopes, xerophytic scrub and coastal thickets, on limestone and serpentine; flowers February to March. **I:** Richter (2010: 40); Guillot Ortiz & Meer (2011: 11); Kattermann (2012: 7); all as *A. legrelliana*; Pilbeam (2013: 122, as *A. legrelliana*; 146); Hochstätter (2015: VII: 95, as *A. ehrenbergii*); Biletzke (2016: 26, 27, as *A. legrelliana*).



**Incl.** *Agave americana* A. Richard in Sagra (1850) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave melanacantha* Lemaire ex Jacobi (1865); **incl.** *Agave laurentiana* Jacobi (1866); **incl.** *Agave legrelliana* Jacobi (1866); **incl.** *Agave coccinea* Lachaume (1876) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave legrelliana* var. *breviflora* Trelease (1913).

[2p] Acaulescent; **Ros** solitary; **L** variably lanceolate, ascending, upper part often recurved in older leaves, thin, rather weak, subacuminate, concave, sometimes conduplicate, 100–160 × 20–30 cm, dark green; **marginal teeth** usually down-curved below, narrowly triangular, acuminate tapered, 2–6 mm, variously brown, 10–15 (–20) mm apart, or from abrupt green prominences whose tops harden in a crescent-shaped manner, intervening margin often concave; **terminal Sp** conically subulate, a little curved, openly or flatly grooved below the middle or involute, smooth, 15–20 × 4–5 mm, brown, dull, scarcely decurrent; **Inf** 6–8 m, paniculate, amply ovoid throughout, part-**Inf** on ascending-recurved branches, not known to be bulbiferous; **Ped** 20–30 mm; **Fl** (55–) 70–80 mm; **Tep** deep orange, tube ±15 mm, lobes 30 × 7 mm; **Fil** 35–60 mm, inserted nearly in the throat of the tube; **Ov** oblong, somewhat contracted at the base and at the top, to 40–45 mm; **Fr** rather narrowly oblong, 40–50 × 15–20 mm, slightly beaked, stipitate; **Se** 7 × 4 mm.

This species and subsequently *A. legrelliana* were both published on the base of exhibited plants seen by Jacobi, having been imported by Mme. Legrelle d'Hanis, Antwerp (Belgium), from “Havana” and “Matanzas” on Cuba, respectively. Material of *A. offoyana* (Cuba, La Habana, Hanis s.n., MO 2056689, not digitized) is apparently preserved. Later authors applied either the former or the latter name to the variable orange-flowered species common on the N coast of Cuba from E of Havana to around Matanzas (Trelease 1913, Berger 1915, Álvarez de Zayas 1985). Trelease (1913) hesitatingly treated both names as conspecific, and Álvarez de Zayas (1995) finally placed *A. legrelliana* in the synonymy of the older *A. offoyana*.

Govaerts (2014+: accessed April 2014) applied the name *A. ehrenbergii* Jacobi (1865) to

this species, and he is followed by some authors (e.g. Acevedo-Rodríguez & Strong (2012)), but this name is a synonym of *A. mitis* (see there and Thiede (2016: 214)). *A. melanacantha* was based on a plant of unknown origin exhibited by de Smet together with *A. offoyana*. It was described as very similar to the latter, and is placed in its synonymy here. The same applies to *A. laurentiana*, which was placed in the synonymy of *A. legrelliana* by Berger (1915: 211). — The taxon was first classified as “Endangered” in the IUCN categories (Berzaín & al. 2005: 17, as *A. legrelliana*), but later classified as of “Least Concern” (González-Torres & al. 2016: 47). Phytotoxic steroidal saponins from leaves and flowers of *A. offoyana* were studied by Pérez & al. (2013) and Pérez & al. (2014).

**A. ornithobroma** Gentry (Agaves Cont. North Amer., 117–119, ills., 1982). **Type:** Mexico, Sinaloa (*Gentry* 18358 [US †; syn: ARIZ, CAS, DES, MEXU, MICH]). — **Lit:** McVaugh (1989: 147); García-Mendoza (2003); Vázquez-García & al. (2007b: 63, t. T); González-Elizondo & al. (2009: 107–108, with ills.). **Distr:** Mexico (S Sinaloa, Nayarit, N Jalisco); volcanic rocks in tropical deciduous forests and ecotones with oak forests, 60–1920 m; flowers November to December. **I:** Etter & Kristen (2011: 57); Richter (2011: 28); Etter & Kristen (2012: 93); Pilbeam (2013: 147); Hochstätter (2015: VIII: 51).

[1d] Stems short; **Ros** asymmetrical, to 1 × 1.5 m, solitary to caespitose, suckering sparingly at maturity; **L** few, narrowly linear, straight-ascending to frequently curving to one side, or falcate, shortly acuminate, convex below from the base to the tip, convex above from the base to the middle of the lamina, smooth, 60–75 × 0.5–0.8 cm, light green to reddish, margins filiferous, reddish to white; **terminal Sp** subulate, weak, fraying, 6–10 mm; **Inf** 2.5–4 m, ‘spicate’, slender, peduncle narrowly bracteate, green to red, fertile part laxly flowered, in the upper ½ of the inflorescence, part-**Inf** with geminate flowers; **Ped** 5–8 mm, thickened at fruiting time; **Fl** slender, 30–48 mm, oriented (nearly) horizontally to slightly ascending; **Tep** green with reddish or purplish flush, tube narrowly funnel-shaped,



triquetrous, finely grooved, 9–13 × 5–6 mm, lobes ± equal, linear-lanceolate, obtuse, recurving, rather thin, 10–17 × 4–5 mm, inner with low rounded keel; **Fil** inserted with the tepal lobes on the rim of the tube, 20–25 mm, red to purplish; **Anth** slender, somewhat excentric, 12–20 mm, green to yellow; **Ov** small, fusiform-angulate, 12–17 mm, neck slightly constricted; **Sty** reddish, longer than the filaments; **Fr** obovoid, small, 7–8 × 6–7 mm, with short and broad beak, dark brown, slightly ascending; **Se** unknown. — **Cytology**: 2n = 90 (Pinkava & Baker 1985).

Closely related to *A. geminiflora*, but separable by its caespitose habit, small, few-leaved rosettes and slender inflorescences with small flowers. The epithet (Greek, = bird's food) alludes to the observation that small parrots eat many of the flowers and buds (Gentry 1982; see also the note under *A. geminiflora*). The triploid *A. ornithobroma* is a putative natural hybrid involving *A. geminiflora* (Pinkava & Baker 1985). According to Jankalski (2008 in Agavaceae@yahoo.com), the second putative parent is *A. rzedowskiana*, which contributes the surculose habit, smaller rosettes, more slender inflorescences and smaller flowers to the hybrid. If this parentage is correct, *A. rzedowskiana*, at present only known from Sinaloa and Jalisco, should also occur in Nayarit (Jankalski l.c.). Vázquez-García & al. (2007b: t. T3) show an infructescence with ripe fruits, albeit fruit formation in sterile triploids should not be possible. Possibly, the species also includes fertile allopolyploids; this is also suggested by its occurrence at localities from where the putative parental species were not reported. Vázquez-García & al. (2007b: 63) and Hernández-Vera & al. (2007a: 505) provide a new record for Jalisco.

The holotype, cited for US in the protologue, appears to be missing, leaving 5 syntypes as cited above. Most probably, Gentry intended the most complete specimen (ARIZ 265553) bearing his stamp "Gentry Herbarium" and his handwriting to be sent to US as holotype.

**A. oroensis** Gentry (Agaves Cont. North Amer., 294–296, ill., 1982). **Type**: Mexico, Zacatecas (Gentry & Engard 23592 [US [3 syn], ARIZ,

ASU, DES, MEXU]). — **Distr**: Mexico (N Zacatecas); cultivated only, silty soil derived from limestone, 1830 m; flowers in August. **I**: Pilbeam (2013: 148); Hochstätter (2015: VII: 19).

[2a] Acaulescent; **Ros** low, openly spreading, to 1 × 2 m, solitary or suckering; **L** linear-lanceolate, straight to recurving, narrow and thickly convex below towards the base, long-acuminate, guttering upwards, slightly asperous, 80–100 × 8–10 cm, green, margins straight to repand; **marginal teeth** mostly straight, 3–6 mm (middle of the lamina), greyish, mostly 20–30 mm apart, smaller and more closely spaced towards the leaf base; **terminal Sp** acicular, narrowly grooved above for ½ of the length, 25–30 mm, greyish, finely decurrent to the uppermost teeth; **Inf** 5–6 m, paniculate, peduncle slender, with small **Bra**, fertile part in the upper ½, part-**Inf** 12–16, laxly flowered, spreading, extending 50 cm or more; **Ped** slender, to 10 mm, with tongue-shaped **Bra**; **Fl** very slender, 70–75 mm; **Tep** yellow, pink in bud, tube urceolate (but funnel-shaped in the drawing), grooved, walls thickened at the filament insertions, thin above, 16–18 mm, lobes linear, scarcely involute, connivent or adherent to one another, rather thin, unequal, 20–21 × 4.5–5 mm, outer bluntly apiculate with reddish rugose cap, inner with a low keel, without ribs within; **Fil** slender, flattened, long-tapering, inserted at slightly different levels 10 and 11 mm above the tube base, yellow; **Anth** slender, excentric, curved or sinuous, 29–30 mm, yellow; **Ov** fusiform, 34–37 mm, greenish, neck grooved; **Sty** much thicker than the filaments, soon exerted beyond the anthers; **Sti** capitate, 3-lobed; **Fr** and **Se** unknown.

A local cultivar in the mining region around Concepción del Oro, unique in Sect. *Agave* (as Group), and well-characterized by its thick, narrow, green leaves and esp. the broad, open, pink-budded panicles with flowers with a tube constricted at the mouth (Gentry 1982: 294). — Gentry's "holotype" at US consists of 3 sheets which are not cross-labelled and thus represent syntypes.

**A. ovatifolia** G. Starr & Villarreal (Sida 20(2): 495–496, ill., 2002). **Type**: Mexico, Nuevo León

(Villarreal & al. 9180 [MEXU, ANSM, ENCB, IBUG, IEB, NY, TEX]). — **Lit:** Starr (2004); Etter & Kristen (2009b); Starr (2012: 162–169, 322–323); all with ills. **Distr:** Mexico (N Nuevo León: Sierra de Lampazos); rocky slopes and mesetas, in calcareous soil, in oak forests, grasslands with *A. lechuguilla* or thorn scrub, 900–1500 m. **I:** Etter & Kristen (2008: 80–81 & title page); Alsemgeest & Roosbroeck (2010: 276); Richter (2011: 57); Pilbeam (2013: 149–152); Greulich (2014b: 62–64); Hochstätter (2015: II: 16); Moore (2016: 221, 230–231).

**Incl.** *Agave noah* Nickels (1894) (*nomen rejiciendum*, Art. 56.1).

[21] **Ros** semiglobular, somewhat compact, 0.6–0.9 (–1.2) × 0.8–1.2 (–1.8) m, solitary (in cultivation rarely sparingly offsetting); **L** 40–50, in 8–10 spiral rows, broadly ovate to elliptic, slightly concave to nearly flat, sometimes with 1–2 dorsal ribs, broadened at the base, apex acute, with brown border, 35–60 × 20–27 (in the middle) cm, silver-blue to greyish sky-blue, margins straight; **marginal teeth** 15–19 per side, slightly down-curved, 4–12 mm or more, evenly spaced and 20–25 mm apart, more closely spaced at the base; **terminal Sp** ±20 mm, decurrent; **Inf** 3.5–4 m, paniculate, peduncle slightly sigmoid, with elliptic-triangular **Bra** 20–25 cm long at the base, most bracts upright, fertile part in the upper ½, elliptic to broadly ovoid, part-**Inf** 13–16, nearly straight to slightly ascending, 30–50 cm, each with 5–6 dense ‘umbels’; **Ped** 4–8 mm; **Fl** 67–74 mm; **Tep** greenish-yellow, tube 15–20 × 15 (in the middle) mm, lobes broadly triangular, 15–17 × 5–7 (at the base) mm, outer with glandular apex; **Fil** 50–60 mm, inserted at the lobe bases, greenish-yellow; **Ov** cylindrical, 30–35 mm, constricted; **Sty** 80–90 mm; **Fr** cylindrical, not beaked, 50–60 × 15–20 mm, coffee-brown; **Se** drop-shaped, 5–6 × 3–4 mm, black, shiny.

Within Sect. *Parryanae* (as Group) closest to *A. havardiana* and *A. parrasana* according to the protologue. It differs from the former in its relatively shorter and broader, elliptic to ovate-elliptic, more bluish leaves with obtuse tip and shorter terminal spine, and its shorter flowers with shorter tepal lobes, and from the latter in its larger and much broader leaves with obtuse tip and

shorter terminal spine, and its larger flowers. Starr (2012: 163, fig. p. 167) mentions 2 further populations from near Monterrey possibly belonging here. Plants introduced as *A. noah* by Anna B. Nickels about 1894 were considered conspecific in the protologue. The name was proposed for rejection by Villarreal & al. (2003), but the nomenclatural committee argued that the name is invalid (Brummitt 2005: 533); in a later vote, the description is regarded as adequate (Wilson 2017a: 189), and the original proposal to reject the name must now be reconsidered (Wilson 2017b: 478).

‘Flipper’ (Starr 2012: 165, 169) and ‘Orca’ (Starr 2014: 224) are variegated cultivars, and ‘Frosty Blue’ (produced by San Marcos Growers) has densely wax-powdery leaves with an almost turquoise hue.

**A. pablocarrilloi** A. Vázquez & al. (Syst. Bot. 38(2): 328–329, ills., 2013). **Type:** Mexico, Colima (*Vázquez-García & al.* 9090 [IBUG, MEXU, MO]). — **Distr:** Mexico (C Colima); limestone outcrops, in succulent woodland, thorn and tropical dry forests, 300–610 m; flowers February to April. **I:** Gentry (1982: 511, figs. 18.4, 18.5); Ullrich (1991b: identification uncertain); Newton (1999); García-Mendoza (2003); Newton (2004); Richter (2011: 82); Pilbeam (2013: 104); Guillot Ortiz & Meer (2016c: 28; fig. 2, 29: figs. 3–5); Moore (2016: 268, 269); all as *A. gypsophila*; Hochstätter (2015: I: 22).

[2n] **Ros** 0.8 × 1.8 m, sparsely to densely surculose; **L** 10–15, narrowly lanceolate, undulate, firm, rigid, wider at the base and above mid-leaf, concave at the lower third, occasionally flat at the distal half, with a semi-amplexicaul sheath, rough, 50–70 (–100) × 7–8.5 cm, bluish-glaucous-grey on both faces, not evidently cross-zoned, margin distinctly crenate in the middle; **marginal teeth** firm, flattened, frequently curved, 2–3.5 mm, dark brown, from broad deltoid bases 2–3 mm wide, usually ascending, intervening margin curved with denticles more frequent at mid-leaf, teeth 9–25 mm apart at mid-leaf, 5–10 mm towards the base, on distinct prominences 4–5 × 5–6 mm; **terminal Sp** short and conical, firm, 4–5 mm, dark brown, not decurrent; **Inf** small, 2.3–4 m, paniculate, peduncle with triangular **Bra** to 12 ×

5 cm at the base, fertile part open, oblong, part-**Inf** few, 8–15 (–19), in the upper ½, with ±50 flowers; **Fl** 28–36 mm; **Tep** orange-yellow, tube somewhat funnel-shaped, 4–5 × 6–8 mm, lobes triangular, fleshy, 10–13 × 3 mm, galeate; **Fil** firm, 7–24 mm, inserted 1 mm above the tube base, orange; **Ov** 14–18 × 3.5–4 mm, neck constricted; **Sty** shorter than the tepals; **Sti** capitate; **Fr** oblongoid, 21–28 × 13–16 mm, stipitate, apiculate; **Se** subtriangular or semicircular, thin, 4–6 × 3–4 mm, black.

The recent study of the *A. gypsophila* complex by Vázquez-García & al. (2013) led to a narrower circumscription of *A. gypsophila* and the description of this and 3 more new species (*A. abisaii*, *A. andreae*, *A. kristenii*). The 3 specimens cited by Gentry (1982: 519) as well as his figs. 18.4 and 18.5 on p. 511, as well as 4 specimens cited from Colima by Vázquez-García & al. (2007b: 55) belong here. *A. pablocarrilloi* differs from *A. gypsophila* in its suckering habit, rough, bluish-glaucous-greyish leaves that are flat in the lower half, closely set firm teeth, smaller panicles with only 8–15 (–19) branches, and occurs at lower elevations. — ‘Ivory Curls’ (ills.: Moore (2016: 14, 268, as *A. gypsophila*)) is a variegated cultivar with yellowish leaf margins.

**A. pachycentra** Trelease (Trans. Acad. Sci. St. Louis 23(3): 135, 1915). **Type:** Guatemala, Dept. Progreso (*Trelease* 2 [ILL]). — **Lit:** Trelease (1915: 140–141, ills., as *A. opacidens* & *A. tenuispina*); Berger (1915: 200–201, as *A. eichlamii* & *A. weingartii*); Standley & Steyermark (1952: 112–115, as *A. hurteri*, *A. opacidens* & *A. tenuispina*); Gentry (1982: 486–488, with ills.); Lott & García-Mendoza (1994: online version with ills.); Véliz Pérez (2013: 240, 242, with ill.). **Distr:** S Mexico (Chiapas), Guatemala, El Salvador, Honduras; volcanic rocky outcrops in tropical deciduous or thorn forests, thorn scrub or grasslands, 220–975 (–1675) m; flowers November to January and March. **I:** Richter (2011: 50, 84); Pilbeam (2013: 153); Hochstätter (2015: VI: 11).

**Incl.** *Agave eichlamii* A. Berger (1915); **incl.** *Agave eichlamii* var. *interjecta* A. Berger (1915); **incl.** *Agave opacidens* Trelease (1915); **incl.** *Agave tenuispina* Trelease (1915); **incl.** *Agave weingartii* A. Berger (1915).

[2o] Acaulescent; **Ros** rather open, to 1 × 1.5–2 m, solitary, rarely surculose; **L** variable, broadly lanceolate, rarely linear-lanceolate, thickly fleshy and gradually narrowed towards the base, acuminate, flat to guttered, rougher or scabrous below, asperous above, (40–) 70–100 × (8–) 12–17 (–20) cm, glaucous-white to yellowish or pale green, margins repand to straight, concave between the teeth; **marginal teeth** variable, 3–6 (–10) mm (middle of the lamina), brown, (10–) 15–40 mm apart, tips straight or variously curved above low broad bases, brown, with intermittent teeth; **terminal Sp** finely subulate to nearly conical from a broad base, broadly to narrowly grooved above, keeled to rounded below, scabrous, 35–50 (–70) mm, long-decurrent to the upper teeth; **Inf** 2–6 m, paniculate, peduncle usually crooked, young white-pruinose, fertile part open, rather irregular, part-**Inf** (6–) 20–30, small, laxly arranged, on stalks 20–30 cm long; **Ped** slender, 5–12 mm; **Fl** (35–) 40–55 (–62) mm; **Tep** yellow, tube funnel-shaped to urceolate, knobby, grooved, 5–11 mm, lobes linear-lanceolate, erect to ascending, incurved, involute, subequal, 13–20 × 4–5 mm, outer closely overlapping the inner at the base, frequently reddish at the apex, inner with narrow thick keel; **Fil** slender, (30–) 40–50 mm, inserted at mid-tube or just above, sometimes on 2 levels; **Anth** centric, regular, straight, 17–22 mm; **Ov** thick-fusiform to slender-cylindrical, (12–) 25–35 mm, green, neck constricted, grooved, short; **Fr** oblong to ovoid, apex rounded, 35–40 × 15–17 mm, nearly beakless, stipitate; **Se** crescent- to drop-shaped, 5–6 × 3–4.5 mm, very finely punctate, marginal wing raised to ± the thickness of the seed.

Highly variable in leaf characters, but generally recognizable by its rather open, medium-sized to rather large rosettes with pale green to nearly white, broadly lanceolate leaves and crooked, laxly flowered, open panicles with small ‘umbels’ (Gentry 1982: 487). *A. hurteri* has similar lax inflorescences, but with compact ‘umbels’, and larger flowers, longer marginal teeth, and larger rosettes (Lott & García-Mendoza 1994). Standley & Steyermark (1952) treated *A. pachycentra* as synonym of *A. hurteri*. — The chromosome count (2n = 210) in Granick (1944: 286) based on a

**Fig. 44** *Agave palmeri*  
(Etter & Kristen 4061:  
Mexico; Sonora, near La  
Huachinera, 1220 m).  
(Copyright: J. Etter &  
M. Kristen)



plant from Texas of uncertain identity is highly doubtful and disregarded here.

‘Chunky Monkey’ and ‘Flying Saucer’ are two nearly identical-looking cultivars (Starr 2014: 220, with ills.).

**A. palmeri** Engelm (Trans. Acad. Sci. St. Louis 3: 319–320, 1875). **Type** [syn]: USA, Arizona (*Rothrock* 496 [F 304130, US 125477]). — **Lit**: Gentry (1972: 101–105, with ills.); Gentry (1982: 443–447, with ills.); Turner & al. (1995: 57–59); Hodgson (1999a: 7–8); Reveal & Hodgson (2002); Klopper & al. (2010: 62–65, with ills.); Starr (2012: 170–172, 324, with ills.); Parker (2017: 256, 258–259, with ills.). **Dist**: USA (SE Arizona, SW New Mexico), Mexico (N Sonora, NW Chihuahua); sandy to gravelly places on limestone in oak woodlands and grama grasslands, 900–2000 m; flowers June to September. **I**: Irish & Irish (2000: t. 29); Heller (2006: 114); Richter (2011: 79, 101, 106); Pilbeam (2013: 154); Hochstätter (2015: IV: 4, 11). – Fig. 44.

[2h] Acaulescent; **Ros** rather open, 0.4–1.3 × 0.6–1.3 m, solitary, rarely suckering with age; **L** numerous, linear-lanceolate to lanceolate, ascending to spreading, rather rigid, thick at the base, widest near the middle, acuminate to long-acuminate, concave towards the apex above, convex towards the base below, somewhat guttered, 35–92 × 3.5–19 cm, pale to glaucous-green or

pale to deep green, sometimes tinged reddish, not cross-zoned, margins almost straight or somewhat crenate, with or without small tubercle-like bases to the teeth; **marginal teeth** variously curved, rather regular, slender, firmly attached, 3–6 mm, (5–) 10–20 mm apart, dark or reddish-brown to pruinose-grey, sometimes with 4–6 smaller intermittent teeth, mostly along the distal  $\frac{2}{3}$  of the leaves; **terminal Sp** acicular, strong, shortly and openly grooved above the base, 30–60 mm, chestnut-brown, reddish-brown or brown to aging grey, decurrent to the 1. or 2. teeth; **Inf** (1.7–) 4–6.5 (–7.2) m, paniculate, peduncle glaucous-green or purple-maroon, with persistent triangular **Bra** 1–5 cm long, fertile part broad, open, part-**Inf** slightly ascending, (8–) 11–26 (–32) in the upper  $\frac{1}{3}$  of the inflorescence, 6–38 cm, with 8–16 congested flowers; **Fl** narrow, erect, cylindrical-urceolate, 45–64 (–75) mm, with strong musky-sour fragrance; **Tep** cream to pale yellow or light green below, conspicuously red to brownish on the calloused tips, reddish in bud, tube urceolate, 10–18 × 10–16 mm, slightly bulging at the base of the lobes, lobes erect, dimorphic, **OTep** 12–18 × 6–11 mm, **ITep** (6.5–) 9–14 × 9–14 mm, persistent and often leathery during and after anthesis, clasping the filaments; **St** long-exserted; **Fil** erect, inserted at 2 levels above mid-tube and near the rim, 40–58 mm, cream, pale yellow or pinkish, apex often tinged with maroon, inserted at 2 levels; **Anth**



11–25 mm, yellow; **Ov** stout, thickish, 18–36 mm, neck slightly constricted, (0.5–) 4–6 mm, angled to roundish; **Sty** 39–62 mm, cream or light yellow, usually tinged with maroon; **Sti** capitate, 3-lobed; **Fr** narrowly oblong to oblong or pyriform, 35–60 × 18–20 mm, dry walls thick and strong, apex short- to long-beaked, shortly and broadly stipitate; **Se** thin, flat, 5–7 × 4–5 mm, sooty black. — **Cytology**: 2n = 60 (Pinkava & Baker 1985, Simpson & al. 2011).

A “stupendously diverse” taxon (Parker 2017: 259), characterized by long lanceolate leaves, typically narrow in the northern part of its range, close-set slender teeth, sometimes with smaller ones between, and reddish tepals about equalling the tube. A smaller form occurs in N Sonora at somewhat lower elevations. The broad, glaucous-green leaves in populations in the Río Bavispe drainage (Sonora, Mexico) resemble those of *A. shrevei*, but its smaller flowers with shallower tubes place the plants in *A. palmeri*. *A. palmeri* shows introgression with *A. chrysantha* in Arizona (see there) and with *A. shrevei* in Sonora (Gentry 1982). For the closely related *A. lyobaa*, see there. The typification is unresolved: 2 of 3 syntypes are available (Rothrock 496, F 304130! [leaves & flowers], US 125477; Palmer s.n. [as *Anonymous*] MO 3949111 [seeds only]); Schott s.n. (“Dr. Schott collected the flowers in 1855”) could not be located.

*A. palmeri* shows some floral shifts from nocturnal bat to diurnal pollination, allowing for multiple pollinators at the N edge of its range where bats become infrequent (Slauson 2000). Scott (2004) observed (almost) no bats during the first 60% of the flowering period, while the migratory nectar-feeding bats were common visitors during the last part of the flowering period. Flowering, nectar and pollen production, sugar concentration, and fruit and seed set in burn-damaged plants are as high as in unburned rosettes (Slauson 2002b).

The seemingly bat-adapted flowers of *A. palmeri* are also visited by the hawkmoth *Manduca sexta*. The hawkmoths feed primarily on *Agave* as a result of learning and behavioural flexibility, and only shift to the moth-adapted flowers of their larval host plant *Datura wrightii* when these become abundant (Riffell & al. 2008). Laboratory

experiments by Alarcón & al. (2010) showed that female hawkmoths feed longer on *A. palmeri* than on *Datura*, whereas male moths feed longer on *Datura*. — For microsatellite primers suitable for population genetic studies in *A. palmeri*, see Lindsay & al. (2012).

**A. palustris** (Rose) Thiede & Eggl (Kakt. and Sukk. 50(5): 112, 1999). **Type**: Mexico, Nayarit (Rose 1943 [US, GH, K, MEXU]). — **Lit**: Rose (1903a: 9, with ill.); McVaugh (1989: 254); García-Mendoza (2003); Feria-Arroyo & al. (2010: with ill.); Solano & Ríos-Gómez (2014: 100, 101, with ill.); all as *Polianthes*. **Dist**: Mexico (Nayarit); on moist pastures and secondary habitats in oak forests, 2100 m; flowers in August. **I**: Barba-Gonzalez & al. (2012: 124); Hochstätter (2016: II: 21); both as *Polianthes*.

≡ *Polianthes palustris* Rose (1903).

[3b1] Herbaceous; corm 0.5–1 × 1.2–1.6 cm, bulb 2–3 × 1.4–2.2 cm, ovoid, completely covered with dried fibrous leaf bases; **R** fleshy, thickened, contractile; **L** drought-deciduous, 2–6, erect, linear, glabrous, attenuate at the base, apex acute, 18–30 × (0.8–) 1.2–1.5 cm, green, margins entire; **Inf** 37–58 cm, erect, ‘spicate’, peduncle with 3–4 **Bra**, linear, lowest 12–18 cm, internodes decreasing in size distally, fertile part 3–13 cm, lax, with 3–8 floral nodes; floral **Bra** ±0.7 cm; **Ped** 0–5 mm, ascending; **Fl** geminate, fragrant, 50–60 mm, divergent; **Tep** white, white-pink at senescence, the basal portion forming a tube 30–60 × 4 mm, curved out near ½ or just below, distally dilated, mouth very slightly oblique, lobes ovate, erect or sometimes spreading, obtuse, equal, 5–6 × 3–4 mm, apex cucullate, with a bundle of white trichomes; **Fil** filiform, 1–2 mm, included, inserted near the distal end of the tube 40 mm above the ovary apex; **Anth** linear, 6–7 mm; **Ov** ellipsoid, ±6 × 3 mm; **Sty** filiform, 35 mm, included; **Sti** 3-lobed; **Fr** and **Se** unknown.

Long known from the type collection only and thought to be possibly extinct (Feria-Arroyo & al. 2010: 20), but recently rediscovered and known from 3 collections in Nayarit (Pérez & al. 2010). Morphologically similar to *A. alboaustralis* (for differences see there), *A. apedicellata* and *A. dolichantha*, which both have longer and



oblong-elliptic lobes, flowers sessile throughout, longer anthers, and leaves usually less than 1 cm broad (see Castro-Castro & al. 2016: 726), and to *A. neonelsonii*, which has narrower leaves and flowers curved downwards with a strongly oblique tube mouth, much longer filaments, and a longer style.

**A. paniculata** (L. Hernández & al.) Thiede (Haseltonia 17: 94, 2012). **Type:** Mexico, Yucatán (Hernández-Sandoval & al. 5815 [CICY, MO, QMEX]). — **Lit:** Hernández-Sandoval & al. (2008); Orellana (2012); Carnevali (2013); all with ills. and as *Manfreda*. **Distr:** Mexico (Campeche, Yucatán, Quintana Roo); open habitats with limestone rocks in secondary tropical sub-deciduous forests, often associated with sinkholes (“cenotes”) or lakes, 5–130 m; flowers November to March. **I:** Hochstätter (2016: I: 32); Pérez-Sarabia & al. (2017: 45); both as *Manfreda*.

≡ *Manfreda paniculata* L. Hernández & al. (2008).

[3a5] Herbaceous; **Ros** caulescent, 0.2–0.4 m, freely suckering through axillary offsets and stolons; rhizomes cylindrical to oblong, 5–30 cm, erect at maturity; **R** thick, succulent; **L** mostly lost during the dry season, some persisting, 20–70, lanceolate to lanceolate-triangular, succulent ( $\pm 2.1$  mm thick at the widest place), lasting for >1 year, channelled, surface almost smooth, 20–55  $\times$  2.5–10 cm, dark green, variegated with darker green to reddish-brown spots, these more vivid on some individuals and when exposed to bright light, margins sinuate, denticulate to spinulose, with chartaceous teeth 0.5–1 mm in mature leaves, apex long-attenuate with a flexible apical tip 10–20 mm long; **Inf** (1–) 1.75–2.5 (–3.8) m, paniculate, peduncle 0.5–1.8 m, with 6–20 internodes, reddish-brown, glaucous, with 13–15 **Bra**, these  $\pm 2$  cm in the upper part, fertile part ovoid to pyramidal, 1- to 3-branched, rhachis 0.2–2 m, mature inflorescences often producing bulbils on some of the distal nodes; **Ped** 3.5–4.5 mm; **Fl** solitary but sometimes appearing almost geminate on young branches, 30–35 mm; **Tep** pale dull greenish-yellow, glaucous outside, shiny pale green inside, tube 6–8 mm, narrowly funnel-

shaped, lobes ovate-lanceolate, 15–20  $\times$  1.5–3.5 (–4.5) mm, reflexed during the male phase of anthesis, later erect, with incurved margins at maturity, apex obtuse, cucullate, with a tuft of glandular white hairs; **Fil** filiform, 40–55 mm, dark shiny reddish-brown; **Ov** cylindrical to fusiform, 15–18 mm, angulate to ribbed, concolourous with the tepals; **Sty** filiform, 50–55 mm, dark shiny reddish-brown; **Sti** clavate to capitate, 3-lobed; **Fr** oblong to pear-shaped, 25–40 mm, dark brown to almost black at maturity; **Se** crescent-shaped, 6–9  $\times$  4–6 mm, black, shiny, marginate.

Most unusual in Subgen. *Manfreda* due to its huge, broadly paniculate inflorescence, solitary pedicellate flowers subtended by a single bracteole, and the production of bulbils, while leaves and flowers are typical. Within the subgenus, *A. paniculata* is closest to *A. petskinil*, likewise from the Yucatán Peninsula, but also similar to *A. sileri* and *A. hauniensis* (Hernández-Sandoval & al. 2008). The species is often cultivated in villages far from the natural populations, and is used medicinally and as ornamental (Hernández-Sandoval & al. 2008). The tropical lowland habitat is untypical and apparently not known for other species of Subgen. *Manfreda* except *A. petskinil*, *A. chamelensis* and *A. littoralis*. *A. paniculata* and the similar *A. petskinil* are both unusual in having paniculate inflorescences and a tendency to become caulescent, as well as having denticulate to spinulose leaf margins and a longer apical tip, suggesting natural hybridization between a species of Subgen. *Manfreda* and a paniculate *Agave* (likely *A. fourcroydes* or *A. angustifolia* as well as the cultivated *A. variegata* (?)) (Jankalski, message in Agavaceae@yahogroups.com, 24. 6. 2008). Material of this species was earlier identified as *Manfreda maculata* (e.g. in the palynological study by Ludlow-Wiechers & Ojeda (1983)).

**A. papyrocarpa** Trelease (Mem. Nation. Acad. Sci. 11: 44, tt. 95–97, 1913). **Type:** Cuba, Isla de la Juventud (*Curtiss* 335 [MO [2 syn], CM, HAC, NY, P, US]). — **Lit:** Berger (1915: 273); Jennings (1917: 32, 95–96); León (1946: 319); Álvarez de Zayas (1985: 11, 13–15, with ills.); Álvarez de Zayas (1995: 41); Acevedo-Rodríguez & Strong

(2012: 86); Greuter & Rankin Rodríguez (2017: 36). **Distr:** Cuba (Isla de la Juventud [Isla de Pinos]); ecology unknown.

For differences from *A. jarucoensis*, see there. The species is considered as “Endangered” by Berazaín & al. (2005). The “holotype” consists of 2 sheets (MO 2056690 & 2056685), which were only cross-labelled at a later stage, and thus represent syntypes. The illustration by Hochstätter (2015: VII: 92) from the W end of Cuba, labelled “*A. papyrocarpa*”, is misidentified and may be *A. tubulata*.

**A. papyrocarpa** ssp. **macrocarpa** A. Álvarez (Revista Jard. Bot. Nac. Univ. Habana 5(3): 7, ills., 1985). **Type:** Cuba, Isla de Pinos (Álvarez 43981A [HAJB [several syn]]). — **Lit:** Álvarez de Zayas (1995: 41); Acevedo-Rodríguez & Strong (2012: 86); Greuter & Rankin Rodríguez (2017: 36). **Distr:** Cuba (W Isla de la Juventud [Isla de Pinos]); ecology unknown.

[2q] Differs from ssp. *papyrocarpa*: **terminal Sp** shorter, 5–8 mm; **Inf** with less compact part-**Inf** at the tip; **Fr** larger, oblong, (22–) 25–45 × 12–20 mm.

Based on a single allopatric population. The type includes 7 sheets, 2 are labelled as “Holotipo”, 5 as “Isotipo”, but the sheets are not cross-labelled and thus represent syntypes. HAJB 00079! contains fruits only about 22 mm long, so that the distinction of this taxon needs restudy.

**A. papyrocarpa** ssp. **papyrocarpa** — **Lit:** Berger (1915: 273, as *A. papyrocarpa*); Jennings (1917: 95–96, as *A. papyrocarpa*); León (1946: 319, as *A. papyrocarpa*); Álvarez de Zayas (1985: 11, 13–15, with ills.); Álvarez de Zayas (1995: 41); Acevedo-Rodríguez & Strong (2012: 86); Greuter & Rankin Rodríguez (2017: 36). **Distr:** Cuba (N & NE Isla de la Juventud [Isla de Pinos]); on open exposed limestone knobs and hills with *Bombax* and *Plumeria*, and on often near-vertical cliffs; flowers in February. **I:** Pilbeam (2013: 155–156, as *A. papyrocarpa*).

[2q] Acaulescent; **Ros** solitary; **L** oblong to elongate-oblong, gradually acute, somewhat concave, sometimes a little conduplicate above, 75–125 × 10–15 cm, green, at first slightly

glaucous and rather dull; **marginal teeth** straight or variously and unequally curved mostly downwards, triangular from scarcely or slightly dilated bases, (1–) 3–4 mm, 10–25 mm apart, occasionally with 1 or several minute intermittent teeth, intervening margin nearly straight or concave on young plants; **terminal Sp** usually a little curved and somewhat conically subulate, narrowly grooved below the middle, smooth or slightly granular below, somewhat polished towards the end, 8–15 × 3 mm, brown, not decurrent; **Inf** 3–4 mm, paniculate, part-**Inf** few, very laxly arranged on slender outcurved nearly horizontal branches 30–40 cm long, in the upper ½ or more of the inflorescence; **Ped** slender, 10–12 mm; **Fl** 36–43 mm; **Tep** light yellow, tube conical, narrow, 4–5 mm, lobes 15 × 4 mm; **Fil** 25 mm, inserted nearly in the throat; **Anth** 12–15 mm; **Ov** fusiform, 20 × 4–6 mm; **Sty** much longer than the filaments; **Sti** capitate; **Fr** globose-oblong, thin-walled, 20–30 × 15–20 mm, little beaked, stipitate or not; **Se** 5–6 × 4–5 mm.

**A. parrasana** A. Berger (Notizbl. Königl. Bot. Gart. Berlin 4: 250, 1906). **Type:** Mexico, Coahuila (*Purpus* s.n. [MO 3346980, US [type collection]]). — **Lit:** Trelease (1912b: 90, tt. 80–81); Berger (1915: 176–177); Breitung (1963: 75); Gentry (1982: 537–538); Ullrich (1992j: 250–252); Ullrich (1992c); García-Mendoza (2003); Starr (2012: 173–178, 322–323); all with ills. **Distr:** Mexico (C, S & SE Coahuila); limestone mountains, chaparral shrub and pine and oak forests above the desert proper, 1200–2480 m; flowers May to June. **I:** Ullrich (1994c); García-Mendoza (2002: 178); Kemble (2004); Heller (2006: 115); Spracklin (2007); Richter (2011: 81); Alsemgeest & Roosbroeck (2012?); Pilbeam (2013: 157); Hochstätter (2015: III: 17); Moore (2016: 257).

**Incl.** *Agave wislizeni* ssp. *parrasana* (A. Berger) Gentry (1975).

[2m] Acaulescent; **Ros** compact, small, 30–50 cm Ø, solitary, with few or no suckers; **L** 40–60, ovate, closely imbricate, thick, rigid, short-acuminate to merely acute, flat to concave above, generally 20–30 × 10–12 cm, glaucous grey-green to green, frequently light grey to bluish-glaucous; **marginal teeth** straight to curved,

slender from small low bases, 5–10 (–15) mm, largest near the leaf tip, rapidly becoming smaller further down, greyish-brown, 10–25 mm apart; **terminal Sp** slender from a broad base, flat to openly grooved above, 20–30 (–40) mm, dark brown to greyish, sharply decurrent to the uppermost teeth; **Inf** 3–4 m, paniculate, peduncle with and part-**Inf** subtended by large reddish to purplish (rarely greenish) **Bra**, fertile part ellipsoid, part-**Inf** compact, 12–15; **Fl** 50–60 mm; **Tep** pale yellow, buds tinged red or purple, tube cylindrical, lightly grooved, 13–14 × 13–14 mm, lobes lanceolate, rather thick, subequal, 13–15 × 5–6 mm, pale yellow, outer more acute, 2 mm longer than the inner, tinged with red at the tip; **Fil** slender, 45–50 mm, inserted near mid-tube; **Anth** centric, 18–19 mm, yellow; **Ov** 25–30 mm, neck short, not constricted; **Sty** slightly longer than the tepals; **Sti** capitate; **Fr** stoutly oblong, shortly stipitate, shortly beaked, 50–53 × 17–20 mm; **Se** 5–6 × 4–5 mm, black.

Only known from a few limestone mountains in Coahuila, and easily distinguished by its short, broad, abruptly short-acuminate leaves. Gentry (1982) placed *A. parrasana* in his Group (now Sect.) *Parryanae*, in which it differs from all other taxa known by its large succulent purplish-coloured bracts on the peduncle that cover the budding part-inflorescences, but these may also be green (habitat photograph in Alsemgeest & Roosbroeck 2012?). Here, it is placed together with *A. gentryi* and *A. montana*, which both have similar large bracts, in Sect. *Hibernicae*. González-Elizondo & al. (2009: 110) mention specimens labelled *A. parrasana* from N Durango which need verification. For the in vitro propagation, see Santacruz-Ruvalcaba & al. (1999). Hardy to –8 °C or more (Spracklin 2007). — ‘Fireball’ is a variegated cultivar, and ‘Meat Claw’ a cultivar with large teeth (Starr 2012: 177).

The typification of *A. parrasana* needs clarification. US 1023807, labelled as “holotype”, was apparently preserved in 1912 (“L[a]. M[ortola]. VIII, 1912”), i.e., after the publication of the name, and includes flowers preserved at a different date than the leaves (“Blüten nachträglich aus La Mortola erhalten”). The leaf from Berger

(MO 3346980) labelled as “isotype” was given as and depicted as “type” by Trelease (1912b: t. 80, 1), this is viewed as (unintended) lectotypification.

**A. parryi** Engelm (Trans. Acad. Sci. St. Louis 3(20): 311–313, 1875). **Type** [lecto]: USA, Arizona (*Rothrock* 274 [MO [3 sheets]]). — **Lit**: Berger (1915: 179–180); Breitung (1963: 74–77, with ills.); Gentry (1982: 538–545, with ills.); Ullrich (1992j); Hodgson (1999a: 8–9); Reveal & Hodgson (2002); González-Elizondo & al. (2009: 111–114, with ills.); Alsemgeest & Roosbroeck (2010: with ills.); Starr (2012: 178–199, 322–323, with ills.); Parker (2018a: 27–28, with ills.). **Distr**: SW USA, NW, N & W-C Mexico.

≡ *Agave applanata* var. *parryi* (Engelmann) Mulford (1896); **incl.** *Agave leopoldii* Rafarin (1874).

*A. parryi* has the most extensive range of any species in Sect. *Parryanae* (as Group) and is distinguished by its compact, multi-leaved, freely suckering, light green to greyish rosettes (Gentry 1982). According to Ullrich (1992j) the earlier but illegitimate name *A. scabra* Salm-Dyck (1858) was based on a collection attributable to *A. parryi*, and so represents a synonym of it. Here, the view of Villarreal & al. (2005) is followed who consider *A. scabra* as illegitimate name for *A. asperriima* (see there). The earlier but rejected name *A. leopoldii* Rafarin is treated as synonym of *A. parryi* on the base of Govaerts (2014+: accessed Oct. 2018).

The protologue cites material from Emory, Bischoff and Rothrock (= syntypes) kept at MO. The designation by Trelease (1912b: 94) as “*Rothrock*, 274, 1874,—to be accepted as the type”) and by Gentry (1982: 539) as “Type: *Rothrock* 274, in 1874” represent first-step lectotypifications since 3 sheets, not cross-labelled, are present at MO.

**A. parryi** ssp. **neomexicana** (Wooton & Standley) B. Ullrich (Sida 15(2): 259, 1992). **Type**: USA, New Mexico (*Standley* 541 [US 498333, ARIZ]). — **Lit**: Wooton & Standley (1913: 115–116, t. 48, as *A. neomexicana*); Gentry (1982: 535–537, with ills., as *A. neomexicana*); Reveal & Hodgson (2002); González-Elizondo &

al. (2009: 104–106, with ills., as *A. neomexicana*); Starr (2012: 188–191, with ills.). **Distr:** USA (S New Mexico, SW Texas), Mexico (Durango, Coahuila?); gravelly to rocky places in grasslands and desert scrub, 1600–2100 m; flowers mid-spring to early summer. **I:** Irish & Irish (2000: t. 27); Heller (2006: 110); Richter (2011: 128); Pilbeam (2013: 139); Hochstätter (2015: III: 15); all as *A. neomexicana*. — Fig. 45.

≡ *Agave neomexicana* Wooton & Standley (1913) ≡ *Agave parryi* var. *neomexicana* (Wooton & Standley) McKechnie (1949).

[21] Differs from ssp. *parryi*: **Ros** flat-topped, smaller, 35–45 × 40–60 cm, generally in smaller groups; **L** lanceolate, more slender, 4–12 cm wide; **Inf** smaller, (2–) 3–4.5 m, part-**Inf** fewer, (7–) 10–17; **Fl** smaller, 55–67 mm; **Tep** yellow to yellowish-green, red to orange in bud, tube longer, 12–18 mm, lobes smaller, 15–20 × 3–4 mm; **Fil** shorter, 35–45 mm, inserted (sometimes irregularly) above mid-tube; **Ov** with shorter neck, 4–7 mm; **Fr** smaller, 25–35 mm. — **Cytology:** 2n = 120 (Granick 1944: as ‘4n’ for *A. neomexicana*).

Ullrich (1992j) reduced *A. neomexicana* to subspecific rank under *A. parryi*, which is followed by Reveal & Hodgson (2002) and Govaerts (2014+: accessed April 2014). The occurrence in Coahuila is based on a single doubtful specimen only and needs verification (Gentry 1982: 547). González-Elizondo & al. (2009) place plants from Durango here, which is a new record for the state. Ssp.

*neomexicana* is difficult to distinguish from *A. ×gracilipes* (see also there). The Mescalero Apaches were so named due to their use of the plant for food (as ‘mescal’). Historical overuse may partly account for its present limited distribution and infrequent occurrence (Reveal & Hodgson 2002). The variability in the nectar sugar composition is studied by Reid & al. (1985: as *A. neomexicana*). — ‘Sunspot’ is a variegated cultivar with creamy-yellow leaf margins (Starr 2012: 191).

**A. parryi** ssp. **parryi** — **Lit:** Gentry (1982: 538–542, with ills.); Ullrich (1992j: with ill.); Hodgson (1999a: 8–9); Reveal & Hodgson (2002); González-Elizondo & al. (2009: 111–114, with ills.); Alsemgeest & Roosbroeck (2010: 33–40, with ills.); Starr (2012: 178–180, 192–195, 322–323, with ills.). **Distr:** S USA (C & SE Arizona, SW New Mexico), NW & W-C Mexico (E Sonora, NW, C & S Chihuahua, W-C Durango, NW Zacatecas, NE Jalisco, Guanajuato, Querétaro?); gravelly to rocky places and open slopes in grama grasslands, oak woodlands, chaparral, desert scrub, pinyon-juniper, and pine-oak-forests, 1200–2800 m; flowers May to July. **I:** Ullrich (1991h); Irish & Irish (2000: t. 30); Heller (2006: 31, 116); Richter (2011: 51, 57, 107, 119, 140); Pilbeam (2013: 158).

**Incl.** *Agave americana* var. *latifolia* Torrey (1859); **incl.** *Agave marcusii* De Smet (1876); **incl.** *Agave patonii* Trelease (1911); **incl.** *Agave chihuahuana* Trelease (1912); **incl.** *Agave*

**Fig. 45** *Agave parryi* ssp. *neomexicana* (Etter & Kristen 178: USA; New Mexico, Culberson County, Guadalupe Mountains National Park). (Copyright: J. Etter & M. Kristen)





*marensii* hort. ex Trelease (1912); **incl.** *Agave marcusea* hort. ex Trelease (1912) (*nom. inval.*, ICN Art. 61.1?); **incl.** *Agave parryi* hort. ex Trelease (1912) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave parreyi* hort. ex Trelease (1912) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave paryi* hort. ex Trelease (1912) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave payrii* hort. ex Trelease (1912) (*nom. inval.*, ICN Art. 61.1).

[21] **Ros** compact, flat-topped or globose, 15–75 × 25–85 cm, freely suckering; **L** 90–160, lanceolate to broadly ovate, closely imbricate, rigid, thick, little constricted above the base, widest just below the middle, short-acuminate to truncate, rounded below, nearly flat to concave towards the apex, 10–65 × 4.5–20 cm, glaucous-grey to light green, margins nearly straight to repand or undulate; **marginal teeth** mostly straight to recurved, small, largest above the middle of the lamina, 3–8 mm, dark brown to greyish, mostly 10–20 (–30) mm apart; **terminal Sp** openly grooved, 15–30 mm, dark brown to grey with age, decurrent to the 1. or 2. teeth; **Inf** 4–6 m, paniculate, peduncle thick, glaucous-green to grey, with large reflexing **Bra**, fertile part with 20–36 slightly ascending congested part-**Inf** in the upper ½ of the inflorescence; **Fl** 43–81 mm; **Tep** greenish to deep yellow, pink to red in bud, tube fleshy, thickly angled, deeply grooved, 6–12 × 11–21 mm, lobes subequal, ascending to erect, thick, soon involute and wilting, linear above the rather open sinuses, papillate within well below the hooded tip, 13–27 × 2–7 mm, **ITep** thickly keeled, 2-costate within; **Fil** broad, (35–) 40–58 (–65) mm, yellow, inserted 4–11 mm above the base of the tube; **Anth** excentric to centric, 12–34 mm, yellow; **Ov** 20–48 mm, usually with a neck (2–) 6–9 mm, slightly angled or rounded, green; **Sty** 52–70 mm, eventually longer than the stamens; **Sti** capitate, 3-lobed; **Fr** oblong to obovate, 35–50 × 15–20 mm, shortly and stoutly stipitate, beaked, strong-walled; **Se** semi-circular, 7–8 × 5–6 mm, with low thick rim and shallow hilar notch.

Alsemgeest & Roosbroeck (2010) provide a richly illustrated account of the typical subspecies and its varieties and forms. Ullrich (1992j) reduced all to the synonymy of ssp. *parryi*, but,

albeit being weakly differentiated, they appear to have some geographical separation and are upheld by Hodgson (1999a) and Reveal & Hodgson (2002). Ssp. *parryi* was recently recorded from NE Jalisco (Hernández-Vera & al. 2007a). Alsemgeest & Roosbroeck (2010: 74) place plants from near Los Trigos in Querétaro here. For plants from Guanajuato named “*A. spatularia*”, see under *A. applanata*. Putative wild populations show higher genetic variability than populations domesticated over 600 years ago. Anthropogenic populations are not simply derived from the closest wild population, but came from more distant wild populations (Parker & al. 2010).

**A. parryi** var. **couesii** (Engelmann ex Trelease) Kearney & Peebles (J. Washington Acad. Sci. 29(11): 474, 1939). **Type:** USA, Arizona (*Coues & Palmer* 253 [MO]). — **Lit:** Trelease (1912b: 94–95, tt. 94–97, as *A. couesii*); Berger (1915: 180, as *A. couesii*); Gentry (1982: 542–543, with ill.); Hodgson (1999a: 8); Reveal & Hodgson (2002); Alsemgeest & Roosbroeck (2010: 38–40, 178–182, with ill.); Starr (2012: 181–184, with ill.). **Distr:** USA (C Arizona); open slopes and gravelly places in grasslands, chaparral, pinyon-juniper, and oak woodlands, 1100–2100 m; flowers June to July. **I:** Heller (2006: 158); Richter (2011: 126); Starr (2012: 16); Pilbeam (2013: 159); Hochstätter (2015: III: 20, as ssp. *couesii*);  
≡ *Agave couesii* Engelmann ex Trelease (1911)  
≡ *Agave parryi* ssp. *couesii* (Engelmann ex Trelease) Hochstätter (2015); **incl.** *Agave parryi* fa. *integrifolia* Breitung (1963).

[21] Differs from var. *parryi*: **Ros** smaller, 35–55 × 40–65 cm; **L** ovate, smaller, 25–42 (–47) × 6.5–11 cm; **Fl** smaller, 43–58 (–60) mm; **Tep** tip more densely papillate, tube 6–9 mm, lobes 13–21 mm; **Fil** shorter, 33–44 mm, inserted 4–8 mm above the tube base; **Ov** shorter, 20–34 mm; **Sty** shorter, 52–62 mm. — **Cytology:** 2n = 120 (Pinkava & Baker 1985).

According to Wolf (1988: 1609) Engelmann annotated the type with the name “couessi”, but this spelling would be erroneous as the name honours Elliot Coues. This taxon represents a variant of smaller growth from the NW border of the species’ range. However, small-leaved forms



occur at random elsewhere (Gentry 1982). *A. parryi* fa. *integrifolia* represents a toothless variant found in populations of this variety; such aberrations are widespread in the genus and do not merit formal taxonomic recognition. In Arizona, the taxon hybridizes with *A. chrysantha* (Hodgson 1999a, Reveal & Hodgson 2002).

This variety as well as var. *huachucensis* and var. *truncata* were reduced to synonyms of *A. parryi* ssp. *parryi* by Ullrich (1992j) who regarded them as mere ecotypes with size modified by more humid or arid conditions, and merging into typical plants in cultivation. All three varieties are weakly differentiated, but appear to have some geographic distinction and are upheld here following Hodgson (1999a) and Reveal & Hodgson (2002).

**A. parryi** var. **huachucensis** (Baker) Little ex L. D. Benson (Amer. J. Bot. 30(3): 235, 1943). **Type:** USA, Arizona (*Pringle* s.n. [K, BR, CM, G, GH, LE, NY, US, VT]). — **Lit:** Trelease (1912b: 91–92, tt. 87–89, as *A. huachucensis*); Berger (1915: 178–179, as *A. huachucensis*); Breitung (1963: 76–77, with ill.); Gentry (1982: 542); Hodgson (1999a: 8); Reveal & Hodgson (2002); Alsemgeest & Roosbroeck (2010: 36–39, 68–74, with ills.); Starr (2012: 185–187, with ills.). **Distr:** USA (SE Arizona), Mexico (NE Sonora, NW Chihuahua?); open slopes in oak woodland and pine forests, 1550–2200 m; flowers (March to) June to July (to August). **I:** Watson (1895); Skinner (1961); Irish & Irish (2000: t. 31); Lyons (2002: 161); Richter (2011: 127); Pilbeam (2013: 160); Hochstätter (2015: III: 21, as ssp.);

≡ *Agave huachucensis* Baker (1888) ≡ *Agave applanata* var. *huachucensis* (Baker) Mulford (1896) ≡ *Agave parryi* ssp. *huachucensis* (Baker) Hochstätter (2015).

[21] Differs from var. *parryi*: **Ros** more robust, 45–75 × 75–85 cm; **L** ovate, larger, 32–65 or more × 10–20 cm; **Inf** broader; **Fl** larger, 62–81 mm; **Tep** tube 8–9 mm, lobes 20–27 mm; **Fil** 46–58 mm, inserted 6–8 mm above the tube base; **Ov** 34–47 mm.

A widely cultivated upland variant with larger growth. The populations studied by Parker & al. (2014) differed significantly morphologically and

genetically from *A. parryi* (ssp./var. *parryi*), with wild populations showing greater genetical diversity than ancient anthropogenic populations planted by native Americans at lower elevations than at which the taxon naturally occurs (ill.: Parker 2018a: 28). — Variegated cultivars are ‘Medio-Picta Pallida’ with leaves with a broad pale yellow mid-stripe, ‘Excelsior’ (also named ‘Medio-Picta’ or ‘Kitsuyoteh Hakafu’) with a clear yellow midstripe (ill.: Greulich 2017c: 159), and ‘Medio-Picta Alba’ with a white midstripe. Further variegated cultivars are ‘Jaggedmeister’, ‘Point of Interest’, and ‘Spring Sun’ of Plant Delights Nursery (USA).

**A. parryi** var. **parryi** — **Lit:** Trelease (1912b: 93–94, tt. 91–93, as *A. parryi*); Gentry (1982: 538–542, with ills.); Ullrich (1992j: with ill.); Hodgson (1999a: 8–9); Reveal & Hodgson (2002); González-Elizondo & al. (2009: 111–114); Alsemgeest & Roosbroeck (2010: 33–37, with ills.); Starr (2012: 192–195, with ills.). **Distr:** S USA (C & SE Arizona, SW New Mexico), NW Mexico (E Sonora, NW, W & SW Chihuahua, W Durango, NE Jalisco, Guanajuato); gravelly to rocky places and open slopes in grama grasslands, oak woodlands, chaparral, desert scrub, pinyon-juniper, and pine-oak forests, 1200–2800 m; flowers June to July. **I:** Irish & Irish (2000: t. 30); Ullrich (1991h); Heller (2006: 31, 116); Richter (2011: 51, 57, 107, 119, 140); Pilbeam (2013: 158); Hochstätter (2015: III: 18, 19). — Fig. 46.

[21] **Ros** (35–) 40–60 × 60–75 cm; **L** linear-ovate, (18–) 25–50 × (4.5–) 8–12 cm; **Fl** 60–77 mm; **Tep** tube 9–12 × 14–18 mm, lobes (17–) 19–24 mm; **Fil** 40–54 mm, inserted 6–11 mm above the base of the tube; **Ov** (27–) 30–47 mm; **Sty** 60–70 mm. — **Cytology:** 2n = 60, 120 (Simpson & al. 2011: as *A. parryi*).

In Arizona, var. *parryi* hybridizes with *A. chrysantha* and *A. schottii* ssp. *schottii* (Hodgson 1999a, Reveal & Hodgson 2002). ‘J. C. Raulston’ and ‘Sierra Estrella’ are normal-leaved cultivars (Starr 2012: 194).

**A. parryi** var. **truncata** Gentry (Agaves Cont. North Amer., 543–545, ills., 1982). **Type:** Mexico, Zacatecas-Durango (*Gentry & Gilly* 10566

**Fig. 46** *Agave parryi* var. *parryi*. (Mexico; Chihuahua, Rosales Mpio., SE Chihuahua towards Delicias). (Copyright: J. Thiede)



[US 2540275, DES 0004758, MEXU 00231534, MICH]). — **Lit:** Alsemgeest & Roosbroeck (2010: 68, 70, 73–74, with ills.); Starr (2012: 196–199, with ills.). **Distr:** Mexico (Durango/Zacatecas border); open rocky limestone slopes in oak-juniper grasslands,  $\pm 2280$  m; flowering in cultivation in July; only known from the region of the type locality. **I:** Irish & Irish (2000: t. 32); Heller (2006: 116); Richter (2011: 100); Pilbeam (2013: 161–162); Hochstätter (2015: III: 21, as ssp.).

≡ *Agave parryi* ssp. *truncata* (Gentry) Hochstätter (2015).

[21] Differs from var. *parryi*: **Ros** copiously surculose with long rhizomes; **L** very short and broad, oblong, 10–30 (sometimes only 7–15)  $\times$  7–12 cm, light grey, tip shortly acuminate to truncate, margins repand to wavy; **marginal teeth** variable, usually flexed downwards, the larger ones 4–8 mm, dark brown; **Inf** infrequently produced.

A diminutive variant at the SE border of the species' range. Its small size appears to result from the arid habitat conditions and the taxon may thus represent a mere modification only; in cultivation, well-watered plants may attain a size comparable to other *A. parryi* variants (Gentry 1982: 544, Etter & Kristen 1997+: accessed 2014). Plants in habitat are somewhat different from those commonly seen in cultivation, which seem to have been derived mostly from plants grown at Huntington Botanical Gardens

(California) (Pilbeam 2013: 161–162); this clone is named as cultivar 'Huntington' (Starr 2012: 198–199, with ill.).

The protologue cites "*Gentry & Gilly* 10566", "June 8, 1951" at US as "holotype", which corresponds to the field-collected US 2540275! (also databased as holotype, and labelled "Holotipo" by A. García-Mendoza 2002); ARIZ-0004758! and MEXU 00231534! are isotypes. Sheets prepared from a plant of the type collection cultivated at Huntington BG (US 2826228! & 2826228!, ARIZ-0004759! & 0004760!, DES 00019018!) were preserved in June or July 1977 and thus represent a different gathering and are not type material.

**A. parva** (Aarón Rodríguez) Thiede (Haseltonia 17: 94, 2012). **Type:** Mexico, Guerrero (*Rodríguez & Pérez-Álvarez* 5518 [IBUG, ENCB, IEB, MEXU, WIS, XAL]). — **Lit:** Rodríguez (2009); Castillejos-Cruz (2009); both with ills. and as *Manfreda*. **Distr:** Mexico (Guerrero: Sierra de Taxco near Taxco); slightly inclined rocky slopes in disturbed pine-oak forests, 1845 m; flowers in July. **I:** Hochstätter (2016: I: 33, as *Manfreda*).

≡ *Manfreda parva* Aarón Rodríguez (2009).

[3a3] Herbaceous; corm 1–4  $\times$  1–2 cm, bulb oblong, 2–2.5  $\times$  1–1.5 cm, covered with dry leaf bases 6–6.5 cm long, these membranous at the base and fibrous above; **R** fleshy, thickened, contractile; **L** (5–) 11–24, semisucculent, extended, linear, falcate, glabrous, tip acute, 10–20 (–25)  $\times$

0.4–0.7 (–0.9) cm, green, margins entire, with a very narrow hyaline band not visible to the naked eye; **Inf** erect, 0.35–0.6 m, peduncle 0.2–0.3 m, with 4–7 **Bra**, fertile part 15–30 cm, with (4–) 9–15 solitary, ascending, sessile and laxly arranged flowers; **Fl** 35 mm, green throughout; **Tep** green with small reddish dots, tube straight or slightly curved towards the rhachis, 15–18 × 4–5 mm, not constricted, lobes oblong, revolute, 7–8 × 4–5 mm, apex thickened, cucullate, with a bundle of white hairs; **St** erect at anthesis, green with red dots, inserted at the mouth of the tube all on the same level, exceeding the tube for 25 mm; **Ov** obclavate, 7 × 4 mm, green with reddish dots; **Sty** ±43 mm, at first ± ½ as long as the stamens, then elongating and finally of the same length; **Sti** 3-lobed, green-yellowish; **Fr** subglobose, triquetrous, 12–17.5 × 8–13 mm, apex with a round scar 4–6 mm Ø; **Se** 4.5–5 × 3.5 mm, shiny.

Unique in Sect. *Herbaceae* due to the small, linear and falcate leaves, and according to the protologue placed in Ser. *Guttatae* (as *Manfreda guttata*-Group). *A. parva* is most similar to *A. bulbulifera*, but has more leaves, shorter filaments, a longer tepal tube and smaller tepal lobes. Both species differ from others in the group by their laxly arranged flowers and inflorescences with a short peduncle measuring about ½ of the inflorescence.

**A. parvidentata** Trelease (J. Washington Acad. Sci. 15(17): 395, 1925). **Type** [lecto]: El Salvador (*Calderón* 2085 [US 92237, ARIZ, ILL, US 92238]). — **Lit**: Gentry (1982: 488–489, with ill.); Ullrich (1992b); Lott & García-Mendoza (1994). **Distr**: El Salvador, Honduras; volcanic rocky slopes in open scrub vegetation, 1000–2500 m; flowers December and March. **I**: Richter (2011: 124).

**Incl.** *Agave compacta* Trelease (1927).

[2o] Stems short; **Ros** dense, to 1 × 1.7 m, solitary; **L** numerous, ascending to out- or incurving, ovate-lanceolate, contracted into the thick base, thickly fleshy, concave above the middle, sometimes plicate, flat, long acuminate, smooth, 80–100 × 15–25 cm, pale green to light glaucous-grey, margins straight or somewhat concave between the teeth; **marginal teeth** deltoid from lenticular bases, nearly straight, 3 (–5) mm (middle of the

lamina), 10–20 mm apart, reduced up- and downwards; **terminal Sp** acicular, involutely grooved to above the middle, smooth, 40–55 mm, dull light brown, somewhat intruded into the leaf tissue and decurrent for more than its length; **Inf** 1.5–3 m, paniculate, peduncle shorter than the leaves to 1.5 (–2) × longer, fertile part oblong, dense, part-**Inf** globose, 30–50, bulbiferous, the lateral branches ± horizontal to ascending, closely ramified, tertiary branchlets with many small bracts; **Ped** 5–15 mm; **Fl** slender, 40–50 mm; **Tep** yellow, tube openly conical, 3–5 mm, lobes linear, spreading, involute, tip acute with small hood, subequal, 10–20 mm; **Fil** slender, ascending-spreading, 35–50 mm, inserted in the orifice of the tube; **Anth** centric, 15–20 mm, yellow; **Ov** fusiform, 20–25 × 3–5 mm; **Fr** oblong, distinctly notched at the base, 36–40 × 18–21 mm, dark brown; **Se** unknown.

Closest to *A. pachycentra* and *A. wercklei*. The very short-peduncled inflorescences branching from the level of the upper leaf tips mentioned as characteristic by Gentry (1982: 488) are not supported by photographs from Volcán Santa Ana from the internet, showing mostly longer peduncles. Similar plants with inflorescences branching from the level of the upper leaf tips also occur in Chiapas (S Mexico) (Ullrich 1992b). The fruit description was added from *Linares* 4930 (US 3459009!). The leaves of *Kimmach* 419 from Honduras (DES 26840 & 26844!) fit very well here; the more robust flowers may result from its cultivation at the Huntington Botanical Garden. For the typification, see Smith & Figueiredo (2014e: 240–241).

Ullrich (1992b) proposes *A. calderonii* Trelease (1923) as oldest name for *A. parvidentata*. Lott & García-Mendoza (1994), however, treat *A. calderonii*, which is known from the type collection only, as a name of doubtful identity (which is accepted here) tentatively assignable to Sect. *Rigidae* (as Group).

**A. parviflora** Torrey (in Emory, Rep. US Mex. Bound. 214, 1859). **Type** [lecto]: Mexico, Sonora (*Schott* s.n. [US, NY]). — **Lit**: Gentry (1982: 200–203, with ills.); Starr (2012: 200–203, 310–311, with ills.). **Distr**: USA (Arizona), Mexico (Sonora).

US 125479, designated as “type” (= lectotype) by Gentry (1982: 201, 213), includes a leaf of a “*Manfreda*”; and the single flower that is much too large for *A. parviflora* might likewise belong to the latter.

**A. parviflora** ssp. **densiflora** G. D. Starr & Devender (Cact. Succ. J. (US) 83(5): 225, ills. (p. 228), 2011). **Type:** Mexico, Sonora (*Reina G. & Devender* 98-1892 [ARIZ, DES, MEXU, MO, USON]). — **Lit:** Starr (2012: 201, 203, 309); Greulich (2018a); both with ills. **Distr:** Mexico (Sonora: near Yécora); rocky hill slopes and rock outcrops, at canyons, in pine-oak forests, oak woodland and rocky grasslands, 1300–1600 m; flowers May and July. **I:** Hochstätter (2015: VIII: 59).

[1e] Differs from ssp. *parviflora*: **Ros** compact, 35–40 × 30 cm; **L** 15 × 1.8–1.9 cm; **terminal Sp** 5–8 mm; **Inf** 2–2.1 m, part-**Inf** with up to 6–8 flowers; **Fl** 16–18 mm, more densely arranged; **Tep** tube 5–7 mm, 2 × as long as the lobes, lobes 2–3 mm; **Fil** erect, 12–13 mm; **Ov** 5–8 mm.

Differs from the other subspecies primarily in its longer and broader leaves and inflorescences with more densely arranged flowers and in groups of 6–8.

**A. parviflora** ssp. **flexiflora** Gentry (US Dept. Agric. Handb. 399: 56–57, ills., 1972). **Type:** Mexico, Sonora (*Gentry* 16638 [US, ARIZ, DES †, MEXU, MICH]). — **Lit:** Gentry (1982: 201–203, with ills.); García-Mendoza (2003); Starr & Devender (2011: 227, 229); Starr (2012: 201). **Distr:** Mexico (NE Sonora); grama grasslands and oak woodlands, 600–1500 m. **I:** Etter & Kristen (2007b: 179); Pilbeam (2013: 164); Ettelt (2014: 115); Hochstätter (2015: VIII: 60).

[1e] Differs from ssp. *parviflora*: **L** dimorphic, linear to lanceolate, 6–10 × 1 cm or 15–18 × 1.2 cm; **terminal Sp** whitish; **Inf** 1.5–2.5 m, part-**Inf** with 1–3 (mostly 2) flowers; **Fl** saccate; **Tep** with anthers and style bent downwards at anthesis, tube 3–4 mm, lobes 3.5–5 mm; **Ov** 6–8 mm. — **Cytology:** 2n = 60 (Palomino & al. 2015, with 3 structurally different cytotypes).

Best differentiated from the other subspecies by its tube and tepal lobes about equal in length and its reflexed flowers (Starr & Devender 2011).

**A. parviflora** ssp. **parviflora** — **Lit:** Trelease (1894: t. 32); Berger (1915: 77–79); Breitung (1960: 79, with ill.); Gentry (1972: 53–56, with ills.); Gentry (1982: 200–203, with ills.); Ullrich (1990e: with ill.); Hodgson (1999a: 9); Reveal & Hodgson (2002); García-Mendoza (2003); Starr & Devender (2011: 227–229, with ills.); Starr (2012: 200–203, 310–311, with ills.); Parker (2017: 262, 264, with ill.). **Distr:** USA (S Arizona), Mexico (NE Sonora); open rocky slopes, mostly in desert grasslands and oak woodlands, 600–1500 m; flowers May to August. **I:** Irish & Irish (2000: t. 33); Heller (2006: 117); Pilbeam (2013: 163); Ettelt (2014: 116); Hochstätter (2015: VIII: 58).

**Incl.** *Agave hartmanii* S. Watson (1891).

[1e] Acaulescent; **Ros** 10–15 × 15–40 cm, solitary or rarely caespitose; **L** ascending to erect, oblong-linear, firm, adaxially flat towards the apex, abaxially convex towards the base, widest at or above the middle, apex abruptly acuminate, 6–10 × 0.8–1 cm, dark green, both faces with white imprints from the central bud, margins straight, conspicuously filiferous, fibres white, tightly and uniformly curled; **marginal teeth** minute, near the leaf base only; **terminal Sp** weakly subulate, 5–8 mm, brown to greyish-white; **Inf** 1–2.1 m, ‘spicate’, peduncle with caducous, narrowly triangular **Bra**, the lowest 1–3 cm long, **Inf** laxly to densely flowered in the upper ½, this part frequently reddish, part-**Inf** with 2–4 flowers; **Ped** < 2 mm; **Fl** strongly recurved, 13–18 mm; **Tep** pale yellow to light greenish-yellow, tube urceolate, 5–7 × 4.5–5.5 mm, lobes erect to incurved, subequal, inner ones nearly orbicular, constricted near the tube, outer slightly longer than the inner, 2–3.5 × 1.5–4 mm; **St** slightly exerted; **Fil** erect, 9–14 mm, pinkish-red, inserted at the base of the tube; **Anth** 5–6 mm, yellow; **Ov** 4–8 × 3–5 mm, neck slightly constricted, 1–2 mm; **Sty** shorter than the filaments; **Fr** globose, 6–8 × 6–10 mm, apex short-beaked, stipe none to short; **Se** semicircular, 3–3.5 × 2–2.5 mm, thinner on the inner edge, thicker on the outer and curved edge. — **Cytology:** 2n = 60 (Bhattacharyya 1968, Zonneveld 2003).

This taxon has the smallest flowers in the genus. It is closely related to *A. polianthiflora*



from which it is only separable with certainty by the distinctive flowers (Gentry 1982: 201).

The name *A. hartmanii* S. Watson caused some confusion. It was based on a sterile cultivated plant whose features correspond to both *A. parviflora* and *A. polianthiflora*, but no original material was preserved (Gentry 1982: 205). Ullrich (1990e) provided an authentic illustration and showed that *A. hartmanii* was collected near Nacori (Sonora), within the area of *A. parviflora* ssp. *flexiflora*, which suggests its identity with the latter. Laferrière (1995a) selected the holotype of *A. parviflora* as neotype for *A. hartmanii*, making the name a homotypic synonym of *A. parviflora*. — The species is listed in CITES Appendix I.

The taxon occurs in Arizona at about a dozen localities, none with more than 200–300 individuals, and is at present the only *Agave* included in the US Endangered Species List, classified as “Endangered” (Parker 2017).

With largely diurnal anther dehiscence and nectar production with a high nectar sugar concentration, *A. parviflora* appears to be predominantly adapted to diurnal insect pollination. Indeed, the flowers are primarily visited by bumblebees; nocturnal bat visitation appears unlikely due to the lack of floral rewards (Slauson 2002a).

**A. pax** Giraldo-Cañas (Caldasia 39(1): 35–38, ills. (pp. 41–46), 2017). **Type:** Colombia, Antioquia (*Giraldo-Cañas & Giraldo-Osorio* 6139 [COL, COL]). — **Distr:** Colombia (Antioquia: Rio Cauca canyon); in tropical deciduous forests, common, 500–800 m; flowers in January.

[2g] Stems to 50 × 18 cm, simple; **Ros** dense, suckering; **L** 32–43, straight, lanceolate, rigid, coriaceous, broadened at the base, guttered, papillose on both faces, veins distinct only when dried, 142–154 × 6.5–12 cm, opaque green, darker on the upper face, pruinose, margins straight; **marginal teeth** absent or as few irregular denticles, 2–3 mm, light to dark brown, shiny, on small prominences; **terminal Sp** conical, rigid, slightly rough, not grooved at the base, 18–22 mm, brown, basally cream, shiny, not decurrent; **Inf** 8–10 m, paniculate, peduncle dark green, with lanceolate **Bra** 35–76 cm long at the base, fertile part

ellipsoid, lax, with 21–24 4-branched part-**Inf** in the upper ½, the basal ones 45–59 cm long, bulbiferous, bulbils scarce, degenerate; **Ped** 2–8 (–10) mm; **Fl** 52–58 (–61) mm; **Tep** light green or yellowish-green, tube urceolate, grooved, (5–) 8–16 × (5–) 7–10 (–12) mm, lobes triangular, longitudinally brownish striate, erect to slightly reflexed, equal, ±18–21 × 2–3 mm; **Fil** filiform, 45–55 mm, light brown, inserted 3–3.2 mm below the tube throat, long-exserted; **Anth** slender, 20–22 mm, yellow; **Ov** fusiform, rounded, 23–30 (–32) × (4–) 5–8 mm, light green, neck 3–4 mm, mostly constricted; **Sty** filiform, longitudinally striate, 50–55 mm, cream, long-exserted; **Sti** capitate, 3-lobed, papillose, cream to dark brown; **Fr** and **Se** never produced.

According to the protologue the sole South American native *Agave* with light green to yellowish-green flowers, and most similar to *A. sisalana*, but differing esp. in its papillose leaves, slightly rough terminal spine, larger inflorescences mostly with more part-inflorescences, ovaries mostly with distinct neck, a shorter style, light brown filaments inserted below the tube throat, smaller anthers, and the scarce degenerate bulbils. — Thought to be endangered (IUCN category EN).

**A. ×peacockii** Croucher *pro sp.* (Gard. Chron. 1873: 1400, fig. 283, 1873). **Type:** [lecto — icono]: Gard. Chron. 1873: 1400, fig. 283, 1873. — **Lit:** Berger (1915: 120–121); Gentry (1982: 165–169, with ills.); Valverde & al. (1996: with ills.); Ullrich (1996a: with ills.); García-Mendoza (2003: with ill.); García-Mendoza (2011a: 42, 44–45, 50); Smith & Figueiredo (2014c: with ills.); all as *A. peacockii*. **Distr:** Mexico (S Puebla, N Oaxaca); thorn forests on arid calcareous hills, 1000–2200 m; flowers December to April. **I:** Curtis’s Bot. Mag. ser. 3, 57: t. 7757, 1901, as *A. peacockii*; Heller (2006: 118, as *A. peacockii*); Richter (2011: 85); Pilbeam (2013: 165); Hochstätter (2015: IX: 46).

≡ *Agave ghiesbreghtii* var. *peacockii* (Croucher) A. Terracciano (1885) ≡ *Agave roezliana* var. *peacockii* (Croucher) Trelease (1914).

[1g × 2n] *A. ×peacockii* is only known from a small area around Tehuacán in S Puebla and, as recently reported by García-Mendoza (2011a), N



**Fig. 47** *Agave pelona*

(Etter & Kristen 3182:  
Mexico; Sonora, ±  
30 km S of Caborca,  
500 m). (Copyright: J. Etter  
& M. Kristen)



Oaxaca. Berger (1915) was the first to suggest a hybrid origin, and Gentry (1982) assumed that the taxon represents the putative natural hybrid between the sympatric *A. kerchovii* and *A. marmorata*. This is above all suggested by the inflorescences that are intermediate between those of species of Subgen. *Littaea* and Subgen. *Agave* (Gentry 1982). A detailed morphometric analysis of the hybrid and comparisons with its putative parents were provided by Valverde & al. (1996). The illustration cited as ‘type’ by Gentry (1982: 165) is to be treated as neotype, but is superseded by designation of the plate accompanying the protologue as lectotype (Smith & Figueiredo 2014c). The taxon is in danger of extinction (Smith & Figueiredo 2014c).

**A. pelona** Gentry (US Dept. Agric. Handb. 399: 76–80, ills., 1972). **Type:** Mexico, Sonora (Gentry & Arguelles 1989 [US [2 syn], ARIZ, DES, MEXU]). — **Lit:** Gentry (1982: 169–172); Turner & al. (1995: 59–61); Starr & al. (2008); Starr (2012: 204–208); Greulich (2017a); all with ills. **Distr:** Mexico (NW & W Sonora: Sierra del Viejo, Cerro Aquituni, Sierrita de Lopez); limestone rocks and cliffs in arid desert mountains, 500–1220 m; flowers February to May. **I:** Etter & Kristen (2001: 166–167, 169–171, 174); Heller (2006: 120); Richter (2011: 52); Pilbeam (2013: 168); Hochstätter (2015: IX: 41); Moore (2016: 291). – Fig. 47.

[lg] Stems short; **Ros** compact, 40–60 × 60–80 cm, solitary; **L** many, linear-lanceolate,

erect to ascending, thick, stiff, sometimes slightly narrowed towards the base, long-acuminate, rounded below, flat above, epidermis smooth, minutely punctate, waxy, 35–50 × 3–5 cm, shiny dark green, turning reddish to purplish during drought or with age, margins with smooth white firm border becoming brittle and detachable on dried specimens; **marginal teeth** none; **terminal Sp** strong, sharp, sharply angled below, grooved or flat above, 40–70 mm, white to reddish, decurrent as a white border down the leaf margins; **Inf** 2–3 m, ‘spicate’, **part-Inf** in the upper ½, with geminate flowers; **Ped** 30–50 mm, bifurcate; **Fl** campanulate, 45–50 mm; **Tep** dark red, tube openly funnel-shaped, lined with a nectariferous tissue, 8–9 × 15–17 mm, lobes linear-ovate, flat and unkeeled, 18 × 8–10 mm, inner wider, 8- to 9-veined, recurved at the tip, tip apiculate, white-papillate; **Fil** 35–40 mm, inserted on the tube rim, red; **Anth** centric, 15–17 mm, red; **Ov** cylindrical, slender, faintly striate, 20 mm incl. neck, light green; **Sty** slightly longer than the tepals, slightly thickened; **Fr** oblong, thin-walled, rounded, 25–30 × 12–15 mm, shortly apiculate, light pruinose; **Se** thick, rugose, irregular in size and shape, mostly 4–5 × 4–5 mm, sooty black.

Without close relatives in Sect. *Heteracanthae* (as Group *Marginatae*) and geographically isolated from its remaining species, but possibly closest to *A. potrerana*, which likewise has a red corolla and a strong tendency towards the reduction of the marginal teeth (Gentry 1982: 169).

*A. pelona* might be misplaced in this group and perhaps belongs to Sect. *Littaea* (as Group *Filiferae*), as indicated by its funnel-shaped flower tube with nectariferous inner lining and red tepals with recurved lobes. Molecular AFLP data (Gil-Vega & al. 2007) place the species among Sect. *Heteracanthae* (as Group *Marginatae*), however. Specimens from the Sierra Seri with smaller, greener leaves and caespitose rosettes were included in the strictly solitary *A. pelona* by Gentry (1972), Gentry (1982) and Turner & al. (1995), but specimens from that area were found to be misidentified by Starr and have been identified as *A. chrysoglossa* by R. Felger (Starr 2012: 205). Gentry's type at US consists of two sheets which are not cross-labelled and thus represent syntypes.

*A. pelona* is an important part of the diet and water source for Bighorn Sheep (*Ovis canadensis mexicana*), which feed on whole plants throughout the year and during the flowering period on inflorescences to meet its food and water demands. In the first half of the twentieth century, the species was harvested at small scale for the production of an alcoholic beverage (Velazco Macías & Alanís Flores 2002), and Seri Indians used to eat the hearts (Turner & al. 1995). Nevertheless, the populations are healthy, with plants of all sizes and ages being found (Velazco Macías & Alanís Flores 2002).

**A. pendula** Schnittspahn (Z. Gartenbau-Vereins Darmstadt 6: 7, 1857). **Type** [neo]: Ex cult. (*Anonymous* s.n. [K]). — **Lit:** Todaro (1876–92: 32–35, t. VIII, 1876, as *A. caespitosa*); Berger (1915: 60–61, as *A. sartorii*); Gentry (1982: 217, 226–228, with ills.); Lott & García-Mendoza (1994); Cházaro Basáñez (2001: with ills.); Cházaro Basáñez & al. (2010a: 3, 10, with ills.); Cházaro Basáñez & Vázquez-García (2013: 59, map). **Distr:** Mexico (C Veracruz, W Chiapas), W Guatemala (Huehuetenango); cliffs and steep canyon walls in tropical deciduous forests, 50–1000 m; flowers January to February. **I:** Curtis's Bot. Mag. 103: t. 6292, 1877, as *A. sartorii*; Cházaro Basáñez (2001); Pilbeam (2013: 169).

**Incl.** *Agave aloina* K. Koch (1860); **incl.** *Agave sartorii* K. Koch (1860); **incl.** *Agave noacksii* Hort. Tonel ex K. Koch (1862); **incl.** *Agave noackii*

Jacobi (1865)  $\equiv$  *Furcraea noackii* (Jacobi) hort. ex Baker (1877); **incl.** *Agave pulcherrima* hort. ex K. Koch (1865) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave rufocincta* Jacobi (1868); **incl.** *Agave rubrocincta* Jacobi (1869); **incl.** *Agave caespitosa* Todaro (1876)  $\equiv$  *Agave sartorii* var. *caespitosa* (Todaro) A. Terracciano (1885).

[1f] Stems long, to 200  $\times$  5–11 cm, bifurcate, sometimes creeping but mostly pendent; **Ros** open, spreading, branching axillary; **L** 20–30, oblong to slenderly lanceolate, softly fleshy, ascending to somewhat outcurving, rounded below, flat to concave above, 40–93  $\times$  4.8–11 cm, light green to yellow-green, with pale yellow mid-stripe, margins not horny, denticulate, denticles  $\pm$  1 mm, absent for 12–16 cm below the tip, brown; **terminal Sp** small, 5–8 mm, brown, not decurrent; **Inf** “lateral” according to Cházaro Basáñez & al. (2010a: 8), but actually likely terminal on rudimentary lateral rosettes, 1.3–1.8 m, ‘spicate’, fertile part slender, drooping, laxly flowered in the upper  $\frac{1}{3}$ – $\frac{1}{2}$  of the inflorescence, part-**Inf** with solitary or geminate **Fl** 30–45 mm long; **Te** greenish or tinged with lavender, whitish inside, tube funnel-shaped, 6–13 mm, lobes linear,  $\pm$  equal, 12–16  $\times$  5–7 mm, with broad adaxial nerve, slightly recurved at the tips; **Fil** 30–50 mm, yellowish-green to brownish; **Anth** 10–18 mm, yellowish to brownish; **Ov** bluntly trigonous, 10–15  $\times$  6–7 mm, neck long, constricted for 4–5 mm; **Sty** thick, strong, longer than the filaments, brownish; **Sti** 3-lobed; **Fr** globose to oblong, thin-walled, rounded at the base, obtuse at the apex, 20–22  $\times$  10–12 mm; **Se** hemispherical, sharply angled, with pronounced marginal wing, 4  $\times$  2.5–3 mm, shiny black. — **Cytology:** 2n = 60 (Vignoli 1936: as *A. sartorii*, Simpson & al. 2011).

Very distinctive with long stems and rosettes with overhanging inflorescence. Additional morphological and distributional data with a first record for Guatemala were published by Cházaro Basáñez & al. (2010a). *A. pendula* is closely related to the recently published *A. gomezpompa* and *A. wendtii* from Veracruz (see there for differences), and more distantly to *A. jimenoii*. Mature clumps flower frequently with several inflorescences (Gentry 1982). Material was distributed

by ISI as ISI 2003-11. Gentry (1982: 226, 234) designated 2 sheets at K as neotype, but this is only a first-step neotypification as the sheets are not cross-labelled.

**A. petiolata** Trelease (Mem. Nation. Acad. Sci. 11: 20, t. 8, 1913). **Type:** Curaçao (*Boldingh* A8 [MO [4 sheets]]). — **Lit:** *Boldingh* (1913: 150); *Boldingh* (1914: 18); *Berger* (1915: 225); *Hummelinck* (1936: 243–244); *Hummelinck* (1993: 104, 106–107, 222, with ill.). **Distr:** Leeward Antilles (Curaçao); cultivated on former plantations, on calcareous flats in xeric shrubland. **I:** Online Flora of Curaçao (2018).

**Incl.** *Agave lurida* Hamelberg (1898) (*nom. illeg.*, ICN Art. 53.1).

[2u] Stems to 1 m, grey; **Ros**  $\pm 2$ –2.5 m  $\varnothing$ , solitary and not suckering; **L**  $\pm 15$ , lanceolate, rather abruptly contracted into a long neck at the base, widest below the middle, gradually acute, 80–130  $\times$  10–20 cm, blue-glaucous, with imprints from the central bud, margins nearly straight between the teeth or prominences; **marginal teeth** rather slenderly subulate, straight or variously curved, downcurved somewhat below the middle, narrowly triangular from half-round bases 5–10 mm wide, purplish chestnut-brown, raised on well to rather strongly developed hardening or green prominences, teeth 5–7 (–11 below and above the middle) mm, granular-roughened, purplish chestnut-brown, 15–30 (–60) mm apart, occasionally with much smaller intermittent teeth; **terminal Sp** acicular, straight or somewhat curved,  $\pm$  flexuous, broadly round-grooved to or beyond the middle, granular-roughened below, covered with very many minute tubercles, smooth towards the tip, 18–35 (–60)  $\times$  3–4.5 mm, chestnut-brown, shortly decurrent, dorsally not intruding into the leaf tissue; **Inf** 3–9 m, paniculate, not further described; **Ped** scarcely 5 mm; **Fl** 35–40 mm; **Tep** tube open, 5 mm, lobes 15  $\times$  3 mm; **Fil** 30 mm, inserted nearly in the throat; **Ov** fusiform, 15 mm; **Fr** and **Se** unknown.

A curious plant, in leaf armature suggesting some of the Mexican species grown for pulque (Trelease 1913). One sheet of the holotype (MO 138457) is annotated as “cultivated; only on two plantations and in small numbers”, which was

repeated by *Boldingh* (1913) (“gekweekt”) and *Boldingh* (1914) (“cultivated”). The species gives *Hummelinck* (1936) “the strong impression of not belonging to the native flora”. It is regarded as introduced by *Hummelinck* (1938: 15) and is today only found in an area where fibre Agaves were formerly cultivated (*Hummelinck* 1993: 107), but on naturally appearing habitats (*Hummelinck* 1993: 106, Fig. 18; Online Flora Curacao 2018). *Hummelinck* (1938: 15) excludes the species from Sect. *Viviparae* (as Group), but does not provide an alternative placement. — The photograph in *Pilbeam* (2013: 170) labelled *A. petiolata* appears to represent *A. vicina* (cf. *Pilbeam* (2013: 230)).

**A. petrophila** García-Mendoza & E. Martínez (*Sida* 18(2): 627, 1998). **Type:** Mexico, Guerrero (*Martínez & al.* 2639 [MEXU, BRIT, ENCB, K, MO]). — **Lit:** García-Mendoza & Martínez (1998); García-Mendoza (2011a: 45–50); Starr (2012: 209–212, 314–316); all with ill. **Distr:** Mexico (E Guerrero, S Puebla, W & N Oaxaca); steep to vertical rocky slopes, in calcareous soil, desert scrubs, tropical deciduous forests and ecotones to pine-oak forests, 850–2100 m; flowers October to December. **I:** *Pilbeam* (2013: 171); *Hochstätter* (2015: VIII: 7).

$\equiv$  *Agave gracilis* García-Mendoza & E. Martínez (1998) (*nom. illeg.*, ICN Art. 53.1).

[1a] Stems procumbent, to 1 m; **Ros** semi-globose, compact, 50–80  $\times$  60–80 cm, caespitose; **L**  $> 100$ , linear, straight or somewhat recurved, flat, flexible, subcoriaceous, with longitudinal striae, 40–70  $\times$  0.4–0.9 (at mid-leaf) cm, broadened to 1–1.5 cm at the base, light glaucous to glaucous-green, margins yellowish, finely denticulate; **terminal Sp** weak, subulate, 3–6 (–8) mm, brownish-reddish; **Inf** 1.8–2 m, ‘spicate’, erect or slightly inclined, peduncle with filiform delicate brown **Bra** 5–15 cm long, fertile part in the upper  $\frac{1}{4}$ – $\frac{1}{2}$  of the inflorescence; floral **Bra** linear, 2–3.5  $\times$  0.1–0.2 cm, much longer than the flowers, persisting; **Ped** 1 mm, at fruiting time 2 mm; **Fl** campanulate, 20–22 (–25) mm; **Tep** oblong, green to greenish-yellow, tips dark reddish, tube sulcate, 3–5 (–8)  $\times$  5–8 mm, lobes deltoid or oblong, divaricate, recurved or straight, 5–9 (–11)  $\times$  2.5–3.5

(–4.5) mm, **ITep** keeled; **Fil** 27–30 mm, inserted at the mouth of the tube, yellow to reddish above; **Anth** centric, 7–9 mm, reddish; **Ov** cylindrical, 7–10 × 2–4 mm, without neck, slightly penetrating into the tepal tube; **Sty** 30–35 mm; **Sti** slightly thickened; **Fr** subglobose, trigonous, ringed at the apex, 9–10 × 8–9 mm, sessile, rostrate, green-brown, with stamens and style persisting; **Se** thickened on the curved side, 3–3.5 × 2–2.5 mm, black.

Sharing morphological characteristics with *A. dasyliroides*, but differing in its small caespitose rosettes, smaller and narrower leaves, erect or slightly inclined inflorescences, much smaller flowers and smaller and globose fruits (García-Mendoza & Martínez 1998). The species was first named *A. gracilis*, but this is an illegitimate later homonym of *A. gracilis* Jacobi (1871). García-Mendoza (2011a) provides a new record from Puebla.

García-Mendoza & Martínez (1998) provisionally placed the plant from Yosondua, Oaxaca referred to *A. dasyliroides* by Ullrich (1990f) here, but that plant is the recently published close relative *A. kavandivi* (see there for differences). *A. graciellae* is a further recently published close relative (see there for differences); and *A. rzedowskiana* has similar flowers but different leaves (see there). Molecular AFLP data (Gil-Vega & al. 2007) place the species closest to *A. stricta* and less close to *A. tenuifolia*, *A. striata* and *A. dasyliroides*, but no further species of Sect. *Juncineae* (as Group *Striatae*) were sampled.

**A. petskinil** (R. A. Orellana & al.) Thiede (Haseltonia 17: 94, 2012). **Type:** Mexico, Yucatán (*Carnevali & Ramírez* 7206 [CICY, MO, QMEX]). — **Lit:** Hernández-Sandoval & al. (2008); Orellana (2012); Carnevali (2013); all with ill. and as *Manfreda*. **Distr:** Mexico (Yucatán); open or shaded areas over limestone, rocky shallow soils in tropical (sub-)deciduous forests, often associated with sinkholes (“cenotes”), 5–30 m; flowers January to April. **I:** Hochstätter (2016: I: 34, as *Manfreda*).

≡ *Manfreda petskinil* R. A. Orellana & al. (2008).

[3a5] Herbaceous, acaulescent; **Ros** 0.3–0.5 m; rhizomes globose, 5–7 cm, producing new

rosettes from lateral meristems at the base of the inflorescence; **R** succulent; **L** mostly lost during the dry season, some persisting, 7–30, linear-lanceolate, recurved, somewhat flaccid, succulent (±1.4 mm thick at the widest section), slightly channelled, surface almost smooth, 18–38 × 1–2 cm, pale to dark green, with darker green to reddish spots, these more vivid on some individuals and when exposed to bright light, margins hyaline, denticulate with small, irregular teeth 0.25–5 mm long, apex long-attenuate with a short soft tip; **Inf** 1.3–1.6 m, a raceme or more often a panicle with 2–5 branches in well-developed plants, peduncle 1.1–1.35 m, with 3–6 internodes, green or reddish, often with darker blotches as in the leaves, with several **Bra** 1–3 cm long, fertile part 20–35 cm, branches suberect, 15–23 cm, densely flowered; **Ped** 1–1.5 (–2) mm; **Fl** solitary, 30–35 mm; **Tep** light green outside, glaucous, dull yellowish-green inside or with reddish tinge, tube 5–7 mm, broadly funnel-shaped, lobes 12–15 × 2–4 mm, reflexed during the staminate phase of the anthesis, then erect, apex cucullate, with a small tuft of glandular white hairs; **Fil** filiform, 40–70 mm, dark shiny reddish-brown; **Ov** cylindrical, 12–18 mm, coloured as the tepal outside; **Sty** linear, 60–68 mm, dark shiny reddish-brown; **Sti** capitate to clavate, 3-lobed; **Fr** trapezoid or asymmetrically oblong to ovoid when unripe, 10–15 × 7–8 mm, ripe **Fr** not seen; **Se** unknown.

Closest to *A. paniculata* according to the protologue, likewise from the Yucatán Peninsula, which is a much larger plant with a larger, more complex inflorescence. *A. petskinil* was included in *A. variegata* by earlier authors, from which it differs in its puberulent and denticulate leaves, ascending flowers, and filament insertion at the throat of the tube. The stamens of *A. petskinil* are widely divergent as opposed to the commonly subparallel stamens in most species of Sect. *Herbaceae*. The tropical lowland habitat is atypical and apparently not known for other species of Subgen. *Manfreda* except *A. paniculata*, *A. chamelensis*, and *A. littoralis*.

*A. petskinil* and the similar *A. paniculata* share the unusual paniculate inflorescences and a tendency towards becoming caulescent, suggesting natural hybrids between Subgen. *Manfreda* and a paniculate



Agave, namely *A. fourcroydes* or *A. angustifolia* (Jankalski, message in Agavaceae@yahoo.com, 2008). Both species have been found primarily near sinkholes and might have been perpetuated as superior medicinal, soap and fibre producing or ornamental plants (Jankalski l.c.); the leaves of *A. petskinil* are used against headache according to the protologue.

**A. ×pfersdorffii** Hort. Besaucèle *ex* André (Rev. Hort. (Paris) 76: 326, 1904). **Type:** not typified. — **Lit:** Berger (1915: 50). **Distr:** Cultivated only.

[1f × 1g] According to Berger (1915: 50), this name was first published by Besaucèle in his elusive (no copies have been traced so far) “Catalogue Raisonné” from 1894 with the statement “Hybride très remarquable, de grandes dimensions. Les feuilles sont larges bleutées” for a hybrid between *A. obscura* (as *A. xalapensis*) × *A. lechuguilla* (as *A. univittata*), raised by Pfersdorff at Paris. André (1904) provides a short description of a plant flowering in the collection of Ch. Simon and states that the second parent is *A. xylonacantha*, a view also expressed by Trelease (1914: 236).

**A. phillipsiana** W. C. Hodgson (Novon 11(4): 410–411, ills., 2001). **Type:** USA, Arizona (Hodgson 11861 [DES, ASU, GCNP, MO [photo], SD]). — **Lit:** Hodgson (1999b: 11–12, with ills., as *A. sp.*); Brian (2000: with ills., as *A. sp. nova*); Reveal & Hodgson (2002); Klopper & al. (2010: 62); Parker (2018a: 22, 25, with ills.). **Distr:** USA (Arizona: Grand Canyon National Park); sandy to gravelly places with desert scrub along permanent waterways, 700–1140 m; flowers September.

[2h] Acaulescent; **Ros** open, 0.75–1 × 0.75–1 m, solitary to caespitose, freely suckering; **L** numerous, ascending to spreading, lanceolate, acuminate, firm, broadest just below the middle, thickish and convex towards the base, concave towards the apex, 76–78 × 10–11 cm, slightly glaucous-green to dark green, very lightly cross-zoned, margins straight or repand; **marginal teeth** variable, upcurved or reflexed, weakly attached, 4–7 mm, red-brown aging to grey, 10–25 mm apart, intermittent teeth (2–) 3–7 along the upper 2/3 of the leaf; **terminal Sp** slender, openly grooved,

25–40 mm, dark brown to grey, decurrent for up to 7.2 cm to the upper teeth; **Inf** 2.5–5.5 m, narrowly paniculate, fertile part open, maroon-glaucous-pruinose, with 9–16 short slightly ascending to horizontal part-**Inf** in the upper 1/3–1/2, with 32–45 densely clustered flowers; **Ped** 5–10 mm; **Fl** 68–86 mm, thick; **Tep** tube very thick, bulging at the lobe bases, 5.5–20 × 15–23 mm, pale creamy yellowish-green, lobes broadly lanceolate, erect, leathery, persistent, clasping the filaments, unequal; **OTep** 20–21.5 × (5–) 8–12 mm, whitish-cream with a light green tinge, becoming dark maroon at anthesis, tips brown-maroon, felt-like, rugose and hooded; **ITep** 15–19 × (4–) 5–8 mm, strongly keeled, similarly coloured; **Fil** 48–64 mm, subequally inserted 7.5–11 and 9–12 mm above the tube base; **Anth** 17–25 mm, yellow; **Ov** thick, 29–46 mm, neck 4–8 mm, slightly constricted, pale creamy yellowish-green; **Sty** 60–78 mm, slightly longer than the filaments, pale creamy yellowish-green flecked with maroon; **Sti** capitate, 3-lobed; **Fr** and **Se** not produced. — **Cytology:** 2n = ±120 (protologue).

The species reproduces exclusively by vegetative means. According to the protologue known from only four places within the Grand Canyon National Park, three of which are near pre-Columbian agricultural features or habitation sites, but Parker (2018a: with map) reports the species from numerous localities across N & C Arizona, allied with the ancient Sinagua culture. It possibly represents an ancient cultivar selected by pre-Columbian people from populations related to *A. palmeri*, *A. colorata*, or other closely related taxa. For further pre-Columbian cultivar species in Arizona, see also under *A. verdensis*.

**A. pintilla** S. González & al. (Acta Bot. Mex. 95: 81–83, ills., 2011). **Type:** Mexico, Durango (Reséndiz & al. 131 [CIIDIR, ENCB, MEXU]). — **Lit:** González-Elizondo & al. (2009: 132–136, as *A. victoriae-reginae* El Mezquital); Thiede (2011: 153–155); both with ills. **Distr:** Mexico (SE Durango); conglomerate slopes in a volcanic area with igneous rock fragments, in calcareous soils in desert scrub, 1440–1580 m. **I:** Roosbroeck (2012: 164); Pilbeam (2013: 172); Ettelt (2014: 122); Hochstätter (2015: IX: 54).



[lg] Acaulescent; **Ros** 30–60 × 20–35 cm, lax, open, caespitose or solitary, surculose; **L** 60–180, narrowly triangular, narrowing gradually towards the apex, very broad at the base, tip acute, with a prominent white apical band 5–10 mm wide around the base of the terminal spine, dorsally rounded or keeled in the upper part, ventrally concave or flat towards the base, 13–22 × 5.8–8 cm, pale green to bluish-green, with white bands on both faces and the margins, margins horny, white, entire, continuous to the leaf base and apex or terminating 2–3 cm below the apex, 3–5 mm wide; **marginal teeth** none; **terminal Sp** narrowly pyramidal to lanceolate, 20–29 mm, broadly channelled above and roundish keeled below, nearly black, not or only very slightly decurrent along the leaf margins, usually with 3 adjacent teeth or at least with 1 very short dorsal spine; **Inf** erect, 1.6–4.3 m, ‘spicate’, peduncle robust, with several chartaceous deltoid **Bra**; **Fl** laxly arranged, usually geminate, 58–65 mm; **Tep** 40–44 mm, whitish to greenish-white, tube funnel-shaped, 3–5 × 8–10 mm, lobes ascending to patent, subequal, broadly linear, 18–22 × 5–7 mm, somewhat conduplicate at the base, flat towards the apex; **Fil** 58–66 mm, inserted above the throat of the tube, greenish-white or with purple tinge; **Ov** thickly fusiform, 18–21 mm, neck short, greenish; **Fr** woody, broadly oblong, rounded at the base, 22–24 × 16–18 mm, shortly apiculate; **Se** suborbicular, semicircular or drop-shaped, 4–5 × 2.5–4 mm, black, shiny or dull black.

First depicted by González-Elizondo & al. (2009: 135, 136) as “*A. victoriae-reginae* El Mezquital, Dgo.”. Two years later, this species was described in the context of the study of the *A. victoriae-reginae* complex by González-Elizondo & al. (2011), in which *A. nickelsiae* was also re-established as species. *A. pintilla* is characterized by 60–180 (vs. 170–280 in *A. nickelsiae*) green to bluish-grey-green, narrowly triangular, not puberulent leaves (vs. grey-green to dull green, puberulent, oblong) with a not or hardly decurrent terminal spine (vs. decurrent). The species propagates by seeds and vegetatively by rhizomes; the latter is commoner (González-Elizondo & al. 2011). In its foliar phenole profile,

the species differs clearly from all other members of the *A. victoriae-reginae* complex (Almaraz-Abarca & al. 2013c).

According to the protologue, *A. pintilla* is restricted to near El Mezquital, SE Durango, ±170 km apart from the closest localities of *A. victoriae-reginae* ssp. *swoboda* in NE Durango. However, the species also occurs ±150 km N of Ciudad Durango and possibly also near Nombre de Dios (Thiede 2011). *A. pintilla* rarely forms natural hybrids with *A. salmiana* ssp. *crassisipina* (González-Elizondo & al. 2011).

**A. planifolia** S. Watson (Proc. Amer. Acad. Arts 22: 479, 1887). **Type:** Mexico, Chihuahua (Pringle 1141 [GH, VT]). — **Lit:** Rose (1903c: 22); Berger (1915: 37); Gentry (1972: 153); Verhoek-Williams (1975: 255–258); Piña Luján (1985: 88–89); García-Mendoza (2003); Castillejos-Cruz (2009: [226]–[231], with ills.); Castro-Castro (2017: 61–63, 68, with ills.); all as *Manfreda*. **Distr:** Mexico (SE Sonora, C & S Chihuahua, C Nayarit); sandy banks near streams and in grasslands, pine or pine-oak forests, 1400–2300 m; flowers September to December. **I:** Hochstätter (2016: I: 35, as *Manfreda*).

≡ *Manfreda planifolia* (S. Watson) Rose (1903) ≡ *Polianthes planifolia* (S. Watson) Shinnors (1966).

[3a3] Herbaceous, medium-sized (for Subgen. *Manfreda*); corm globose to subglobose, 3–4 × 3–3.8 cm, bulb globose, 3.5–4 × 3–3.5 cm, covered almost entirely with dry leaf bases 3.8–7 cm long; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, 4–5, spreading-arching, oblong to narrowly elliptic, narrowed towards the clasping, petiole-like, 1.5–2 cm long base, tip acuminate, with a short point, channelled in the petiolar portion and at the tip, nearly flat in the middle, semisucculent, drying leathery, smooth, with raised ribs below, 20–32 × (2.5–) 3–7.5 cm, green, unspotted, margins with a narrow hyaline band, minutely and irregularly to regularly denticulate; **Inf** 1.2–1.6 m, erect, ‘spicate’, light green to yellow, peduncle with 5–8 truncate, narrowly elliptic, slightly amplexicaul **Bra**, upper ones lanceolate, fertile part short,

dense, (6–) 10–12 cm, with 6–14 sessile flowers; floral **Bra** 8–12 × 3–5 mm; **Fl** 18–28 mm, ascending; **Tep** yellowish-green, tube cylindrical, at a slight angle to the ovary, 5–7 × 4–5 mm, slightly constricted at the apex of the ovary, lobes oblong to narrowly elliptic, recurved to reflexed, apex cucullate, with a tuft of short white hairs, 12–19 × 4–5 mm, yellow-green; **Fil** erect at anthesis, 26–40 (–56) mm, inserted at the same level at mid-tube, reddish-green with small purple dots; **Anth** 12–15 mm, yellow; **Ov** cylindrical to slightly ellipsoid, 9–15 × 5–7 mm, extending 1–4 mm into the tepal tube; **Sty** 36–55 mm, exceeding the tube by 35–42 mm at anthesis, yellowish-green; **Sti** clavate, 3-lobed; **Fr** ovoid to subglobose, 15–20 × 15–18 mm, with a scar near the apex, base of style and dry perianth persistent; **Se** deltoid, plane-concave, 4–5 × 3–4 mm, with a narrow margin, black, shiny.

Characterized by broad leaves flattened in the middle and channelled at the base and tip, and the narrowed leaf base forming a pseudopetiole (Castillejos-Cruz 2009). Closely related to *A. guttata*, but distinctive because of its elliptic leaves with the appreciably narrowed and clasping base and acuminate tip, as well as the more N range (Verhoek-Williams 1975: 257, Castillejos-Cruz 2009). The species shares the flower shape, the size of the tepal tube as well as the size and shape of the lobes with *A. guttata* and the undescribed *Manfreda riosramirii* (from Puebla) but both these species do not have the fragile and brittle leaves of *A. planifolia* and its unpleasant floral odour (Castillejos-Cruz 2009) (as *Manfreda*). — The species is known from few collections only and is listed as threatened with extinction (Rodríguez & Castro-Castro 2006, Rodríguez & Castro-Castro 2007) (both as *Manfreda*).

**A. platyphylla** (Rose) Thiede & Eggli (Kakt. and. Sukk. 50(5): 112, 1999). **Type:** Mexico, Jalisco (Rose 2598 [US, GH, MEXU, MO, NY]). — **Lit:** Rose (1903a: 11); McVaugh (1989: 255–256, with ills.); García-Mendoza (2003); Feria-Arroyo & al. (2010: with ill.); all as *Polianthes*. **Distr:** Mexico (S Durango, S Zacatecas, Nayarit, Jalisco); grasslands, rocky mesas among grasses, hillsides in pine, pine-oak or oak

and tropical deciduous forests, 1400–2520 m; flowers June to November. **I:** Hochstätter (2016: II: 22); Castro-Castro & al. (2016: 721); Castro-Castro (2017: 137); Solano & al. (2019: 5, 8, 9, with ills.); all as *Polianthes*.

≡ *Polianthes platyphylla* Rose (1903) ≡ *Bravoa platyphylla* (Rose) Conzatti (1947).

[3b1] Herbaceous; corm ±0.5–0.8 × 1–1.2 cm, bulb 1.8–3.5 × 1.2–2.3 cm, ovoid, nearly completely covered with dried leaf bases, these membranous at the base and fibrous above; **R** fleshy, thickened, tapering, to 3–7 cm, contractile, in a dense cluster; **L** drought-deciduous, (1–) 2–6 (–10), lying flat on the ground, elliptic-lanceolate to narrowly ovate, narrowed at the base to a short subpetiolar part to 5 mm wide, apex long-acute, apiculate, 7–16 × 1–4 cm, green, with purple dots near the base, margins entire, with a narrow hyaline band; **Inf** 27–60 cm, erect, ‘spicate’, peduncle with 2–3 **Bra**, bracts lanceolate-attenuate, 2–10 cm, internodes decreasing distally, fertile part (4–) 6–13 cm, lax, with 3–25 remote floral nodes; floral **Bra** deltoid-ovate, 0.8–1.2 cm; **Ped** none; **Fl** geminate, fragrant with *Gardenia*-like scent, 15–22 mm; **Tep** white, cream or rose to red at senescence, tube cylindrical, ±10–16 (–21) × 2.5–3.5 mm (near the filament insertion), curved outwards just above the ovary, diffuse to divaricate, mouth oblique, lobes equal, ovate to orbicular, 2–2.5 (–3) × 2–2.5 (–3) mm, **OTep** nearly erect, **ITep** reflexed, apex cucullate, rounded, with a bundle of white trichomes; **Fil** filiform, 1–5 mm, included, inserted 3–6 mm below the mouth of the tube; **Anth** linear, 3–4 mm; **Ov** ellipsoid, ±3.5–4 × 2.5–3 mm, erect at anthesis or nearly so; **Sty** filiform, 10–18 mm, white, tips exerted; **Sti** 3-lobed, white; **Fr** narrowly ellipsoid to subglobose, stoutly stipitate, 7–13 × 7–10 mm, with persisting tepals; **Se** crescent-shaped, flat, 2.5–4 × 2–3.4 mm, shiny or opaque.

*A. platyphylla* is distinct in Ser. *Polianthes* of Sect. *Polianthes* esp. in its mostly broader, lanceolate leaves and its sessile flowers with short tube. *A. rosei* has a similarly short tube, but differs in its ensiform, narrower leaves and pedicellate flowers. Feria-Arroyo & al. (2010) assess the extinction risk and classify the species as “Endangered”.

**A. polianthiflora** Gentry (US Dept. Agric. Handb. 399: 51–54, ills., 1972). **Type:** Mexico, Chihuahua (*Gentry* 8013 [US, ARIZ, MEXU]). — **Lit:** Gentry (1982: 202–205); Ullrich (1989c); García-Mendoza (2003); Starr & Devender (2011:

220–230); Starr (2012: 213–216, 310–311); all with ills. except García-Mendoza. **Distr:** Mexico (E & SE Sonora, W, SW & C Chihuahua); infrequently in small clones on rock outcrops, slopes and grazed pastures, in pine-oak or oak forests, 1220–2000 m; flowers June to July. **I:** Thiede & Eggli (1999: 109); Etter & Kristen (2003a: 10); Heller (2006: 121, 122); Richter (2011: 64, 107); Pilbeam (2013: 173); Ettelt (2014: 116); Hochstätter (2015: VIII: 61); Greulich (2018a: 31–33). — Figs. 48 and 49.

[1e] Acaulescent; **Ros** 8–20 × 12–30 cm, solitary or caespitose; **L** linear-lanceolate, widest in the middle, convex below, flat above, 10–20 × 1–1.3 cm, green, both faces with white impressions from the central bud, margins conspicuously white-filiferous; **marginal teeth** minute, near the leaf base only; **terminal Sp** weak, 7–10 mm, greyish; **Inf** 1.2–2 m, ‘spicate’, axis red, with deltoid-lanceolate subulate chartaceous **Bra** 1–2 cm long, part-**Inf** in the upper ½ of the inflorescence, usually with 2 (or 1 or 3) laxly arranged flowers; floral **Bra** triangular, 3–6 mm; **Ped** short; **Fl** 37–42 mm; **Tep** pruinose-pink, tube long, very narrow and curved below, 22–32 × 6–8 (at the mouth) mm, lobes ovate to deltoid, subequal, 4–7 mm; **Fil** 27–37 mm, inserted 4–6 mm above the tube base; **St** shortly exerted, reddish before anthesis, yellow afterwards; **Ov** ovoid, 9–12 × 3.5–5 mm, red; **Sty** slender, exerted before anthesis; **Sti** thickened; **Fr** globose to ovoid, rugose,



**Fig. 48** *Agave polianthiflora* (Cultivated material without known wild origin). (Copyright: U. Eggli)

**Fig. 49** *Agave polianthiflora* (Eggli & al. 2038: Mexico; Sonora, Yecora, 1600 m). (Copyright: U. Eggli)



10–15 mm, apiculate, pruinose; **Se** thick, 3.5–4 × 2.5–3 mm, black.

Differs from all other members of Subgen. *Littaea* by its long tubular flowers with very short lobes, similar to those of Sect. *Polianthes*. Moreover, as the style is exerted before anther dehiscence, its flowers are not proterandrous, as in other agaves (Gentry 1982). *A. polianthiflora* is difficult to distinguish from *A. parviflora* vegetatively, but its leaf tip is at a less obtuse angle than in *A. parviflora*, its leaves tend to be widest below the middle (vs. broadest at or above the middle), and the leaf marginal fibres tend to be either straight or slightly curved back (vs. fibres shaped like an inverted U; Starr 2012: 311). The species was first collected by Pringle back in 1888 (Pringle 1995; MO, US) and first depicted by Jacobsen (1954: 149, as *A. parviflora*).

In moist or more fertile situations and if watered frequently in cultivation, the leaves become much larger than in its natural habitat (Gentry 1982). The Wariho Indians manufactured a sweet food from pit-baked plants, and used the inflorescence stalks as arrow shafts (Gentry 1982).

**A. potatorum** Zuccarini (Flora 15:2(Beiblatt 2): 96–97, 1832). **Type** [neo]: Mexico, Puebla (Gentry & al. 20427 [MEXU 116053, ARIZ, US]). — **Lit:** Berger (1915: 185–187); Gentry (1982: 468, 490–493); Arias Toledo & al. (2000: 18); Forster (2006); García-Mendoza (2010: 73–78, 90–92); García-Mendoza (2011a); Starr (2012: 217–222, 312–323); all with ills. **Distr:** Mexico (Puebla, Oaxaca, W-C Veracruz); plains or slightly inclined sites in soils derived from calcareous rocks, in tropical deciduous forests and xerophytic scrub with cacti or oaks, and ecotones of both with oak forests, 1240–2400 m; flowers end of August to November. **I:** Curtis's Bot. Mag. 91: t. 5493, 1865, as *A. saundersii*; Refug. Bot. 5: t. 306, 1872, as *A. verschaffeltii*; Refug. Bot. 5: t. 328, 1872, as *A. scolymus*; Ettelt & Riedel (1998); Heller (2006: 123, 162); Richter (2011: 84, 112); Pilbeam (2013: 174–176).

**Incl.** *Agave potatorum* var. *minor* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave scolymus* Karwinsky ex Salm-Dyck (1834); **incl.** *Agave elegans* hort. ex Salm-Dyck (1859); **incl.** *Agave*

*latifolia* Karwinsky ex Salm-Dyck (1859); **incl.** *Agave pulchra* hort. ex Salm-Dyck (1859); **incl.** *Agave quadrata* Lemaire (1864); **incl.** *Agave saundersii* Hooker fil. (1865); **incl.** *Agave schnittspahnii* Jacobi (1865); **incl.** *Agave verschaffeltii* Lemaire ex Jacobi (1865) ≡ *Agave potatorum* var. *verschaffeltii* (Lemaire ex Jacobi) A. Berger (1915); **incl.** *Agave scolymus* var. *polymorpha* A. Terracciano (1885); **incl.** *Agave auricantha* Baker (1888).

[2o] Acaulescent; **Ros** compact to openly spreading, 30–50 × 40–60 cm, solitary, rarely with 1–3 offsets on stolons; **L** 30–60 (–100), erect, ovate, oblong or (shortly) lanceolate, softly fleshy but rather rigid, thickened and narrowed towards the base, flat to somewhat concave above towards the apex, 15–35 × (5–) 8–10 cm, glaucous to glaucous-green, margins repand to deeply crenate, with tubercle-like prominences 4–7 (–10) mm long, esp. above mid-leaf; **marginal teeth** on low broad bases, straight, recurved or antrorse, at mid-leaf 4–6 (–12) × 4–6 (–8) mm, chestnut-brown to greyish-brown, mainly 10–30 mm apart; **terminal Sp** broad at the base, sharply pointed, straight or sinuous, broadly grooved to flat above, 30–40 × 4–7 mm, chestnut- to greyish-brown, sharply decurrent as a ridge to the uppermost teeth; **Inf** 3–5 (–6) m, paniculate, peduncle green to reddish-brown, with triangular chartaceous reddish-brown **Bra** 12–20 cm long, fertile part open, with (7–) 11–25 small compact part-**Inf** in the upper 1/3 or 1/2 of the inflorescence, these 10–30 cm and separated for 15–30 cm, with (15–) 20–40 flowers; **Ped** 10–15 mm; **Fl** campanulate to somewhat urceolate, (50–) 55–70 mm; **Tep** light green to yellowish-green, frequently tinged red or purplish in bud, tube cylindrical to funnel-shaped, sulcate, (10–) 13–16 × (8–) 13–18 mm, lobes erect, triangular to oblong, thick, outer 1–2 mm longer than the inner, margins involute, tip cucullate, hard, keeled on the inner face; **Fil** 30–40 (–45) mm, inserted at mid-tube or above, yellowish, sometimes with purple tinge; **Anth** 15–25 mm, yellow; **Ov** cylindrical to slightly triquetrous, 25–30 × 4–6 mm, green, neck 2–3 (–5) mm; **Sty** 55–60 mm; **Sti** clavate, 3-lobate; **Fr** oblong, (35–) 40–60 × 15–20 mm, stipitate, rostrate; **Se** crescent-shaped, flat, faintly winged, 5–6 × 4–5 mm,



black. — **Cytology:**  $2n = 45-60, 60 (= 2 \times)$  (Gómez-Pompa & al. 1971: as *A. verschaffeltii*, Lv & al. 2009, Simpson & al. 2011).

This very polymorphic species is widely distributed in horticulture and vegetatively characterized by its compact rosettes with a large number of flat leaves with small prominences and teeth. In the central valleys of Oaxaca, it shows a great variation in vegetative and reproductive features which is probably due to genetic exchange with the sympatric and synchronously flowering, closely similar *A. seemanniana*. The latter differs in its recurved to erect leaves which are longer and broader, spatulate to ovate, and have larger and more widely spaced teeth on larger prominences (Gentry 1982, García-Mendoza 2010, García-Mendoza 2011a). In C Oaxaca, it forms apparent intermediate hybrids with *A. seemanniana* (García-Mendoza 2010: 77). Forster (2006) illustrates the variability of the species. Rivera-Hernández & al. (2015: 52) provide a new record from W-C Veracruz.

Eguiarte & al. (2013), based on population genetic studies, conclude that *A. potatorum* and *A. cupreata* represent one species only in the evolutionary sense, which is adapted to different climates either in upland forests and open areas (*A. potatorum*) or in the lower areas in the Balsas basin slopes (*A. cupreata*). *A. schnittspahnii* is here included as synonym on the base of Govaerts (2014+), while Berger (1915: 174) placed it in the synonymy of *A. applanata*. — Gentry (1982: 490) designated 2 specimens at M as neotypes, which constitutes a first-step neotypification; García-Mendoza (2010: 75) subsequently designated on of the specimens as the neotype cited above.

Its traditional management and use (for mescal, medicine and fodder), and strategies for its sustainable use are described by Delgado-Lemus & al. (2014). Aguirre-Dugua & Eguiarte (2013) report on the conservation and sustainable use of wild populations for mescal production. Félix-Valdez & al. (2016) show that the extraction of plants for mescal production from wild populations does not significantly decrease the genetic diversity. Torres & al. (2015) calculate a 30–90% population decline in the next 30 years due to continued extraction of adult plants

for mescal production, and show that the population regeneration would be most effective when 1- or 2-year old seedlings are transplanted, and this size class also predominates in nature. Seeds from different localities show significant differences in size, weight, and germinability; germinability decreases with age (Ortiz-Hernández & al. 2018).

A small form with green leaves has been named ‘Minor’ (Heller 2006: 123, with ills.). ‘Kichijokan’ and the variegated ‘Kissho Kan’ (with several different spellings) are cultivars assigned to this species (Starr 2012: 120–126, with ills.), and ‘Cubic’ is selected from seedlings of ‘Kichijokan’ (Starr 2014: 218). ‘Snowfall’ is a variegated cultivar (Starr 2012: 222, with ill.); Moore (2016: 283) illustrates further variegated forms.

**A. potosina** B. L. Robinson & Greenman (Proc. Amer. Acad. Arts 29: 393–394, 1894). **Type** [syn]: Mexico, San Luis Potosí (*Pringle* 3745 [ARIZ, B, BM, BR, COLO, E, F, G, GH, GOET, K, LE, MA, MEXU, MO, MSC, MU, NY, P, PH, PUL, S, US, VT]). — **Lit:** Rose (1903c: 18); Verhoek-Williams (1975: 182–186); Piña Luján (1985: 29, 58–60, with ills.); García-Mendoza (2003: with ill.); Castillejos-Cruz (2009: [232]–[237], with ills.); all as *Manfreda*. **Distr:** Mexico (S Coahuila, SW Nuevo León, E Durango, C Zacatecas, W-C San Luis Potosí); dry desert and limestone mesas, in desert scrub, 1300–2400 m; flowers June to July. **I:** Hochstätter (2016: I: 36, as *Manfreda*). — Fig. 50.

≡ *Manfreda potosina* (B. L. Robinson & Greenman) Rose (1903) ≡ *Polianthes potosina* (B. L. Robinson & Greenman) Shinnery (1966); **incl.** *Delpinoa gracillima* Ross (1898).

[3a1] Herbaceous, small (for Subgen. *Manfreda*), corm shortly cylindrical, (1–) 2–3 × 1.1–2 cm, bulb 3–5 × 1.8–2.5 cm, covered almost entirely with dry leaf bases 2.8–9.5 cm long, these almost entirely membranous, with fibrous top; **R** fleshy, fusiform, with filiform ramifications, contractile; **L** evergreen, 2–7, succulent, semi-erect, recurved, lanceolate to linear-lanceolate, channelled, verrucose on both faces, 8–16 × 1.2–2 cm, light green to glaucous, margins with irregular cartilaginous



**Fig. 50** *Agave potosina*

(Etter & Kristen 4228:  
Mexico; San Luis Potosí, ±  
20 km NE of Huizache,  
1420 m). (Copyright:  
J. Etter & M. Kristen)



teeth, these coarse, broad and usually truncate, blunt, usually incised at the acute to slightly caudate tip, occasionally retrorse, 2–5 (–14) mm apart; **Inf** (15.5–) 24–54 (–75) cm, ‘spicate’, erect, green-grey to red, peduncle with 2–4 **Bra** with truncate base, the lower linear-lanceolate, similar to the leaves, the upper caudate-lanceolate to deltoid, fertile part 9–29.5 cm, semidense to open above, with 6–15 (–31) nodes; floral **Bra** 4–7 × 2–3 mm; **Ped** none to short; **Fl** erect, sessile, 10–18 mm, ascending to appressed to the axis, mostly solitary, rarely geminate; **Tep** yellowish-green to green-glaucous, tube straight, tubular, constricted above the ovary, 6–14 mm, lobes erect, elongate to narrowly lanceolate, extended to appressed to the axis, apex apiculate, with a tuft of short white hairs, 2–5 × 1–2 mm; **Fil** erect at anthesis, 18–22 mm, of 2 lengths, inserted at the base and the middle of the tube, yellowish-green; **Anth** 5–8 mm, yellow; **Ov** ellipsoid to slightly ovoid, 6–14 × 2–3 mm, not constricted, not extending into the tube; **Sty** 12–18 mm; **Sti** 3-lobate, yellowish-green; **Fr** ± globose to subglobose, (9–) 10–13 (–15) × 8–14 mm, without a scar near the apex, dried perianth persisting; **Se** deltoid, plane-concave, granular, 3–4 × 2–3 mm, dull.

The small, narrow flowers, short style and two lengths of the filaments are characteristic features of this species (Verhoek-Williams 1975: 184, Castillejos-Cruz 2009). Fleshy, succulent leaves with irregularly dentate margins are also found in

*A. brunnea*, *A. longiflora*, *A. maculosa*, *A. variegata*, *A. sileri* and *A. virginica*; *A. potosina* is distinguished from these by its smaller stature and flowers (Castillejos-Cruz 2009) (as *Manfreda*).

The lectotypification attempt by Verhoek-Williams (1975: 182) is ineffective because the work was not effectively published. The specimen *G. B. Hinton* 27200 (GBH, MO, TEX) is a new record for Nuevo León. The species is listed as threatened with extinction.

**A. potrerana** Trelease (Contr. US Nation. Herb. 23: 138, 1920). **Type:** Mexico, Chihuahua (*Pringle* 802 [MO, B, BR, COLO, JE, LL, KFTA, MEXU, MICH, MIN, NDG, NY, P, S, UC, US, VT]). — **Lit:** Gentry (1977b: 76–79 & front cover, with ills.); Gentry (1982: 172–174, with ills.); McVaugh (1989: 148); Vázquez-García & al. (2007b: 66–67, t. O4-O5); González-Elizondo & al. (2009: 115); Starr (2012: 223–226, with ills.); Greulich (2016a: 35, 38, with ills.). **Distr:** Mexico (C, S & SW Chihuahua, N Coahuila, W Zacatecas?); oak-pine grasslands in volcanic ranges, 425–2500 m. **I:** Richter (2011: 117); Pilbeam (2013: 177); Hochstätter (2015: IX: 42).

[1g] **Ros** thick-stemmed, regularly spreading, 0.7–1 × 1.5–2 m, solitary; **L** numerous, lanceolate, straight, rigid, widest below the middle, convex below, roundly guttered above, mostly 40–80 × 6–7 cm, glaucous to light or dark green, margins horny, continuous, straight, firm, brown

towards the base, grey above; **marginal teeth** mostly straight, generally small, 2–4 mm, commonly 20–30 mm apart, lacking or reduced to serrations below mid-leaf; **terminal Sp** acicular, sharply angled below, flat to broadly canaliculate above, 25–40 mm, light brown to grey; **Inf** 4–8 m, ‘spicate’, peduncle with narrow scarious **Bra**, fertile part stout, straight or arching, densely flowered through the upper  $\frac{2}{3}$ , part-**Inf** with 2–4 flowers; floral **Bra** long attenuate, shorter than the flowers; **Ped** geminate, 4–15 mm; **Fl** 46–58 mm; **Tep** pink to red or yellow, tube thick-walled, 3–6 mm, lobes linear to ovate, erect, obtuse, clasping the filaments after anthesis, nearly equal, 17–24 × 5–7 mm, outer  $\pm$ 1 mm longer and closely overlapping the inner, inner broader, with a wide keel; **Fil**  $\pm$ 50 mm, inserted at the lobe base, yellow or red; **Anth** centric or excentric, 14–21 mm, yellow; **Ov** cylindrical, slender, 25–32 mm, neck smooth, constricted; **Sty** up to as long as the filaments; **Fr** oblong, rarely pear-shaped, strong-walled, rounded at the base, 25–40 × 10–15 mm, glaucous, shortly beaked; **Se** crescent-shaped, with low broad circumferential margin, hilar notch shallow, 4–5 × 3–3.4 mm.

Distinct and without close relatives in Sect. *Heteracanthae* (as Group *Marginatae*). It differs by its solitary habit, tall inflorescences with large usually red flowers, and the long-acuminate leaves with reduced or lacking teeth on the lower  $\frac{1}{2}$  of the margin (Gentry 1982: 174). The epithet is sometimes erroneously spelled ‘potreriana’, rather than ‘potrerana’ as in the protologue, where the collection number of the type is erroneously cited as ‘302’ instead of ‘802’. The disjunct record from W Zacatecas of Gentry (1982: 193) is based on *Rose* 2404 (US 301314!), which consists of two leaves only and needs confirmation (McVaugh 1989). González-Elizondo & al. (2009) mention the possible, but not yet documented occurrence in Durango.

**A. pratensis** A. Berger (Agaven, 37, 1915). **Type:** Mexico, Nayarit (*Rose* 1994 [US 300886 [lecto], K, MEXU, US 300887]). — **Lit:** *Rose* (1903c: 22); Verhoek-Williams (1975: 245–247); Piña Luján (1985: 86–87); McVaugh (1989:

233–234); Castillejos-Cruz (2009: [265]–[269], with ills.); all as *Manfreda rubescens*. **Distr:** Mexico (N Nayarit, S Jalisco); small grassy openings along road cuts and little streams, in oak and tropical deciduous forests, 700–1500 m; flowers August to September. **I:** Hochstätter (2016: I: 40); Castro-Castro & al. (2017: 62); both as *Manfreda*.

$\equiv$  *Manfreda rubescens* *Rose* (1903)  $\equiv$  *Polianthes rubescens* (*Rose*) *Shinners* (1966).

[3a3] Herbaceous, small (for Subgen. *Manfreda*); corm 1.5–4 × 1–2 cm, cylindrical, bulb 2–6.8 × 2.5–3 cm, cylindrical, completely covered with dried fibrous leaf bases 6–8 cm long; **R** fleshy, with filiform ramifications, contractile; **L** drought-deciduous, 3–6 (–10), recurved to erect, linear to linear-lanceolate, thin, slightly canaliculate, lower face papillose on the veins, upper face glabrous, apex acute, 17–30 (–60) × 0.6–1.4 cm, shiny green, margins entire, with a hyaline band; **Inf** 60–85 (–135) cm, erect, ‘spicate’, glaucous green, peduncle with 6–8 **Bra**, base truncate, lowest similar to the foliage leaves, fertile **Inf** part 6–10 (–18) cm, dense, with 5–9 (–16) flowers; floral **Bra** 8–10 × 6 mm; **Fl** 23–27 mm, solitary, sessile, ascending to diffuse; **Tep** greenish-red to purple-brownish dorsally, tube broadly funnel-shaped to campanulate, (3–) 5–6 × 4 mm, lobes oblong, extended to irregularly reflexed, 12–14 × 2–3 mm, tip cucullate with a soft tip, with a bundle of short white trichomes; **Fil** 20–27 mm, erect at anthesis, exceeding the tube for 18–23 mm, inserted at  $\frac{3}{4}$  of the tube length on the same level, reddish-green with purple dots; **Anth** 8–10 mm, yellowish-green; **Ov** ellipsoid, 7–10 × 3–5 mm, greenish, prolonging 1–2 mm into the tube, not constricted above; **Sty** 28–30 mm; **Sti** 3-lobed, greenish-red; **Fr** cylindrical to ellipsoid, 20–22 × 13–16 mm, with a scar near the apex and persisting tepals; **Se** deltoid, plane-concave, 3–4 × 4 mm, dull.

Perhaps nearest to *A. guttata* and sharing the short tepal tube, the compact inflorescence and the flower shape, but differing by purple (vs. greenish-yellow) flowers and thin and glabrous leaves (Verhoek-Williams 1975: 246, Castillejos-Cruz 2009; both as *Manfreda*). *A. pratensis* is morphologically also similar to *A. bulbulifera* and *A. littoralis* (Castillejos-Cruz & Solano 2008: as

*Manfreda*). McVaugh (1989: 234) and Castro-Castro & al. (2017: 61, 63) provide records for Jalisco. Rose's type at US consists of 2 sheets (US 300866! & 300887!). The attempted lectotypification by Verhoek-Williams (1975: 245) fails as the work was not effectively published, but the designation by McVaugh (1989: 234) "US300886!, the lectotype" represents a lectotypification.

**A. pringlei** Engelm. *ex* Baker (Handb. Amaryll., 182, 1888). **Type:** Mexico, Baja California Sur (*Orcutt* s.n. [K, CAS, MEXU, MPU, NY, US]). — **Lit:** Trelease (1912b: 54, t. 44); Berger (1915: 263–264); Gentry (1978: 20–22, with ill.); Gentry (1982: 380–382, with ill.); Turner & al. (1995: 51, 53, with ill.); Starr (2012: 85–86, 89); the last 4 references as *A. deserti* ssp.; Webb & Starr (2015: 83–84, with ill.); **Distr:** Mexico (N Baja California); desert plains and slopes, 595–1830 (–2300) m; flowers mainly April to August, also August and October. **I:** Heller (2006: 81); Richter (2011: 37, 103); Pilbeam (2013: 73); Hochstätter (2015: V: 10); all as *A. deserti* ssp.

≡ *Agave deserti* ssp. *pringlei* (Engelm. *ex* Baker) Gentry (1978) ≡ *Agave deserti* var. *pringlei* (Engelm. *ex* Baker) W. C. Hodgson & Reveal (2001); **incl.** *Agave scaberrima* Hort. Peacock *ex* Baker (1888).

[2i] Acaulescent; **Ros** 40–70 × 50–80 cm, rather strict, caespitose, offsetting closely from the root crown; **L** ascending, narrowly triangular-lanceolate, deeply canaliculate, thick and widest at the base, very long-acuminate, guttered and thinner above, smooth, mostly 40–70 × 5–7 cm, green to yellowish-green or light glaucous-grey, margins nearly straight; **marginal teeth** slender and little curved, more rarely smaller or more broadly flattened and irregularly flexed, triangular, lenticular at the base, mostly 5–10 mm, grey, rather regularly spaced 10–20 mm apart; **terminal Sp** acicular, usually narrowly grooved for a short distance at the base, 30–40 mm, reddish-brown to light grey, decurrent as a corneous margin to the upper teeth or to mid-leaf; **Inf** 3–6 m, paniculate, fertile part very narrow or more ample with longer part-**Inf** with larger 'umbels', part-**Inf** 10–15; **Fl** 40–60 mm; **Tep** yellow, tube ample, 3–8 ×

12–15 mm, bulging, strongly furrowed from the tepal sinuses, lobes linear, spreading, rounded over a finely cucullate apex, nearly equal, 14–20 × 5–7 mm, **ITep** broader and with broad low keel; **Fil** 30–35 mm, inserted on the rim of the nectary in the orifice of the tube; **Anth** 14–15 mm; **Ov** fusiform, roundly angular, 20–35 mm, neck furrowed; **Fr** mostly oblong, 30–55 × 12–15 mm, short-stipitate, beaked, greyish straw-coloured; **Se** crescent-shaped, 5–7 × 3–4.5 mm, black.

This taxon, apparently restricted to the Sierra San Pedro Mártir and Sierra Juárez, was reduced to a subspecies of *A. deserti* by Gentry (1978) and Gentry (1982), based on "apparent introgression" and a "hybrid swarm" between both at San Matias Pass. Hodgson (2001a) went even further and reduced it to a variety of *A. deserti*, whose range it borders and partly overlaps to the S and W. Webb & Starr (2015: 82) found both species in that area clearly separated and with little evidence of a hybrid swarm (only isolated hybrids were found), thus justifying species status as *A. pringlei*, based on clear differences from *A. deserti*: Green, long triangular-lanceolate leaves often with a conspicuous brown ring around the marginal teeth, and shorter inflorescences. The brown ring on the teeth is otherwise typical of *A. cerulata* and suggests a closer link with it rather than with *A. deserti* (Webb & Starr 2015). This view is, however, contradicted by molecular data (Navarro-Quezada & al. 2003), which associate *A. pringlei* with *A. deserti*, and apart from *A. cerulata*, but the analysis may be influenced by inclusion of hybrids.

**A. producta** Thiede & Egli (Kakt. und Sukk. 50(5): 112, 1999). **Type:** Mexico, Guerrero (*Chisholm* s.n. in *Section Plant Introduction USDA* 11260 [US, NY]). — **Lit:** Rose (1905: 437, as *Polianthes elongata*). **Distr:** Mexico (Guerrero); flowers in October. **I:** Hochstätter (2016: II: 10, as *Polianthes elongata*).

≡ *Polianthes elongata* Rose (1905).

[3b2] Herbaceous; corm ±1.2 × 2 cm, bulb ovoid, 3.5 × 1.2 cm, completely covered with dried light brown membranous leaf bases to 5.5 cm long; **L** drought-deciduous, erect, elongate, oblanceolate, trough-shaped below, flat above,

30 × 1–1.2 (near the tip) cm, green, hardly if at all glaucous, margins entire; **Inf** 80–90 cm, erect, ‘racemose’, reddish at the base, glaucous above, glabrous, peduncle with 6–7 **Bra**, these much reduced upwards, fertile part 22–24 cm, lax, with 12–18 flowering nodes; floral **Bra** ovate-linear, acuminate, 1–1.5 cm, reddish; **Ped** 10–15 mm; **Fl** ±24 mm, geminate; **Tep** reddish, forming a tube, bent just above the base almost at right angles with the ovary axis, tube ±20 mm, lobes short, somewhat spreading, ±1 mm, tip rounded; **Fil** included, inserted near the base of the tube; **Anth** 6 mm, tips just projecting from the mouth of the perianth; **Ov** ellipsoid, ±4 × 2 mm; **Sty** finally projecting a short distance beyond the mouth of the perianth; **Sti**, **Fr** and **Se** unknown.

Known from the type collection only (depicted by Hochstätter (2016)); the description was added from both cited specimens. The holotype (US 399706!) was annotated as *Polianthes geminiflora* var. *geminiflora* (= *A. coetocapnia* ssp. *coetocapnia*) by E. Solano in 2000, the sole other species of Sect. *Polianthes* in Guerrero. Castro-Castro & al. (2015: 141), in contrast, recognize *Polianthes elongata* as distinct, which is followed here. *A. producta* differs from *A. coetocapnia* mainly in its narrower, unspotted, not glaucous leaves, inflorescences with a shorter fertile part, and flowers with filaments inserted near the base of the tube and somewhat spreading and much shorter perianth lobes. Castro-Castro (pers. comm. to author, Nov. 2018) found a population close to the type locality which may belong here. — When transferring *Polianthes elongata* to *Agave*, a new name was necessary to avoid homonymy with *A. elongata* Jacobi (1865).

**A. pubescens** Regel & Ortgies (Gartenflora 23: 227–228, t. 804, 1874). **Type**: Ex cult. BG St. Petersburg (*Anonymous* s.n. [LE 00011016]). — **Lit**: Berger (1915: 31); Verhoek-Williams (1975: 298–300); Piña Luján (1986: 15–17, 35, with ill.); Castillejos-Cruz (2009: [248]–[254], with ill.); the last 3 as *Manfreda*. **Distr**: Mexico (Michoacán, Mexico, Morelos, Guerrero, Oaxaca, Chiapas, Veracruz); rocky slopes in mountain regions, in tropical deciduous forests, thorn forests, pine-oak forests, (semi-) evergreen rain forests, and

montane cloud forests, 300–2500 m; flowers July to August. **I**: Hochstätter (2016: I: 38, as *Manfreda*).

≡ *Agave brachystachys* var. *pubescens* (Regel & Ortgies) A. Terracciano (1885) ≡ *Manfreda pubescens* (Regel & Ortgies) Espejo & López-Ferrari (1993).

[3a2] Herbaceous; corm cylindrical, 2–6 (–12) × 2–3 cm, bulb ovoid, 3.5–6 × 1.5–2.5 cm, covered with fibrous dry leaf bases 4–7 (–9.5) cm long; **R** fleshy, contractile; **L** drought-deciduous, 3–4 (–9), linear-lanceolate to lanceolate, ribbed, prostrate, narrowing towards the base, tip acute, densely pubescent on both faces, 18–28 (–70) × 2.2–4.2 (–6) cm, dark green with abundant purple spots, margins entire, slightly wavy, with a hyaline band; **Inf** erect, 60–160 (–185) cm, ‘spicate’, peduncle reddish to greenish, pubescent at the base, with 5–8 **Bra**, these truncate at the base, lower ones linear-lanceolate and similar to the leaves, fertile part 15–40 (–55) cm, with 10–22 solitary, laxly arranged flowers; floral **Bra** 4–11 × 3–4 mm; **Fl** sessile, ascending, 32–40 mm, tubular to infundibuliform; **Tep** yellowish-green, tube 18–26 × 4–5 mm, constricted at the tip of the ovary, lobes narrowly elliptic to oblong, revolute, 11–18 × 4–5 mm, apex cucullate, with a bundle of white hairs; **Fil** erect, 26–45 mm, exceeding the tube for 22–38 mm, inserted all on the same level at mid-tube, greenish-yellow with reddish dots; **Anth** 8–12 mm, yellow; **Ov** ellipsoid, 10–16 × 2–4 mm, not extending into the tube; **Sty** first bent downwards, straight at maturity, 36–53 (–60) mm; **Sti** clavate, 3-lobed, green-yellowish; **Fr** cylindrical to subellipsoid, 16–25 × 12–15 mm, apiculate, without an apical scar, remains of perianth persisting; **Se** deltoid, plane-concave, with narrow margin, 3–4 × 3 mm, black, shiny.

Characterized by its large corm and large and pubescent leaves narrowed at the base. Apart from *A. maculata*, this is the only species in Sect. *Manfreda* with pubescent leaves, but distinguished by its generally larger size with larger inflorescences, lobes and filaments and much more exerted stamens and styles (Verhoek-Williams 1975: 299, Castillejos-Cruz 2009) (as *Manfreda*).

**A. × pumila** De Smet ex Baker pro sp. (Handb. Amaryll., 172, 1888). **Type** [neo]: Cult. (*Anonymous* s.n. in *Huntington* BG 16230 [ARIZ,



HNT]). — **Lit:** Trelease (1911: 13–15, with ills.); Berger (1915: 90–91); Breitung (1960: 91, 121, with ills.); Gentry (1982: 174–176, with ills.); Ullrich (1991c: with ills.); Thiede (2011: 152–153); Roosbroeck (2012: 165–166, with ill.); all as *A. pumila*. **Distr:** Known from cultivation only. **I:** Kuppen (2000: 185); Heller (2006: 124); Richter (2011: 69); Pilbeam (2013: 179–180); Hochstätter (2015: IX: 42); all as *A. pumila*; Walker (2017: 166, as *A.* ‘Pumila’).

**Incl.** *Agave simonis* hort. ex Hirscht (1898) (*nom. inval.*, ICN Art. 38.1a).

[1g × 1g] Plants dimorphic, **juvenile form** persisting for 8–12 years; **Ros** small, 5–8 cm Ø, surculose; **L** ovate-orbicular, thickly succulent, broader than long, base broadly clasping, rounded below, deeply concave above, 2–4 × 3–4 cm, glaucous, lower face striped, margins thin, friable, white; **marginal teeth** several, weak and small; **terminal Sp** conical, flexuous, small; **adult form** thick-stemmed; **Ros** open, short, 40–50 × 60–70 cm, not suckering; **L** deltoid-lanceolate, rigid, patulous, thickened at the base, upper face concave, lower face convex, 30–38 × 4–4.5 cm, glaucous, without stripes below, margins narrowly horny, detaching, white; **marginal teeth** small, weak, 1–2 mm, 10–15 mm apart; **terminal Sp** conical, slender, 15 mm, decurrent along the leaf margins and along the keel in the middle of the lower face; **Inf**, **Fl** and **Fr** unknown. — **Cytology:** 2n = 120 (4×) (Zonneveld 2003).

Long known only from the stunted juvenile form, but developing into large ‘normal’ rosettes when given enough space (Gentry 1982); such a dimorphism is unknown in other Agaves. First brought into the trade in 1877 by De Smet (Berger 1915). Trelease (1911) placed the species close to *A. lechuguilla* due to the shared presence of longitudinal stripes on the lower leaf face. Gentry (1982) assumes an origin as (natural) hybrid, probably *A. nickelsiae* (as *A. victoriae-reginae*) × *A. lechuguilla*, adding the narrow detachable leaf margins as further character shared with the latter. The stunted juvenile growth form might result from incongruence of chromosome numbers of its putative parental species: *A. nickelsiae* is di-, tetra- and hexaploid, and *A. lechuguilla* as well as *A. ×pumila* are tetraploid (Thiede 2011).

González-Elizondo & al. (2011) equated *A. pumila* with the natural hybrid *A. nickelsiae* × *A. asperrima* (see under *A. ×santilloensis*), arguing that the leaf shape of adult plants points towards *A. asperrima* as one parent. However, the presence of longitudinal stripes on the lower face of the leaves of *A. ×pumila*, which are a typical feature of *A. lechuguilla* but are absent in *A. asperrima*, strongly favours *A. lechuguilla* as putative parent.

Gentry (1982: 174, 193) selected a neotype at US, but the specimen does not appear to be extant; however, the specimen ARIZ 0004769 with Gentry’s handwriting “Neotype” and his stamp “Gentry herbarium” was apparently intended as neotype, but was not sent to US. ‘Green of Jealousy’ (Roosbroeck 2012: 166, with ill.) is a cultivar with green leaves.

**A. quilae** (Art. Castro & Aarón Rodríguez) Thiede & Govaerts (Phytotaxa 306(3): 238, 2017). **Type:** Mexico, Jalisco (*Rodríguez & Castro-Castro* 7149 [IBUG, CIIDIR, ENCB, IEB, MEXU, XAL]). — **Lit:** Castro-Castro & al. (2016: protologue, with ills.). **Distr:** Mexico (C Jalisco); with grasses in deep and acid soils or on rocks in pine-oak forests, 1500–2350 m; flowers late July to early August.

≡ *Polianthes quilae* Art. Castro & Aarón Rodríguez (2016).

[3b2] Herbaceous; corm 0.8–1.5 × 0.9–1.2 cm, oblong, bulb (2.5–) 3.3–4.5 × (1.3–) 1.6–2.5 cm, ellipsoid or ovoid in saxicolous individuals, completely covered with dried fibrous leaf bases; **R** fleshy, thickened, contractile; **L** drought-deciduous, 3–6, mostly erect, sometimes prostrate or slightly elevated from the surface, ensiform, chartaceous and soft, hyaline, glabrous, apex acute, (10–) 15–24 (–36) × (0.5–) 0.8–1.4 cm, shiny green, margins entire; **Inf** 55–94 cm, erect, ‘spicate’, glaucous, peduncle with 2–4 **Bra**, these ensiform, 4–21 cm, base truncate, internodes decreasing in size distally, fertile **Inf** part ±32 cm, lax, with 4–12 remote floral nodes; floral **Bra** 8–33 × 2–4 mm; **Ped** 9–21 mm at anthesis, 12–24 mm in fruit, ascending; **Fl** geminate, unscented, 14–25 mm, divergent to inclinate; **Tep** bicoloured, the bottom ⅓ orange-reddish,



the upper  $\frac{1}{3}$  and the lobes purple-glaucous, forming a ventricose tube, middle portion inflated, and the distal portion tapered, not curved,  $\pm 18 \times 5$  mm at the base of the lobes, lobes unequal, ascending, imbricate,  $2-3 \times 2-3$  mm, **OTep** ovate, acute, **ITep** circular, hyaline, obtuse, apex with a bundle of white trichomes; **Fil** filiform, 12–16 mm, included, inserted 3–5 mm above the ovary apex, orange-yellowish; **Anth** linear, 4–5 mm, yellow, at anthesis below the upper portion of the mouth of the tube; **Ov** ellipsoid,  $3.6-4 \times 2.5-3$  mm; **Sty** filiform, 18–20 mm, orange, distally yellowish, included; **Sti** 3-lobed, papillose; **Fr** globose to ellipsoid,  $8-10 \times 7-9$  mm, with persisting tepals; **Se** deltoid, flat,  $3-3.5 \times 2.2-2.5$  mm, shiny.

According to the protologue morphologically closest to *A. cernua* (as *Polianthes*) and *A. coetocapnia* ssp. *clivicola* (as *P. geminiflora* var.), which share esp. oblong corms, ellipsoid or ovoid bulbs, entire hyaline and glabrous leaves, ensiform sterile bracts, and globose to ellipsoid fruits. It differs, however, in its ensiform erect leaves, glaucous inflorescences with 4–12 floral nodes, pedicels 9–21 mm long at anthesis, and esp. in the orientation, length, shape, and colour of the perianth. The species is considered to be endangered (IUCN category EN).

**A. quotepecensis** García-Mendoza & S. Franco (Acta Bot. Mex. 126: e1461: 9, ills. (pp. 10, 15), 2019). **Type:** Mexico, Oaxaca (*García-Mendoza & al.* 10349 [MEXU, ENCB, MEXU, MO, OAX]). — **Distr:** Mexico (N Oaxaca: middle and upper río Papaloapan basin); on sandy reddish soils in low tropical deciduous forests, 525–845 m; flowers December to March.

[lg] Acaulescent; **Ros** lax, solitary,  $1.4-1.5 \times 2-2.5$  m; **L** 40–70, lanceolate, ovate in young plants, erect, rigid, thickened at the base, flattened or slightly canaliculate, slightly keeled on the lower face, apex long acuminate, involute and grooved,  $70-90 \times 10-13$  (–20) cm,  $5-7$  (–10)  $\times$  longer than broad, yellowish-green, sometimes with a lighter longitudinal midstripe, margins straight, corneous, continuous, greyish or brown, dentate; **marginal teeth** deltoid to irregular,

straight, antrorse or rarely retrorse, (10–)  $15-28 \times 8-20$  mm at mid-leaf, greyish to occasionally brown, (25–)  $50-90$  mm apart at mid-leaf, sometimes with smaller interstitial teeth; **terminal Sp** keeled on the lower face, (30–)  $40-55 \times 6-10$  mm, greyish, decurrent for 14–20 (–35) cm, corneous base penetrating 2–7 (–15) mm into the lower leaf face; **Inf** erect, 4–5 m, ‘spicate’, peduncle green, with deltoid coriaceous **Bra** 12–20 (–28)  $\times 1.5-4$  cm, fertile part dense, in the upper  $\frac{1}{2}$  or  $\frac{3}{4}$  of the inflorescence; lowest floral **Bra** 10–20  $\times 2-5$  cm; **Ped** short; **Fl** 45–50 mm; **Tep** greenish-yellowish, tube campanulate,  $1-4 \times 7-10$  mm (at the mouth), lobes oblong, straight to slightly recurved at anthesis,  $19-23 \times 3-6$  mm; **Fil** 50–67 mm, yellowish, inserted in the distal part of the tube; **Anth** 12–16 mm, yellowish; **Ov** cylindrical,  $25-28 \times 3-4$  mm, neck 6–8 mm; **Sty** 40–50 mm, yellow with purplish tinge; **Sti** 3-lobed, yellow with purplish tinge; **Fr** ellipsoid,  $20-21 \times 10$  mm; **Se** semicircular, unwinged,  $3-4 \times 2-3$  mm, black.

In the protologue placed in Sect. *Heteracanthae* (as Group *Marginatae*). It is closely related to *A. titanota*, which occurs to the NW and differs in its longer leaves with long acuminate apex, straight margins with more distant teeth, a shorter terminal spine decurrent for a longer distance, a spine base intruding for a shorter distance into the lower leaf face, and larger flowers with longer filaments and longer ovaries. However, the protologue applies a restricted range of character expressions; with the data given in this handbook for *A. titanota*, the differences in the distance of the teeth, the length of the terminal spine, the flower size, and the length of the filaments disappear or show broad overlap. One of the paratypes (*García-Mendoza & Palma* 5712) was formerly included in *A. titanota* by García-Mendoza (2011a: 64) (see also under the latter). — Vernacular name: “rabo de león”. The leaves are used for making ropes, complete inflorescence are used as fodder, and boiled flower buds (“cacayas”) are eaten as vegetables. Classified in the IUCN Red List Category “Near Threatened”.

**A. revoluta** Klotzsch (Allg. Gartenzeitung 8: 274, 1840). **Type:** Ex cult. BG Berlin

(*Anonymous* s.n. [B]). — **Lit:** Rose (1903c: 21); Berger (1915: 34); Verhoek-Williams (1975: 295–297); Piña Luján (1986: 16); Castillejos-Cruz (2009: [255]–[259], with ills.); all as *Manfreda* except Berger. **Distr:** Mexico (México); clay bluffs, in pine or oak forests, 1300–2200 m; flowers July to August. **I:** Hochstätter (2016: I: 39, as *Manfreda*).

≡ *Manfreda revoluta* (Klotzsch) Rose (1903)  
 ≡ *Polianthes revoluta* (Klotzsch) Shinnery (1966).

[3a2] Herbaceous; corm cylindrical, 5–9 × 1.8 cm, bulb conical, 3–6 × 1.8–2.5 cm, covered with dry leaf bases 4.5–6 cm long and fibrous above; **R** fleshy, contractile; **L** drought-deciduous, 5–6, linear-lanceolate, prostrate to semi-erect, channelled, narrowed towards the base, apex attenuate, acute, with small and recurved tip, glabrous, 12–20 × 1.5–2 cm, greenish-yellow to dark green, margins hyaline, narrow, entire or finely papillose to erose-papillose, revolute; **Inf** 0.8–1 (–2) m, erect, ‘spicate’, with 6–12 somewhat inclined **Bra** with truncate bases, the lower leaf-like, the upper reduced, fertile part (15–) 20–30 (–40) cm, with 20–30 solitary, laxly or sometimes densely arranged flowers; **Fl** sessile, erect, 22–26 mm, tubular to funnel-shaped; **Tep** greenish-red to greenish-yellow, semisucculent, tube 12–15 × 5–7 mm, not constricted, lobes oblong, reflexed to revolute, 8–12 × 5–8 mm, tips thickish, cucullate, with a bunch of white hairs; **Fil** erect, exceeding the tube for 19–34 mm, greenish-yellow, adnate to the tube, all inserted at the same level; **Anth** 10–12 mm, greenish-yellow to greenish-red; **Ov** ellipsoid, 7–12 × 5 mm, greenish-yellow; **Sty** 30–47 mm; **Sti** 3-lobed, greenish-yellow; **Fr** ellipsoid, triquetrous, 15–22 × 15–18 mm; **Se** plane-concave, 3–4 × 4 mm, black, dull.

This species belongs to Ser. *Scabraea* within Sect. *Herbaceae*. It differs from other members by its short revolute leaves. The specimen at B (cult. Horto Bot. Berol., Jun [18]40; not digitized] appears to represent the type material of Klotzsch (Verhoek-Williams 1975: 296). It is morphologically similar to *A. galvaniae*, but distinguished by larger, ellipsoid fruits and smaller floral bracts (Castillejos-Cruz 2009).

**A. rhodacantha** Trelease (Contr. US Nation. Herb. 23: 117, 1920). **Type** [neo]: Mexico, Nayarit (*Gentry & Gilly* 10704 [ARIZ 266622, ARIZ, MEXU [2 sheets], US [3 sheets]]). — **Lit:** Gentry (1972: 141–143, with ills.); Gentry (1982: 580–582, with ill.); McVaugh (1989: 140–141); Vázquez-García & al. (2007b: 67–68, t. X); González-Elizondo & al. (2009: 116–118, with ills.); García-Mendoza (2011a: 51–52); **Distr:** Mexico (Sonora, Sinaloa, Durango, Zacatecas, Nayarit, Jalisco, México, Puebla, Oaxaca); in arid scrub and tropical (sub-) deciduous pine-oak, oak, thorn or short-tree forests, 50–2080 m; flowers May to July. **I:** García-Mendoza (2002: 179); Pilbeam (2013: 181); Hochstätter (2015: VII: 45).

[2g] Stems none or 50–90 cm or more; **Ros** truncate, large, 1.7–3 × 2.5–5 m, solitary or caespitose; **L** 100–200, ascending, lanceolate to linear-lanceolate, hard-fibrous, rigid, straight, much thickened and scarcely narrowed at the base, smooth, (80–) 100–250 (–300) × (5–) 6–18 cm, green to faintly glaucous-green, margins straight to repand; **marginal teeth** upcurved, firm, slender, very sharp, regular, 4–10 × (4–) 6–12 mm, dark brown to blackish, mostly 10–30 mm apart, not decurrent; **terminal Sp** conical but frequently with subulate tip, with short open groove above, 10–30 × 5–6 mm, dark brown; **Inf** 6–9 m, paniculate, peduncle green, with triangular chartaceous **Bra** 30–38 cm, fertile part lax, rhomboidal to oblong, part-**Inf** 25–45, large, remote, in the upper ½ of the inflorescence, 40–55 cm long; **Ped** 5 mm; **Fl** 55–65 mm; **Tep** green, yellowing at anthesis, tube urceolate, 8–10 × 9–10 mm, lobes linear to oblong, erect, strongly involute, rounded and strongly hooded at the apex, subequal, 16–23 × 4 mm, wilting at anthesis and soon reflexing; **Fil** 40–45 mm, inserted in the upper ¼ of the tube; **Anth** 14–28 mm; **Ov** cylindrical to fusiform, 25–35 mm incl. the short neck; **Fr** oblong, 70–80 × 25–30 mm, shortly beaked, long-stipitate (but not always), stipe 10–15 mm; **Se** 10–11 × 7–8 mm, oblique, curved margin not wing-like, hilum notch shallow. — **Cytology:** 2n = 60 (Moreno Salazar & al. 2007, Simpson & al. 2011).

The taxon is difficult to characterize and is distinguished from its close relative *A. angustifolia* by its many, very long, rigid leaves with large,

robust and narrow teeth, and large inflorescences with long part-inflorescences and large fruits (Gentry 1982: 582, García-Mendoza 2011a). According to Gentry (1982), the fruits are long-stipitate, but this character has not been seen in the material studied by García-Mendoza (2011a). Some forms may be indistinguishable from *A. angustifolia* (Gentry 1972, McVaugh 1989). New records are provided by Gentry 18298 (MEXU 109971) for Zacatecas, *Matuda* 32069 (MEXU 160226) for México, Hernández-Vera & al. (2007a: 501) for Jalisco, and González-Elizondo & al. (2009) for Durango.

The protologue indicates “Lundstrom, in 1909” “from Mocerito” at MO as “type” which was thought to be lost so that Laferrière (1995b) designated a neotype. However, MO houses 2 specimens collected by A. A. Lundström 1909 at Mocerito, which appear to represent syntypes: MO 1800295, filed as *A. fourcroydes* (det. H. S. Gentry), and MO 1800296, filed as *A. tequilana* (both without digital image).

Zizumbo-Villarreal & al. (2013) report a landrace of the taxon as being used locally in S Jalisco for sustainable mescal and tequila production. According to ethnobotanical and morphological studies (Vargas-Ponce & al. 2007), wild populations of *A. rhodacantha* and *A. angustifolia* as well as unclassified putative hybrids between both are the primary gene pools from which traditional landraces have been selected in S Jalisco. Genetically, *A. rhodacantha* and *A. tequilana* ‘Sigüin’ and ‘Chato’ form a group separate from *A. angustifolia* and *A. tequilana* ‘Azul’ (Trejo & al. 2018). Five landraces from Jalisco showed a clearly higher genetic diversity than the commercial *A. tequilana* ‘Azul’ (Vargas-Ponce & al. 2009).

**A. ×romanii** Hort. De Smet *ex* Anonymous [J. C.] (Gard. Chron., ser. 3, 33: 325, 1903). — **Lit:** Baker (1888a: 166); Trelease (1914: 236–238); Berger (1915: 74); all as *A. romanii*. **Distr:** Cultivated only. **I:** Richter (2011: 86).

[1d × 1f] According to Baker (1888a) and Trelease (1914) a garden hybrid *A. filifera* × *A. obscura* (as *A. xalapensis*), raised by the Belgian nursery of L. de Smet. A specimen prepared by

Berger (a single leaf with fraying margins) which fits Berger’s description taken from Besaucèle is kept at US (US 1023732!). Plants designated as *A. romanii* presently offered or cultivated in the USA and in Europe include plants with dark fraying margins corresponding to the description, but also plants apparently not belonging here, either with small marginal teeth, or with entire margins and partly broader leaves. For the latter the parentage is given as *A. filifera* × *A. mitis* (as var. *albidior*). Here included is the cultivar ‘Shadow Dancer’ with light leaf colouration esp. during summer (photograph in Greulich 2017c: 159).

**A. rosei** Thiede & Egli (Kakt. and. Sukk. 50 (5): 112, 1999). **Type:** Mexico, Nayarit (*Rose* 2178 [US, GH, MEXU]). — **Lit:** Rose (1903a: 11); McVaugh (1989: 259–260); Solano & al. (2019: 5, 8, 9, with ills.); all as *Polianthes montana*. **Distr:** Mexico (Nayarit, Jalisco); ecology unknown, 1500–2040 m; flowers July to August. **I:** Barba-Gonzalez & al. (2012: 124); Hochstätter (2016: II: 17); both as *Polianthes montana*.

≡ *Polianthes montana* Rose (1903).

[3b1] Herbaceous; corm unknown, bulb ±4 × 1–1.5 cm, oblong, completely covered with dried fibrous leaf bases; **R** unknown; **L** drought-deciduous, 2–3, erect, linear-ensiform, nearly smooth, not narrowed at the base, apex attenuate, acute, ±20–30 × 0.27–0.8 cm, margins obscurely papillose; **Inf** 110–120 cm, erect, ‘spicate’, ± glaucous, peduncle with 6 distant **Bra**, these ensiform, lowest 19.5–25 cm, upper ones much smaller, internodes decreasing in size distally, fertile part 6.5–18 cm, lax, with 4–12 remote floral nodes; floral **Bra** ±0.4 cm; **Ped** 2.5–4 (–6) mm, ± ascending; **Fl** geminate, strongly fragrant, ±20–24 mm, ± divergent; **Tep** white, pink when senescent, forming a cylindrical tube (slightly) curved near the base, ±14–15 mm, lobes erect, 4–9 × 2.9–4.3 mm, ovate, rounded; **Fil** filiform, 7–25 mm, longer than the anthers, inserted much below the middle of the tube; **Anth** 4.3–4.7 mm, included; **Ov** ellipsoid, ±1.25 × 2.5 mm; **Sty** 10–14 mm, included; **Sti** unknown; **Fr** 6 × 7 mm; **Se** unknown.

An incompletely known species, long known only from the type specimen, but recently

collected in Jalisco (Solano Camacho 2002) and now known from 12 records from 6 localities (Solano & Feria 2007: 1988). Solano & al. (2019) provide additional morphological data. Within Ser. *Polianthes* of Sect. *Polianthes* easily distinguishable by its short tube, linear-ensiform leaves, and pedicellate flowers (see also under *A. platyphylla*). McVaugh (1989) suggests the possibility that the specimen regarded as type, which much resembles *A. duplicata* (*Polianthes geminiflora*), has erroneously been substituted for the original white-flowering type specimen of *A. rosei* ( $\equiv$  *Polianthes montana*). Locally used as ornamental (Barba-Gonzalez & al. 2012: 125). — The new name was necessary to avoid homonymy with *A. montana* Villarreal 1996.

**A.  $\times$  rosselloana** D. Guillot & P. Van der Meer (Flora Montiber. 27: 55, 2004). **Type:** Ex cult.: Spain, Valencia (Guillot & Van der Meer s.n. [VAL 151001]). — **Distr:** Cultivated only.

[1f  $\times$  1f] This is the garden hybrid *A. obscura* (as *A. polyacantha* var. *xalapensis*)  $\times$  *A. warelliana* found in the Botanical Garden of Valencia (Spain). The original spelling ‘rossellonensis’ is to be corrected as shown above, as the epithet honours Sr. Rosselló.

**A.  $\times$  rovelliana** Todaro *pro sp.* (Index Seminum Panormitani 1888: 36, 1889). **Type:** not typified. — **Lit:** Pax (1893: with ills.); Berger (1915: 58–59); Ullrich (1992: 87, 89, 92, with ill.); Richter (2011: 45–47: with ill.); all as *A. terraccianoii*. **Distr:** Cultivated only. **I:** Greulich (2018b: 78, as *A. rovelliana*).

**Incl.** *Agave terraccianoii* Pax (1893).

[1f?  $\times$  3a] This most probably represents an artificial hybrid between a species of Subgen. *Littaea* (possibly *A. mitis*) and a species of Sect. *Herbaceae* of Subgen. *Manfreda*, as strongly indicated by the spotted leaves not present in Subgen. *Littaea* and flowering nodes with 1–2 flowers intermediate between both groups (Ullrich 1992, Richter 2011). Ullrich (1992: 89) depicts a plant with spotted leaves labelled “*A. terraccianoii*” in his collection purportedly going back to Pax’s original plants at BG Berlin. A plant labelled “*A. terraccianoii*” cultivated at BG Berlin

and possibly going back to Pax flowered there in 2002 (Richter 2011). The plant depicted by Richter has unspotted leaves possibly due to shady cultivation; plants kept more sunny seen in the botanical collection at Berlin in 2002 by the writer were intensely spotted. Vignoli (1936: 193–194) reported an aberrant aneuploid chromosome number of  $2n = 50$  for *A. rovelliana*, which, if not a miscount, might be related to its hybrid origin.

**A. rutteniae** Hummelinck (Recueil Trav. Bot. Néerl. 33: 238, 1936). **Type** [syn]: Aruba (Hummelinck 19a + b [U]). — **Lit:** Hummelinck (1938: 19–20); Hummelinck (1993: 10–11, with ills.); Thomson (2014: with ills.). **Distr:** Leeward Antilles (Aruba: slopes of the Hooiberg); debris of igneous rocks, 60–90 m; flowers May to June; only known from the type locality. **I:** Pilbeam (2013: 182); Hochstätter (2015: VII: 46).

[2u] Acaulescent; **Ros** 1  $\times$  0.9–1.5 m  $\varnothing$ , suckering; **L**  $\pm$  15–25, narrowly elliptic or lanceolate, straight or very slightly S-curved, acute, narrowed towards the 4–5 cm broad base, widest at or somewhat above the middle, tip usually slightly curved upwards, guttered, 40–70  $\times$  7.5–9 cm; **marginal teeth** slender-acicular, usually somewhat recurved below the middle of the leaf, 4–5 mm (5–7 mm below the middle), 9–17 per 10 cm, on small or rather well-developed, hardening or partly green prominences; **terminal Sp** acicular, straight, often somewhat flexuous, narrowly and usually shallowly grooved below or beyond the middle, involute or slightly involute towards the base, smooth or with some very small denticles at the margin, 22–30  $\times$  2–3 mm, decurrent, dorsally not intruding into the leaf tissue; **Inf** 1.4–3.6 m, paniculate, peduncle with rather few, toothed **Bra**, the lowest one 5–17.7 cm, fertile part oblong or obovate, 16–145 cm, with (3–) 10–15 part-**Inf**, on slightly S-curved,  $\pm$  ascending branches 6–21 cm long, in the upper  $\frac{1}{4}$ – $\frac{1}{3}$  of the inflorescence, axis distinctly swollen below the insertion of the branches, forming fruits and at the same time freely bulbiferous; **Ped** (4–) 5–6 (–8) mm; **Fl** 40–45 mm; **Tep** yellow, tube conical, 4.5–8 mm, lobes 14–21 mm; **Fil** 25–30 mm, inserted 0–2 mm below the tube throat, long-exserted; **Anth** 14–17 mm; **Ov** not described;

**Sty**  $\pm 40$  mm, long exserted, slightly exceeding or equalling the filaments; **Fr** shortly oblong, 24–30  $\times$  15–18 mm, not or nearly not beaked, stipitate, only rarely formed; **Se** 5.5–6.5  $\times$  4–5 mm.

Hummelinck differentiates *A. rutteniae* in the protologue from *A. vicina* (as *A. vivipara*) on account of its generative features only: The inflorescence axis is distinctly swollen below the insertion of the branches, the flower tube is longer, and the fruits are only 1.5–1.75 $\times$  as long as broad (Hummelinck 1938: 16), and from *A. arubensis* esp. in its shorter leaves, shorter inflorescences, shorter perianth lobes, and smaller fruits (Hummelinck 1993: 223). The species was thought to have possibly disappeared, but was recollected by Howard (Howard 20311, US 3567226! & NY 0140250!, Jan. 1986) and Thomson (2014).

**A. rzedowskiana** P. Carrillo & al. (Brittonia 55 (3): 240–242, ill., 2003). **Type:** Mexico, Jalisco (Carrillo-Reyes & Cabrera 1503 [IBUG, GUADA, MEXU, NY]). — **Lit:** Cházaro Basáñez & al. (2004a: with ill.); Vázquez-García & al. (2007b: 68–69, 73, t. Y). **Distr:** Mexico (S Sinaloa, Nayarit, Zacatecas, C Jalisco); igneous rocky slopes and cliffs, in oak or oak-pine forests, 1600–2500 m; flowers February to April. **I:** Etter & Kristen (2007a: 58); Richter (2011: 56); Etter & Kristen (2012: 84); Pilbeam (2013: 183–184); Ettelt (2014: 125); Hochstätter (2015: VIII: 8).

[1a] Stems repent, to 50 cm; **Ros** hemispherical, compact, 25–45 (–65)  $\times$  20–40 cm, caespitose, given as “polycarpic” and flowering repeatedly from “lateral” inflorescences, which are actually likely terminal on rudimentary lateral rosettes; **L** 100–260, linear-triangular, straight or falcate, rigid, acuminate, striate on both surfaces, (11–) 20–35 (–50)  $\times$  (0.7–) 0.8–1.2 (–1.4) cm (in the middle, at the base to 2.1 cm), glaucous or green, margins hyaline, minutely serrulate with 17–30 teeth per cm; **terminal Sp** rigid, (8–) 10–19 (–23) mm, reddish-brown; **Inf** inclined to decumbent, occasionally sinuous, (42–) 70–170 cm, ‘spicate’, fertile part 10–32 (–53) cm, dense, in the upper  $\frac{1}{8}$ – $\frac{1}{3}$ , with 50–200 flowers; peduncular **Bra** 2.5–9  $\times$  0.5–0.7 cm; floral **Bra** longer than the flowers; **Ped** < 1 mm; **Fl** funnel-shaped, (20–)

22–23 (–24) mm; **Tep** greenish-purple, tube 7–7.5 (–10)  $\times$  9–10 mm, lobes ovate-elliptic, incurved, subequal, the inner slightly narrower than the outer, 4–6 (–8)  $\times$  2–4 (–6) mm, with a tuft of microscopic hairs at the apex; **Fil** (22–) 28–38 (–45) mm, inserted at mid-tube; **Ov** cylindrical to fusiform, glabrous, 7–9  $\times$  3–3.5 (–4) mm, slightly protruding from the tube; **Sty** filiform, sinuate when young, straight at anthesis 40–48 (–51) mm; **Sti** capitate; **Fr** subglobose, erect or appressed to the axis, 7–13  $\times$  6–9 mm, smooth or verrucose; **Se** hemispherical, triangular in cross section, 2.4–3.1  $\times$  1.2–2.1 mm, black.

According to the protologue, the species clearly belongs to Sect. *Juncineae* (as Group *Striatae*) due to its narrow, striate, hard and thick leaves with scabrous serrulate margins and flowers without neck and the ovary slightly protruding from the tube. Its leaves resemble those of *A. striata* ssp. *falcata*, but its floral morphology is more similar to *A. petrophila* and *A. dasyliroides*, with which it shares a short floral tube about as long as the tepals. According to the protologue distinguished from *A. petrophila* by its wider leaves, longer floral tube and shorter tepal lobes, and from *A. dasyliroides* by its caespitose habit, narrower leaves and shorter flowers. In the protologue, the inflorescences are given as inclined to decumbent; a habitat photograph by Etter & Kristen (2007a) shows that the inflorescences may indeed bend down to the ground. Etter & Kristen (2007a: 58) list the plant for Nayarit and Zacatecas. According to Vázquez-García & al. (2007b: 69, 73), *A. rzedowskiana* belongs to the *A. striata* complex and should be compared with its infraspecific taxa, and the population at Cerro El Gallo, Bolaños (Jalisco) assigned to the former may in fact represent *A. striata* ssp. *falcata*.

**A. salmiana** Otto ex Salm-Dyck (Bonplandia 7: 88, 1859). **Type:** not typified. — **Distr:** Mexico.

$\equiv$  *Agave atrovirens* var. *salmiana* (Otto ex Salm-Dyck) Trelease (1920).

**A. salmiana** ssp. **crassispina** (Trelease) Gentry (Agaves Cont. North Amer., 609, ill. (pp. 597, 609), 1982). **Type:** not typified. — **Lit:** González-



Elizondo & al. (2009: 122). **Distr:** Mexico (Coahuila, Zacatecas, San Luis Potosí, NE Jalisco, Guanajuato, Hidalgo, Puebla, C Veracruz); in desert scrub, 1450–2700 m. **I:** Martínez-Morales & Meyer (1985: 63); Irish & Irish (2000: t. 35); Heller (2006: 125); Richter (2011: 9); Pilbeam (2013: 186).

≡ *Agave crassispina* Trelease (1914); **incl.** *Agave crassispina* var. *culta* Trelease (1920).

[2b] Differs from ssp. *salmiana*: **Ros** smaller, 0.8–1.2 m; **L** fewer and smaller, 60–90 × 16–25 cm (rarely larger), margins repand to crenate; **marginal teeth** firm, with a broad base, mostly 7–12 mm, dark brown becoming grey with age, 10–30 mm apart.

This subspecies represents the extensive wild populations of *A. salmiana* differing from the cultivated ssp. *salmiana* mainly in its smaller size and stronger marginal teeth (Gentry 1982: 610). It rarely forms natural hybrids with *A. pintilla* (González-Elizondo & al. 2011). Hernández-Vera & al. (2007a) provide a new record from NE Jalisco. In W San Luis Potosí, wild plant are intensively collected for mescal production leaving soil and offsets exposed, and overgrazing is a major problem for the establishment of offsets (Martínez-Morales & Meyer 1985). In Zacatecas, human population increase with increased *Agave* exploitation has led to ecological deterioration of the local plant stands, without contributing to socio-economic improvements (Martínez-Salvador & al. 2007).

**A. salmiana** ssp. *salmiana* — **Lit:** Berger (1915: 134–137); Breitung (1964: 13–14, as *A. atrovirens* var.); Gentry (1982: 605–608); González-Elizondo & al. (2009: 119–122); García-Mendoza (2011a: 53–54); Starr (2012: 230–233, 325–327); all with ills. **Distr:** Mexico (Coahuila, Durango, Zacatecas, San Luis Potosí, Colima, Jalisco, Guanajuato, Querétaro, Hidalgo, Michoacán, México, Distrito Federal, Puebla, Oaxaca); cultivated only; flowers March to July; neophyte in Spain, Portugal, and RSA. **I:** Heller (2006: 126, 154); Richter (2011: 11); Pilbeam (2013: 185); Smith & Figueiredo (2014a: 15, as var.);

**incl.** *Agave latissima* auct. (s.a.) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave jacobiana* Salm-Dyck

(1859); **incl.** *Agave ferdinand-cortez* Hort. Tonel ex K. Koch (1862); **incl.** *Agave montezumae* Hort. Tonel ex K. Koch (1862); **incl.** *Agave maximiliana* P. Blázquez & I. Blázquez (1865); **incl.** *Agave atrovirens* Heldreich (1867) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave lehmannii* Jacobi (1869); **incl.** *Agave cochlearis* Jacobi (1870) ≡ *Agave salmiana* var. *cochlearis* (Jacobi) A. Terracciano (1885); **incl.** *Agave chinensis* F. P. Smith (1871) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave ragusae* A. Terracciano (1897) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave salmiana* var. *glauca* Becker (1898); **incl.** *Agave quioitifera* Trelease ex Ochoterena (1913); **incl.** *Agave compluviata* Trelease (1914); **incl.** *Agave whitackeri* hort. ex Trelease (1914) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave caratas* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave dyckii* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave potatorum* hort. ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave salmiana* var. *contorta* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[2b] Stems short, thick; **Ros** massive, 1.5–2 × ±3–4 m, closely surculose; **L** broadly linear-lanceolate, thickly fleshy, acuminate, tip sigmoidally curved, deeply convex below at the base, concave to guttered upwards, 100–200 × 20–35 cm, green to glaucous-greyish, margins of the upper ½ often ± repand, sometimes with small prominences; **marginal teeth** mostly 5–10 mm (largest at mid-leaf), brown to greyish-brown, 30–50 mm apart, tips straight to curved from low broad bases; **terminal Sp** subulate, stout, long, 50–100 mm, dark brown, grooved above for >½ of the length, long decurrent (sometimes to the middle of the lamina) as heavy horny margin; **Inf** 7–8 m, paniculate, peduncle with closely imbricate large fleshy **Bra**, fertile part broad, stout, part-**Inf** large, several times compound, 15–20 in the upper ½ of the inflorescence; **Fl** 80–110 mm, thickly fleshy; **Tep** yellow, tube funnel-shaped, thick-walled between the lobe sinuses, 21–24 × 20 mm, lobes lanceolate, curling inwards with progressing anthesis, unequal, outer 21–25 × 6 mm, bulging at the base, narrowed above, with thin involute margins, bluntly galeate,

inner 2–3 mm shorter, with a broad keel; **Fil** 55–70 mm, inserted just above mid-tube, those in front of the outer tepals frequently 1–3 mm taller than the others; **Anth** excentric, 30–35 mm, yellow; **Ov** cylindrical, thick, 50–60 mm, green, neck not constricted; **Sty** exceeding the stamens after anthesis; **Fr** 55–70 × 20–22 mm, stipitate, beaked, brown; **Se** drop-shaped, 8–9 × 6–7 mm, black, hilar notch shallow, apical. — **Cytology**:  $2n = 120$  (Simpson & al. 2011).

Consisting of many forms cultivated in the pulque industry. It is generally recognizable by its broad, heavy, well-armed green leaves with long-acuminate sigmoid tips and large peduncular bracts subtending broad large pyramidal ‘panicles’ (Gentry 1982: 605). *A. salmiana* as well as *A. mapisaga* both include several cultivars which are morphologically and genetically different but show low genetic diversity within each cultivar due to low levels of gene flow (Alfaro Rojas & al. 2007). A detailed study of 48 morphological characteristics from 62 populations of the *A. salmiana* group (Mora-López & al. 2011) showed a gradient of domestication in the sequence *A. salmiana* ssp. *crassispina* (wild) → *A. salmiana* ssp. *salmiana* (cultivated only), concomitant with the increase in rosette and leaf size and the reduction of the marginal teeth and terminal spines (see also under *A. mapisaga*).

Brunel & Rull (2010) report this species and *A. atrovirens* as hosts of the Ulidid fly *Pseudodyscrasis scutellaris*, whose larvae develop in the leaf tissue and cause necrotic spots and discolourations. Previous herbivore damage by beetles and lepidopterans seems to promote *Pseudodyscrasis* attacks, as its adults feed on herbivory-associated rotting *Agave* tissues, etc. Caterpillars of the moth *Comadia redtenbacheri* feed on the plants and may eventually kill them. The boiled and fried caterpillars are eaten as “gusano rojo” or “red agave worms” (Acuña & al. 2011: 159). Plant communities change after long-time use towards *Opuntia* spp. (nopaleras) as replacement of the original communities, and *A. salmiana* density decreases concomitantly (Martínez Salvador & al. 2012). Gómez-Aíza & Zuria (2010) report that flowers of plants in an urban area are visited by 39 species of birds.

The taxon is mentioned as neophyte in Spain (Guillot Ortiz & Meer 2008a, Peña Ramos & Sánchez Gullón 2016), Portugal (Silva & al. 2015) and RSA (Eastern Cape) (Smith & Figueiredo 2012).

**A. salmiana** var. **mitriformis** (Jacobi) A. Berger (Gard. Chron., ser. 3, 33: 294, 1903). **Type**: not typified. — **Lit**: Berger (1915: 132–134, with ill., as *A. ferox*); Breitung (1964: 11–13, with ills., as *A. ferox* and *A. mitriformis*); Gentry (1982: 611–612, with ills., as *A. salmiana* var. *ferox*); García-Mendoza (2011a: 55–57, as *A. salmiana* ssp. *tehuacanensis*); Starr (2012: 231, 233, as *A. salmiana* var. *ferox*). **Distr**: Mexico (México, Puebla, Oaxaca); mainly cultivated but apparently also spontaneous; neophyte in Spain and New Zealand. **I**: Heller (2006: 5, 14, 40, 125); Pilbeam (2013: 187); Smith & Figueiredo (2014a: 15); Zimer (2014: 100); all as *A. salmiana* var. *ferox*.

≡ *Agave mitriformis* Jacobi (1869); **incl.** *Agave tehuacanensis* Karwinsky ex Salm-Dyck (1859) ≡ *Agave salmiana* ssp. *tehuacanensis* (Karwinsky ex Salm-Dyck) García-Mendoza (2011); **incl.** *Agave ferox* K. Koch (1860) ≡ *Agave salmiana* var. *ferox* (K. Koch) Gentry (1982) ≡ *Agave salmiana* ssp. *ferox* (K. Koch) Hochstätter (2015); **incl.** *Agave coarctata* Jacobi (1869); **incl.** *Agave bonnetiana* Peacock ex Baker (1877); **incl.** *Agave coelum* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[2b] Differs from ssp. *salmiana*: **Ros** 1–1.5 × ±2–3 m; **L** broadly oblanceolate, outcurving, thick, tip shortly acuminate, 50–90 × 15–30 cm, light shiny green, margins crenate with strong prominences; **marginal teeth** (5–) 10–15 × 10–20 mm, on prominent broad-based tubercles; **Inf** 3.5–5 (–6) m, peduncle with coriaceous **Bra**, fertile part with (6–) 10–15 part-**Inf**; **Fl** more slender, 70–85 mm. — **Cytology**:  $2n = 120$  (Simpson & al. 2011: as *A. ferox*).

An easily recognizable variant of uncertain systematic status (Gentry 1982: 611). In a classification of 13 morphological characters, it is multiply nested within (and possibly derived from) *A. salmiana* ssp. *crassispina* (Mora-López & al. 2011). García-Mendoza (2011a) elevated this

taxon to subspecific rank as *A. salmiana* ssp. *tehuacanensis*, but the retention of varietal rank is deemed more appropriate due to geographical overlap with ssp. *salmiana*. This taxon was previously treated as *A. salmiana* var. *ferox*, but the name used here has nomenclatural priority.

Reported as neophyte from Spain (Guillot Ortiz & al. 2008: 72–73, Mesquida & al. 2016: 50–53), and New Zealand (Zimer 2014: 100). — ‘Butterfingers’ is a normal-leaved cultivar of smaller size (Starr 2012: 233, sub *A. salmiana* var. *ferox*).

**A. ×santilloensis** Hort. B. Ullrich (ined., 1991). **Nom. inval.**, ICN Art. 29.1. — **Lit:** Gentry (1967: as *A. asperrima* × *A. victoriae-reginae*); Shields (1972: 96, as *A. nigra* etc.); Gentry (1982: 185, as *A. scabra* × *A. victoriae-reginae*); Ullrich (1993c: as *A. asperrima* × *A. victoriae-reginae*); Thiede (2011: 151, 152, as *A. nickelsiae* × *A. scabra*); González-Elizondo & al. (2011: 87, 88, as *A. nickelsiae* × *A. asperrima*); Starr (2012: 240–243, as *A.* ‘Sharkskin’); all with ills. **Distr:** Mexico (Coahuila: NE Saltillo); on limestone ridges in desert scrub, 1220–1525 m; flowers June to July. **I:** Kuppen (2000: 186, as *A. victoriae-reginae* × *A. asperrima*); Heller (2006: 146, as *A. nigra*); Richter (2011: 87, as *A. nigra*); Roosbroeck (2012: 164, as *A. nickelsiae* × *A. asperrima*).

**Incl.** *Agave victoriae-reginae* fa. *viridis* Breitung (1960); **incl.** *Agave ferdinandi-regis* var. *nigra* Shields (1972) (*nom. inval.*, ICN Art. 36.3, 39.1); **incl.** *Agave nigra* Shields (1972) (*nom. inval.*, ICN Art. 36.3, 39.1); **incl.** *Agave victoriae-reginae* var. *nigra* Shields (1972) (*nom. inval.*, ICN Art. 36.3, 39.1).

[1g × 2a] This is the natural hybrid *A. asperrima* × *A. nickelsiae*, known from extensive, very variable introgressive hybrid swarms in the vicinity of Saltillo with all intergrades between its putative parents. The hybrids were dealt with in detail by Gentry (1967) and Gentry (1982: 185), and represent the best-known natural hybrid in *Agave*.

It is widely cultivated esp. under the name *A. nigra*, which was invalidly published by Shields (1972). In an unpublished manuscript in 1991,

B. Ullrich coined the name *A. santilloensis* for these hybrids, which is adopted here. See also the note under *A. ×pumila*. ‘Sharkskin’ is a cultivar selected from the hybrid swarm (Starr 2012). In habitat, most plants of the hybrid swarm, esp. the horticulturally more attractive plants, were missing in 2012 and had apparently been illegally collected (P. Spracklin, pers. comm. Nov. 2012).

**A. sanpedroensis** W. C. Hodgson & Salywon (Syst. Bot. 43(3): 735–738, ills., 2018). **Type:** USA, Arizona (*Hodgson & Salywon* 29603 [DES [3 sheets], NY, US]). — **Distr:** USA (S Arizona: Tucson region); on pre-Columbian agricultural fields in the Arizona Upland subdivision of the Sonoran Desert, 915 m; flowers late July to August.

[2h] Acaulescent; **Ros** open, 0.5–0.75 × 0.5–0.75 m, caespitose, freely suckering; **L** numerous, erect-spreading, linear-lanceolate to linear-oblongate, acuminate, firm, broadest at, just below, or just above the middle, canaliculate, thick at the base, 44–49 × 5–7.3 cm, glaucous-grey, cross-zoned with alternating bands of grey and grey-green, with conspicuous white imprints from the central bud, margins repand; **marginal teeth** strongly recurved, occasionally porrect or upturned in the basal and distal 1/6–1/4, weakly attached, ±1.5–3.5 mm, glaucous-grey (-brown), with brown ring at the base, 12–25 mm apart, intermittent teeth (0–) 4–6 along the lower 2/3 of the leaf; **terminal Sp** slender, openly grooved, 24–35 mm, grey with dark grey-mahogany-brown at the tip, decurrent for ±40 mm to the upper teeth; **Inf** 4.75–6 m, narrowly paniculate, maroon-green glaucous, fertile part open, with 9–13 short, perpendicular to sigmoid/sinuuous-ascending part-**Inf** in the upper 1/3–2/5, to 22 cm long, with 21–31 flowers; **Bra** broadly lanceolate, acuminate to long acuminate; **Ped** very short; **Fl** 55–65 mm, with sweet-musky fragrance at anthesis; **Tep** tube thick, bulging at the lobe bases, 11.5–14 × (11–) 13.5–17 mm, light green, lobes broadly lanceolate, persistently erect, becoming leathery with age, margins sometimes strongly involute, clasping the filaments, (slightly) unequal to equal; **OTep** 15.2–19.25 mm, creamy light yellow (to very light chartreuse-green), sometimes lightly flushed with maroon, tips brown,

papillose, cucullate; **ITep** 13.5–16.25 mm, creamy light yellow (to very light chartreuse-green), strongly keeled, tips less cucullate and lighter; **Fil** 51–60 mm, unequally to subequally or equally inserted 5–6.9 mm above the tube base, light chartreuse-cream, sometimes becoming lightly flushed with maroon distally; **Anth** 15–19 mm, yellowish; **Ov** 24–30 × 8–9 mm, neck 1.5–4.7 mm, slightly constricted, light chartreuse-green-cream or chartreuse-green; **Sty** 32–59 mm, ± as long as the filaments, cream or light chartreuse-green-cream with or without slight maroon flush; **Sti** capitate, 3-lobed; **Fr** and **Se** not observed.

According to the protologue similar to *A. phillipsiana* and *A. palmeri* in its flower colour, but these two species differ in having darker green leaves without conspicuously thickened bases and without imprint of the central bud.

*A. sanpedroensis* is known from less than a dozen sites with roughly 200 individuals, all occurring within pre-Columbian agricultural fields with numerous rock piles and terraces; no occurrences at non-anthropogenic sites are known. It appears to be sterile; only two flowering specimens were observed which did not produce any fruit. The species reproduces vegetatively via rhizomatous offsets and thus has persisted for centuries in these fields since they were abandoned. For further pre-Columbian cultivar species in Arizona, see also under *A. verdensis*.

**A. santanamichelii** (Art. Castro & Aarón Rodríguez) Thiede & Gideon F. Smith (Bradleya 37: 262, 2019). **Type:** Mexico, Jalisco (*Carrillo-Reyes & Tinoco-Villa* 8160 [IBUG, CIIDIR, MEXU]). — **Dist:** Mexico (W Jalisco); ecotone between open pine-oak forests and savannoid vegetation, in deep acidic soils, 920–1060 m; flowers in November.

≡ *Manfreda santanamichelii* Art. Castro & Aarón Rodríguez (2018).

[3a3 × 3b2?] Plants herbaceous; corm 2–2.8 × 1–1.3 cm, cylindrical, with conspicuous buds, bulb 3.5–4.8 × 2–2.5 cm, oblong-ovoid, nearly completely covered with tunicate reddish-brown dried leaf bases; **R** fleshy and thickened, 2–7.5 cm, contractile; **L** drought-deciduous, 7–10, erect, linear, falcate, involute, thin to

leathery, lower and upper face papillate, apex acute and soft, 30–45 × 0.2–0.5 cm, greyish-green, uniformly coloured, margins hyaline, retrorsely and antrorsely denticulate; **Inf** 90–135 cm, erect, green, ‘spicate’, peduncle with 6–9 **Bra**, the lowermost similar to vegetative leaves, **Int** decreasing in length upwards, fertile part 26–36 cm, lax, with 12–17 floral nodes; floral **Bra** 3–45 × 0.2–2 mm; bracteoles 2 per node; **Ped** 4–25 mm, glaucous; **Fl** ±25–30 mm, geminate, ascending, actinomorphic, funnel-shaped; **Tep** yellowish-green or pale red-yellowish on the outer face and pale yellow inside, forming a tube 9–15 × 3–4 mm at the base of the lobes, slightly tapering towards both ends, not curved, lobes ovate to lanceolate, extended, 7–9 × 3–4 mm, tip with a bundle of short white trichomes; **Fil** subulate, 3.7–5.6 mm, erect at anthesis, exceeding the tube for its length, inserted at the base of the lobes on the same level, yellow; **Anth** 4.5–5.5 mm, yellow; **Ov** ovate, 5–7 × 3–5 mm, greenish, slightly constricted above; **Sty** filiform, 17–21 mm, whitish, exerted for 3–5 mm at anthesis; **Sti** capitate, 3-lobed; **Fr** globose, 12–16 × 10–15 mm, with persisting tepals; **Se** deltoid, plane-concave, 3–3.5 × 2.2–2.5 mm, shiny black.

According to the protologue resembling *A. involuta* and *A. singuliflora* (both as *Manfreda*). In its geminate flowers, *A. santanamichelii* differs from all other species of Sect. *Herbaceae* (with single flowers), but resembles Sect. *Polianthes* (with geminate flowers). It might have originated as a spontaneous natural hybrid or allopolyploid between the sympatric *A. involuta* (Sect. *Herbaceae*) with similarly coloured flowers and *A. bulliana* (Sect. *Polianthes*, = *Prochnyanthes mexicana*; A. Castro, pers. comm. Nov. 2018). Artificial hybrids between species of Sect. *Polianthes* and Sect. *Herbaceae* were raised by Lindstrom (2006); some of these have flowers very similar to *A. santanamichelii* (webpage J. T. Lindstrom on <https://www.flickr.com/photos/jonsplants/3642338622>, accessed 6. 11. 2018).

**A. scabra** Ortega (Nov. Pl. Descr. Dec. 2: 13, 1797). **Type:** not typified. — **Lit:** Rose (1903c: 20); Berger (1915: 32); Standley & Steyermark



(1952: 108–110, with ills.); Verhoek-Williams (1975: 265–282); all as *Manfreda brachystachys* except Berger; Piña Luján (1986: 12–13, 35, with ill., as *M. brachystachya*); McVaugh (1989: 234–235, fig. 37, as *M. scabra*); Ullrich (1992k: with ill., as *M. brachystachya*); Robbins (2001: online version with ills., as *M. scabra*); Castillejos-Cruz (2009: [270]–[281], with ills., as *M. scabra*). **Distr:** Mexico (Durango, Zacatecas, San Luis Potosí, Nayarit, Aguascalientes, Jalisco, Guanajuato, Querétaro, Hidalgo, Michoacán, México, D. F., Morelos, Puebla, Veracruz, Guerrero, Oaxaca, Chiapas), Guatemala, Honduras, El Salvador, N Nicaragua; rocky slopes in oak or pine-oak forests, tropical deciduous forests, thorn forests, (semi-) evergreen forests, cloud forests, and grasslands, 100–3100 m; flowers July to September, in Chiapas and C America October to November. **I:** Edwards's Bot. Reg. 25: t. 55, 1839, as *A. saponaria*; Verhoek-Williams (1978b: 126, as *Manfreda brachystachya*); Rodríguez & Castro-Castro (2006: 621); Rodríguez & Castro-Castro (2007: 4); Richter (2007: 41); Hochstätter (2016: I: 41); Castro-Castro & al. (2017: 62); as *M. scabra* when not mentioned otherwise.

≡ *Manfreda scabra* (Ortega) McVaugh (1989); **incl.** *Agave brachystachys* Cavanilles (1802) ≡ *Manfreda brachystachys* (Cavanilles) Rose (1903) ≡ *Polianthes brachystachys* (Cavanilles) Shinnars (1966); **incl.** *Agave spicata* De Candolle (1813) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave polyanthoides* Schlechtendal & Chamisso (1831); **incl.** *Agave saponaria* Lindley (1838); **incl.** *Agave humilis* M. Roemer (1847); **incl.** *Agave polianthoides* M. Roemer (1847) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave brachystachys* var. *strictior* Jacobi & C. D. Bouché (1865); **incl.** *Agave sessiliflora* Hemsley (1880) ≡ *Manfreda sessiliflora* (Hemsley) Matuda (1961); **incl.** *Agave langlassei* André (1901); **incl.** *Manfreda oliveriana* Rose (1903) ≡ *Agave oliveriana* (Rose) A. Berger (1915) ≡ *Polianthes oliveriana* (Rose) Shinnars (1966); **incl.** *Manfreda malinaltenangensis* Matuda (1976).

[3a2] Plants herbaceous, large (for Subgen. *Manfreda*); corm (2.5–) 4–7.2 × (1.7–) 2.5–4.5 cm, cylindrical, reproducing vegetatively by buds, bulb 4–7 × (1.5–) 2.5–4 cm, covered with fibrous

dry leaf bases separating into coarse fibres 7.5–12 cm long; **R** fleshy and thickened, with filiform ramifications, contractile; **L** drought-deciduous, 2–5, recurved to arched, broadly or narrowly linear-lanceolate, spreading, glabrous on both faces, coriaceous to herbaceous, slightly canaliculate, often gently undulate, 40–60 (–95) × 2–4 (–5) cm, light green, often glaucous, glossy, tip acute, with a short and soft tip, veins prominent on the lower face, each vein usually with a single row of papillae, margins with a narrow hyaline band, entire or slightly scabrous and papillate, slightly revolute; **Inf** 1.2–1.4 (–1.6) m, erect, ‘spicate’, green-glaucous, peduncle with 8–10 **Bra**, base truncate, similar to the leaves, decreasing in size upwards, fertile part elongate, lax, 20–40 (–70) cm, with 20–30 flowering nodes; floral **Bra** (0.6–) 1.4–3.8 (–4.4) cm, narrowly deltoid; **Fl** sessile, 28–32 mm, ascending, tubular; **Te**p greenish-yellow to reddish-green, tube narrowly funnel-shaped, slightly recurved, 13–28 × 4–7 mm, lobes oblong, reflexed to revolute, (10–) 12–18 (–23) × 4–6 mm, cucullate, with a soft tip and a tuft of short white trichomes; **Fil** erect, 36–55 mm, exceeding the tube for 26–36 (–45) mm, inserted at  $\frac{3}{4}$  from the base of the tube all on the same level, yellowish-green with purple dots; **Anth** 11–16 mm, greenish-yellow; **Ov** cylindrical, 12–16 (–20) × 4–5 mm, not extending into the tube, not constricted; **Sty** 30–42 mm, yellowish-green with purple dots; **Sti** capitate, 3-lobed; **Fr** cylindrical, slightly apiculate, (15–) 20–26 (–30) × 12–16 mm, with persisting tepals; **Se** deltoid, plane-concave, 4.5–6 × 4–6 mm, dull.

McVaugh (1989: 234) has replaced the well-established name *Manfreda brachystachys* (based on *Agave brachystachys*, as ‘*brachystachya*’) by the new combination *Manfreda scabra*, based on the earlier name *Agave scabra*. *A. scabra* is the most widely distributed species of Subgen. *Manfreda* and with the exception of the Guatemalan *A. fusca* the only one reaching Central America. It is less variable in the N and rather variable in the C and S part of its area (Castillejos-Cruz 2009) and is characterized by leaves with prominent veins with a row of papillae and margins which are entire or equally papillate, as well as the elongate open inflorescence, a semihorizontal



flower position during anthesis and ascending at maturity, and the tepal tube, which is longer than the ovary and the lobes (McVaugh 1989, Castillejos-Cruz 2009).

*A. scabra* is morphologically similar to the recently published *A. justosierrana* (see there). *Manfreda malinaltenangensis* was placed in the synonymy of *A. hauniensis* in the first edition of this handbook, but represents a synonym of *A. scabra* (Castañeda Rojas & al. 2005). The main pollinator is a long-nosed bat species, minor pollinators are other bats, hawkmoths, and hummingbirds, and perching birds and bees rob nectar (Eguiarte & Búrquez 1987).

**A. scaposa** Gentry (Agaves Cont. North Amer., 303–304, ills., 1982). **Type:** Mexico, Oaxaca (Gentry 22472 [US [syn], ARIZ, DES, MEXU, MICH]). — **Lit:** García-Mendoza (2011a: 58–59). **Distr:** Mexico (S Puebla, NW Oaxaca); on igneous or limestone rocks, in dry scrub, oak-palm grasslands or oak forests, 1980–2550 m; flowers June to August. **I:** Pilbeam (2013: 188); Hochstätter (2015: VII: 20).

[2a] Stems short; **Ros** dense, 1.5–2.2 × 2.5–3 m, solitary; **L** 60–100, broadly lanceolate, ascending, outcurving to spreading, coriaceous, somewhat flexible, heavily succulent, slightly narrowed above the thick base, upper face almost flat to concave, smooth, 90–120 × 20–28 cm, light to dark green or yellowish-green, with glaucous transverse bands, margins straight or repand to crenate; **marginal teeth** numerous, usually straight, closely set, on broad flattened reddish bases, sometimes on small prominences, 3–6 (–8) × 7–10 mm, confluent or 10–20 (–25) mm apart, dark brown or brownish to greyish, sometimes with few smaller intermittent teeth placed at random; **terminal Sp** subulate, base conical, with deep narrow groove above, 25–60 × 3–5 mm, dark brown or greyish, decurrent to ¼–½ of the lamina; **Inf** 6–10 (–13) m, paniculate, peduncle green to greyish-green, 5–7 m, with narrow chartaceous triangular reflexed **Bra** 30–40 cm, fertile part lax, broadly oblong to ovate, part-**Inf** 25–40 in the upper ½–¼ of the inflorescence, 25–40 cm long; floral **Bra** small, scarcely persistent; **Ped** 5–15 mm, slender; **Fl** (45–) 50–60 (–65)

mm; **Tep** intense greenish-yellow, tube 4–10 × (8–) 10–18 mm, lobes oblong, erect, thick, subequal, 14–20 (–25) × 3–5 mm, the outer slightly larger, the inner ribbed; **Fil** (30–) 35–45 mm, inserted at the mouth of the tube, yellowish; **Anth** 20–22 mm, yellow; **Ov** cylindrical to somewhat triquetrous, 30–38 × 5–10 mm, green, neck 3–5 mm; **Sty** 50 mm; **Fr** oblong, strong-walled, 50–60 × 20–30 mm, stipitate, shortly beaked; **Se** drop-shaped, 7–9 × 5–6 mm, dull black.

Characterized by its large rosettes with dark to yellowish-green leaves with repand to crenate margins with small, narrow teeth, and small, intense greenish-yellow flowers on large inflorescences overtopping the tree stratum (García-Mendoza 2011a). Rarely observed in habitat. Its tall narrow panicles with dry small scapose peduncular bracts relate it with Sect. *Agave* (Gentry 1982, as Group *Americanae*). The flowers were unknown to Gentry (1982) and the description is added from García-Mendoza (2011a).

The caterpillars of the butterfly *Aegiale hesperiaris* feed within the leaves esp. of *A. scaposa* and represent a most valued delicacy in the traditional food system (“conduchos” or “white agave worms”; Acuña & al. 2011). This species, *A. aff. atrovirens*, and *A. salmiana* occurring in areas cleared for agriculture are protected by transplanting young individuals to areas or terraces surrounding the plots in order to favour retention of soil and water and to make use of them as fodder, fuel, food, and wood (Blancas & al. 2010). — The holotype at US consists of 3 sheets thus representing syntypes; 2 of the sheets were apparently cross-labelled later.

**A. schidigera** Lemaire (Ill. Hort. 8(6): in adnot. ad t. 289, 1861). **Type:** [neo — icono]: Ill. Hort. 9(7): t. 330, 1862. — **Lit:** Berger (1915: 74–76 [but ill. placed in *A. colimana* by Gentry (1982: 120)]); Breitung (1963: 118); Gentry (1982: 119–121); McVaugh (1989: 142–143); Ullrich (1992h); Vázquez-García & al. (2007b: 70–71, t. BB); Hernández-Vera & al. (2007a); González-Elizondo & al. (2009: 69–74, as *A. filifera* ssp.); Starr (2012: 234–239, 317–318); all with ills. except McVaugh. **Distr:** Mexico (Sonora, Chihuahua, Sinaloa, Durango, Zacatecas, San Luis

Potosí, Nayarit, Jalisco, Guanajuato, Aguascalientes, Michoacán, Guerrero?); tropical deciduous forests, pine-oak-forests and ecotones, 875–3000 m; flowers mainly June to November, also records for February, March, May, and December. **I:** Curtis's Bot. Mag. 93: t. 5641, 1867; Curtis's Bot. Mag. 135: t. 8271, 1909, as *A. wrightii*; Heller (2006: 127); Richter (2011: 44, 109, 110, 118); Pilbeam (2013: 83, as *A. filifera* ssp.).

≡ *Agave filifera* var. *schidigera* (Lemaire) A. Terracciano (1885) ≡ *Agave filifera* ssp. *schidigera* (Lemaire) B. Ullrich (1992); **incl.** *Agave filifera* var. *ignescens* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave filifera* var. *adornata* Scheidweiler (1861); **incl.** *Agave filifera* var. *pannosa* Scheidweiler (1861); **incl.** *Littaea roezlii* Roezl (1861) (*nom. inval.*, ICN Art. 36.1b); **incl.** *Agave filifera* var. *angustifolia* Lemaire (1865); **incl.** *Agave schidigera* var. *angustifolia* Lemaire (1865); **incl.** *Agave schidigera* var. *ignescens* Lemaire (1865); **incl.** *Agave schidigera* var. *plumosa* Lemaire (1865); **incl.** *Agave vestita* S. Watson (1890); **incl.** *Agave taylorii* Hort. Besaucèle ex A. Berger (1894) (*nom. illeg.*, ICN Art. 53.1) ≡ *Agave schidigera* var. *taylorii* (Hort. Besaucèle) H. Jacobsen (1955); **incl.** *Agave wrightii* J. R. Drummond (1909) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave perplexans* Trelease (1914); **incl.** *Agave schidigera* ssp. *huicholensis* Ullrich ex I. Richter (2011) (*nom. inval.*, ICN Art. 38.1a, 40.1).

[Id] Stems short or none; **Ros** symmetrical, solitary, 0.4–1.14 × 0.9–2 m, not surculose; **L** > 100, linear, straight, sometimes falcate, relatively thin, pliable, widest at or below the middle, acuminate, convex below towards the base, flat above, smooth, 30–40 (–50) × (1.3–) 1.5–3 (–4) cm, green to greyish-green or yellowish-green, rarely reddish, with white imprints from the central bud, margins brown to white, coarsely white-filiferous; **terminal Sp** flat above, round below, 5–16 (–20) mm, brown to grey with age, shortly decurrent; **Inf** 2–3.5 m, 'spicate', peduncle with narrow **Bra**, fertile part slender, laxly flowered in the upper ½, part-**Inf** with 1–2 flowers; **Ped** short; **Fl** 30–45 mm; **Te** green to yellow or purplish, tube narrowly funnel-shaped, grooved, 7–10 mm,

lobes linear, acute, recurving, thin, overlapping at the base, equal, 13–20 mm, greenish to yellow or tinged purple; **Fil** slender, 35–50 mm, pale-coloured to purple, inserted on the tube rim; **Anth** very slender, frequently excentric, 13–21 mm, yellow to purplish; **Ov** fusiform, angled, 12–20 mm, neck furrowed; **Sty** longer than the filaments; **Sti** capitate; **Fr** variable in size and shape, ovoid and 12 × 6–7 mm, or oblong and 18–20 × 6–9 mm, usually beaked, shortly stipitate; **Se** thick, deltoid and 2 × 1.5 mm, or crescent-shaped and 3.5 × 2 mm, sharply cornered rather than winged, rugose or irregularly veined on the faces. — **Cytology:** 2n = 52, 180 (Simpson & al. 2011: as *A. wrightii*).

Closely related to *A. filifera*, but separable by its non-surculose habit, its mostly larger rosettes with longer, thinner, more pliable leaves and coarse rather than finely filiferous margins, and its longer floral tube (Gentry 1982: 120, McVaugh 1989, Starr 2012: 317). Narrow-leaved forms may vegetatively be indistinguishable from *A. colimana*, but the latter usually has a shorter terminal spine (5–8 mm; McVaugh 1989). González-Elizondo & al. (2009: 72) show a caespitose form from Durango as well as natural hybrids with *A. asperrima* and a further unknown species. For a form from the Sierra Huichol (Saucito, Nayarit) with esp. long and narrow leaves collected by A. B. Lau, the unpublished name *A. schidigera* ssp. *huicholensis* is used (Richter 2011: 109, with ill.). González-Elizondo & al. (2009) mention the species for Sonora (possibly based on *Reina-G. & Van Devender*, ARIZ 348293, from S Sonora). The records for Hidalgo (González-Elizondo & al. 2009) and México (McVaugh 1989) need specimen citations. The record cited by Gentry (1982: 122) for Guerrero is uncertain.

Ullrich (1992h) reduced this taxon as well as *A. multifilifera* to subspecific rank under *A. filifera*, based on mere literature interpretations, which was followed in the first edition of this handbook for practical reasons. Vázquez-García & al. (2007b) and Govaerts (2014+) reinstated Gentry's (1982) concept of separate species, and this is followed here.

Horticultural selections are distributed as 'Black Widow' and 'Durango Delight', and 'Shira Ito No Ohī' is a variegated cultivar (Starr 2012).

**A. schneideriana** A. Berger (Agaven, 256, 1915). **Type:** not typified. — **Distr:** Mexico (Puebla: Tehuacán?); ecology unknown.

[2g] Stems short, laxly leafy along the whole length, covered with leaf sheaths; **L** ±17–20, linear-lanceolate, upright-projecting, somewhat irregularly curved inwards or outwards, leathery, little fleshy, at mid-leaf ±4 cm broad, from there long attenuate towards the tip and narrowed to 2.5 cm at the base, there 9–10 mm thick, convex below, dull dark green, smooth but rough towards the tip, above flatly concave, somewhat canaliculate towards the tip, smooth, dull dark green, margins fine, pale, hyaline and cartilaginous; **marginal teeth** remote, somewhat irregular and relatively large, the larger ±30–40 mm apart, on flat, fleshy prominences with crescent-shaped to lenticular base ±6 mm long, tip of the teeth narrowly deltoid, curved hook-like, 2–3 mm, mostly up-flexed, sometimes with small intermittent teeth, upper teeth more remote and becoming smaller, basal teeth somewhat narrower, young chestnut-brown, later black-brown; **terminal Sp** slender, nearly straight, subulate, narrowly and shortly grooved above, 17–30 mm, 52 (sic!, 5.2?) mm thick, black-brown, shiny, not decurrent, sharply offset from the green tissue; **Inf, Fl, Fr** and **Se** unknown.

This “forgotten” name was not mentioned by Gentry (1982), and was listed as unplaced in the first edition of this handbook. Recently, it was recognized as a distinct species by Espejo Serna & López Ferrari (1993) and Govaerts (2014+), which is followed here. The plant was sent in 1906 from Mexico by C. A. Purpus to his brother A. Purpus at BG Darmstadt (Germany), from where Berger received material. According to the protologue, it is a very distinct species closest to *A. karwinskii*, but with a much laxer rosette, a different stem, and the leaves reminiscent of *A. cantala*. Ullrich (1993b: 56) placed *A. schneideriana* for the time being in the synonymy of *A. karwinskii*. Purpus may have collected the material from the *A. karwinskii* localities around Tehuacán (Puebla) from where he sent many plants, esp. in 1906, and it may have represented a natural hybrid with a narrow-leaved species such as *A. angustifolia*.

**A. schottii** Engelm (Trans. Acad. Sci. St. Louis 3: 305–306, 1875). **Type:** USA, Arizona (*Schott* s.n. [MO 3347375, NY 320043]). — **Lit:** Gentry (1982: 205–207, with ills.); Turner & al. (1995); Parker (2017: 262). **Distr:** USA (Arizona, New Mexico), Mexico (Sonora).

The types are the two specimens cited above from the “Serra del Pajarito” in S Arizona, collected in July 1855.

**A. schottii** var. **atricha** Trelease (Contr. US Nation. Herb. 23: 140, 1920). **Type:** not typified. — **Lit:** Toumey (1901: with ills., as *A. treleasei*); Berger (1915: 76–77, as *A. treleasei*); Gentry (1982: 207, with ill.); Hodgson (1999a: 10); Reveal & Hodgson (2002); Parker (2018a: 21, with ill.); the last 4 as *A. schottii* var. *treleasei*. **Distr:** USA (S Arizona); gravelly to rocky places, mostly in desert scrub, grasslands, juniper and oak woodlands, 1100–2000 m; flowers May to July.

**Incl.** *Agave treleasei* Toumey (1901) ≡ *Agave schottii* var. *treleasei* (Toumey) Kearney & Peebles (1939).

[1e] Differs from var. *schottii*: **L** larger, thicker and wider (1.2–2.5 cm), deep green, without imprints from the central bud, margins not filiferous; **terminal Sp** longer, 12–19 mm; **Inf** subspicate to narrowly racemose-paniculate; **Fl** larger, 35–50 mm.

For this taxon, the name *A. schottii* var. *treleasei* (published 1939) is commonly applied, but that name is antedated by *A. schottii* var. *atricha* (1920) which, according to the protologue, is “without marginal threads” and thus belongs here and not to the synonymy of var. *schottii* as previously thought.

According to Gentry (1982: 207) a doubtful variant in need of better study, occurring sympatrically with var. *schottii* (Gentry 1972: 77). It appears to be based on scattered aberrant specimens. At the type locality, only few plants were found in 1940 (Little 1981: 68) and none later in the 80ies (Reichenbacher 1985: 103). The taxon may be of hybrid origin involving *A. schottii* var. *schottii* and *A. chrysantha* or *A. palmeri* (Reveal & Hodgson 2002). According to Parker (2018a), it is the hybrid *A. schottii* var. *schottii* × *A. chrysantha*, occurring in few small clumps in the

**Fig. 51** *Agave schottii* var. *schottii* (Eggl s.n.: USA; Arizona, Organ Pipe National Monument). (Copyright: U. Eggl)



Santa Catalina Mts. near Tucson, Arizona. Hybridisation with a member of Subgen. *Agave* is also indicated by its inflorescences, partly with branchlets to 4 cm long with up to 6 flowers (Hodgson 1999a). If the hybrid origin can reliably be documented, the taxon should be treated as *A. ×treleasei*. — Plants are consumed by wildlife, perhaps rodents (attributed to “Hodgson & al. 1994” by Turner & al. (1995).

**A. schottii** var. **schottii** — **Lit:** Berger (1915: 71–72, with ill.); Gentry (1972: 67–60, with ill.); Gentry (1982: 205–207, with ill.); Ullrich (1992e); Turner & al. (1995); Hodgson (1999a: 9–10); Reveal & Hodgson (2002); Starr & Devender (2011: 230, with ill.). **Distr:** USA (S & SE Arizona, SW New Mexico), Mexico (N Sonora); gravelly to rocky places, mostly in desert scrub, grasslands, juniper and oak woodlands, 900–2000 m; flowers April to August. **I:** Curtis’s Bot. Mag. 123: t. 7567, 1897; Irish & Irish (2000: t. 38); Heller (2006: 129); Richter (2011: 128); Pilbeam (2013: 189); Hochstätter (2015: VIII: 62, 64). — Fig. 51.

**Incl.** *Agave geminiflora* var. *sonorae* Torrey (1859) ≡ *Agave sonorae* (Torrey) Mearns (1907); **incl.** *Agave schottii* var. *serrulata* Mulford (1896); **incl.** *Agave mulfordiana* Trelease (1920).

[1e] **Ros** small, densely caespitose; **L** narrowly linear, straight, incurved, or falcate, pliable, widest at the base, deeply convex below, flat or somewhat convex above, smooth on both faces, 25–40

(–50) × 0.7–1.2 cm, yellowish-green to green, with conspicuous imprints from the central bud on both faces, margins with a narrow border and sparse brittle threads; **terminal Sp** delicate, rather weak and brittle, 8–12 mm, greyish; **Inf** 1.6–2.5 m, ‘spicate’, peduncle with straw-coloured filiform acicular **Bra** 2–4 cm long, fertile part slender, frequently crooked, in the upper ¼–½, part-**Inf** with 1 or 2–3 flowers; floral **Bra** thread-like, 10–15 mm at the lower nodes but shorter further up; **Ped** stout, <2 mm; **Fl** 29–42 mm; **Tep** yellow, tube deeply funnel-shaped, very narrow below, 8–11 (–14) × 5–8 mm, lobes unequally spreading at anthesis, unequal, 8–11 (–14) × 5–8 mm, outer without keel, light yellow; **Fil** 15–22 mm, inserted 6–13 mm above the tube base; **Anth** 10–15 mm, light yellow; **Ov** 8–15 mm incl. the 4–6 mm long neck, greenish-yellow; **Sty** shorter than the filaments; **Sti** slightly thickened; **Fr** rounded to apiculate, 10–20 mm; **Se** with hilar notch at one corner, variably thickened, 3–3.5 mm along the straighter thinner edge. — **Cytology:** 2n = 60, 120 (Granick 1944, Zonneveld 2003, Simpson & al. 2011).

The flowers of *A. schottii* have a long tubular appearance due to the slender tube and the long narrow neck of the ovary. The taxon is easily confused with narrow-leaved forms of *A. felgeri*, but the latter has a short flower tube (Gentry 1982: 207). In *A. schottii*, the leaves are longer and taper more towards the tip than those of the



habitually similar *A. parviflora*, and have thinner, more irregular marginal fibres, while the rosette has a more open appearance (Starr & Devender 2011). *A. schottii* var. *schottii* hybridizes with *A. deserti* ssp. *simplex*, *A. chrysantha*, and possibly *A. palmeri* or *A. parryi* var. *parryi* (Reveal & Hodgson 2002).

*A. geminiflora* var. *sonorae* Torrey (1858) is treated as homotypic synonym by Govaerts (2014+: accessed Dec. 2018), but is according to the protologue based on “Sierra del Pajarito, Sonora, August, Schott” and thus from the Sonoran (Mexican) side of the Pajarito Mts.; the type appears to be *Schott* s.n., 1855, from “Sonora” (US 125669!).

The flowers are visited by hummingbirds, bees, wasps, ants, and bats. Nectar production is mainly nocturnal suggesting bat pollination, but the sweet fragrance, low protein content of the pollen, and the yellow flowers might favour bee pollination. Possibly, the species undergoes a shift from bat to bee pollination (Turner & al. 1995). Pollination experiments and genetic analyses showed that the taxon experiences inbreeding depression and a trend towards outbreeding depression; individuals 1 m apart had a higher genetic similarity than plants further apart (Trame & al. 1995). — The taxon has been used for washing clothes and hair and is unpalatable to livestock (Turner & al. 1995).

**A. sebastiana** Greene (Bull. Calif. Acad. Sci. 1: 214, 1885). **Type:** Mexico, Baja California (*Greene* s.n. [CAS 0000141, CAS, UC]). — **Lit:** Trelease (1912a: 47–48, tt. 23–26); Berger (1915: 172); Breitung (1963: 49–50, with ills.); Gentry (1978: 96–97, t. 6); Gentry (1982: 645–646, with ills.); Turner & al. (1995: 63); Webb & Starr (2014a: 93, 95–96, with ill.); Heim (2014: 7, 19–23, with ills.); Webb & Starr (2015: 91–92, with ill.). **Distr:** Mexico (Isla San Benito, Isla Cedros and Isla Natividad off the coast of Baja California); low desert scrub, 0–600 m; flowers March to May. **I:** Greulich (2005a: 28); Heller (2006: 129); Richter (2011: 75); Klaassen (2011: 28–30); Pilbeam (2013: 190–191); Hochstätter (2015: IV: 31); Moore (2016: 218, 220, 221, 275); Vanderplank & al. (2017: 25, 26); Greulich (2018b: 95).

≡ *Agave shawii* var. *sebastiana* (Trelease) Gentry (1949); **incl.** *Agave disjuncta* Trelease (1912).

[2f] **Ros** elongate, 0.6–0.9 × 0.75–1 m, single or mostly prolifically caespitose; **L** closely imbricate, broadly linear, broadly linear-lanceolate, broadly linear-ovate, or ovate, shortly acuminate, thick and rigid, sometimes slightly narrowed towards the base, rounded below, flat to slightly hollowed above, generally 25–45 × 8–24 cm, silvery-blue, blue-grey or glaucous blue-green, with imprints left by the central bud, margins rather straight, usually thick-horny, dark brown; **marginal teeth** frequently down-flexed, slender, larger teeth (at mid-leaf) 5–10 mm, reddish-brown, 10–20 mm apart, or smaller and more numerous; **terminal Sp** stout, variously grooved above, 20–30 mm (rarely shorter), black to somewhat grey, decurrent to the 5. or 6. tooth; **Inf** 2–3 m, paniculate, peduncle stout, with small deltoid scarious appressed pink to yellow **Bra**, fertile part short, widely spreading, rounded to nearly flat at the top, congested with 8–12 large part-**Inf** in the upper ¼ of the inflorescence; **Fl** thickly fleshy, 70–90 mm; **Tep** green in bud, opening yellow, tube broadly funnel-shaped, 14–20 × 18–22 mm, lobes lanceolate, markedly cucullate and glandular-floccose at the tip, 16–25 × 5–7 mm, inner shorter, strongly keeled; **Fil** stout, 50–60 mm, inserted at mid-tube 8–14 mm above its bottom; **Anth** 20–21 mm, yellow; **Ov** cylindrical, 35–55 mm; **Fr** large, ±60–80 × 30 mm, beaked but scarcely stipitate; **Se** 7 × 11 mm, glossy black.

Closely related to *A. shawii*, but differing significantly in the pale green somewhat glaucous leaves with more slender teeth, the smaller more remote and scarious peduncular bracts and the broader flatter inflorescences (Gentry 1978, Gentry 1982). Plants from the Bahia Tortugas area assigned here by Gentry (1982) belong to *A. vizcainoensis*, and *A. sebastiana* is thus absent from mainland Baja California (Webb & Starr 2014a). No other Agaves are known from Isla San Benito and Isla Natividad (Webb & Starr 2015), but from Isla Cedros, *A. cerulata* has recently been reported (see there). Greulich (2005a) describes a flowering hybrid of cultivated origin with a species of Subgen. *Littaea*.



**A. seemanniana** Jacobi (Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss. 1868: 154, 1869). **Type** [neo]: Honduras (*Gentry* 20684 [US, DES, MEXU]). — **Lit**: Trelease (1915: 137–138); Standley & Steyermark (1952: 116); *Gentry* (1982: 494–499, with ill.); Ullrich (1992g: with ill.); Lott & García-Mendoza (1994); Cseh (2008: with ill., p.p. as *A. pygmaea*); García-Mendoza (2010: 86–92, with ill.); García-Mendoza (2011a: 59–60). **Distr**: Mexico (Oaxaca, Chiapas), Guatemala, Honduras, El Salvador, N & NW Nicaragua, Costa Rica; dry rocky slopes, in soils derived from calcareous or granitic rocks, in dry scrub, savannas, tropical deciduous or subtropical oak or pine-oak forests, 100–2600 m; flowers September to January. **I**: Irish & Irish (2000: t. 34, as *A. pygmaea*); Richter (2011: 55, 84, 124); Pilbeam (2013: 192–193, as ssp. *seemanniana* and ssp. *pygmaea*); Smith (2014).

≡ *Agave scolymus* var. *seemanniana* (Jacobi) A. Terracciano (1885); **incl.** *Agave seemannii* var. *nana* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave seemannii* W. Bull (1868); **incl.** *Agave seemannii* K. Koch (1869) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave seemannii* T. Moore & Masters (1869) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave seemannii* var. *acuta* W. Bull (1870); **incl.** *Agave seemannii* var. *papillosa* W. Bull (1870); **incl.** *Agave seemannii* var. *parvispina* W. Bull (1870); **incl.** *Agave seemannii* var. *rotundifolia* Peacock (1873) (*nom. inval.*, ICN Art. 38.1); **incl.** *Agave caroli-schmidtii* A. Berger (1915); **incl.** *Agave guatemalensis* A. Berger (1915); **incl.** *Agave seemanniana* var. *perscabra* Trelease (1915); **incl.** *Agave tortispina* Trelease (1915); **incl.** *Agave seemannii* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave pygmaea* *Gentry* (1982) ≡ *Agave seemanniana* ssp. *pygmaea* (*Gentry*) B. Ullrich (1992) ≡ *Agave seemanniana* var. *pygmaea* (*Gentry*) B. Ullrich ex Espejo & López-Ferrari (1993); **incl.** *Agave pygmaea* *Gentry* (1982) (*nom. inval.*, ICN Art. 61.1).

[2o] Acaulescent; **Ros** compact, open, ((±0.3–) 0.8–) 1–1.5 × ((±0.4–) 1.3–) 1.5–2 mm, solitary; **L** (16–) 30–40, spatulate, broadly lanceolate or ovate, recurved or erect, thickly succulent, thickened and strongly narrowed at the base, flat

to slightly guttered, ((12–) 22–) 30–55 (–65) × (6–) 10–16 (–22) cm, glaucous, greenish-glaucous to yellowish-green, zonate, margins repand to sharply crenate; **marginal teeth** mostly straight or curved, deltoid, (2–) 6–10 (–15) × (±5–) 10–14 mm, dark to greyish-brown or greyish, ((10–) 30–) 40–55 mm apart, with broad bases covering the top of the marginal prominences, these (7–) 10–15 (–20) mm; **terminal Sp** subulate, very broad at the base, sinuous, broadly grooved above, (15–) 20–45 (–50) × 5–10 mm, dark brown to greyish, conspicuously decurrent as a sharp ridge to the upper teeth for 2–6 cm; **Inf** (2–) 4–6 (–7) m, paniculate, peduncle short, with triangular chartaceous **Bra** 15–22 cm long, fertile part open, ovate to oblong in outline, with (8–) 12–30 (–50) spreading part-**Inf** in the upper 1/3–1/2 of the inflorescence, with ((±20–) 40–) 60–80 flowers, primary branches (10–) 15–30 (–50) cm, 15–30 cm apart; **Ped** (3–) 8–17 mm; **Fl** slender, (31–) 40–70 mm, salver-shaped to broadly campanulate; **Tep** yellow, tube broadly funnel-shaped, (4–) 7–10 (–13) × 7–10 (–12) (at the apex) mm, lobes linear, erect, thick, slightly unequal, (11–) 13–20 (–24) × 3–5 mm, outer slightly larger, involute, sometimes purple-tinged, inner linear, erect, thickish, keeled, cucullate at the tip; **Fil** (20–) 30–45 mm, yellow, inserted at ± different levels 1–2 (–3) mm below the base of the lobes; **Anth** versatile, 12–20 mm, yellow; **Ov** slender, triquetrous, fusiform to cylindrical, (15–) 25–38 × 5–7 mm, green, neck 3–5 mm, slightly furrowed; **Sty** (±30–) 45–60 mm; **Sti** 3-lobed; **Fr** oblong, (30–) 45–50 (–65) × (14–) 20–25 mm, shortly rostrate, shortly stipitate; **Se** crescent-shaped, applanate, unwinged, 5–7 × 3.5–6 mm, black. — **Cytology**: 2n = 60 (M. Baker 1997, label on DES00040525, as *A. pygmaea*).

Characterized by open compact rosettes with few recurved, spatulate to broadly lanceolate leaves with margins with distinct prominences and marginal teeth with broad, decurrent bases (García-Mendoza 2011a: 59–60). The species exhibits considerable variation in leaf characters and is within its geographical range recognizable by its open compact rosettes with broad flat leaves markedly narrowed at the base (*Gentry* 1982). It is

close to *A. potatorum*, but the latter differs in its shorter and narrower, erect leaves with smaller and less distant teeth on smaller prominences (García-Mendoza 2010). Grayum (2003) provides a new record for Costa Rica.

The species is commonly assumed to have been discovered by the eponymous B. Seemann in Nicaragua in 1866 (see Ullrich 1992g). However, the species was first collected by A. S. Ørsted who sent plants from Nicaragua to Copenhagen in 1848 where they flowered after 70 years in 1918 and were identified as *A. guatemalensis* (Ostenfeld 1924: 47).

The caespitose *A. pygmaea* (distributed as ISI 2009-11) was described by Gentry (1982: 494–495) as “a depauperate form generated by the arid limestone on which it was found” in E Chiapas (Mexico). Lott & García-Mendoza (1994) and García-Mendoza (2010) place *A. pygmaea* in the synonymy of *A. seemanniana*. Similar small caespitose forms are reported locally from arid limestone rocks in S Nicaragua where they are threatened by extending human settlements (Cseh 2008).

**A. shaferi** Trelease (Mem. Nation. Acad. Sci. 11: 35, t. 57, 1913). **Type:** Cuba (*Shafer* 3800 [MO, NY]). — **Lit:** Berger (1915: 209); León (1946: 318); Acevedo-Rodríguez & Strong (2012: 86); Greuter & Rankin Rodríguez (2017: 36). **Distr:** E Cuba (Sierra de Nipe); rocky peaks and steep slopes of karstic serpentine dome hills (mogotes), in pine-*Agave*-woodland, 400–1000 m; flowers January to February. **I:** Hochstätter (2015: VII: 74); Fernández Velázquez & al. (2018: 37).

[2p] Acaulescent; **Ros** hemispherical, to >2 m Ø, solitary; **L** elongate-lanceolate, erect, recurved in the upper part, rather gradually pointed, guttered, ±75 – ±150 × 10 – ±20 cm, light green to green, not glaucous; **marginal teeth** straight or slightly curved upwards or downwards, triangular from lenticular bases, 1–2 mm, brown, 10–25 mm apart, intervening margin slightly concave; **terminal Sp** conically subulate, unguiculate recurved, openly V-grooved to the middle, smooth, 10–20 × 3 mm, brown, dull, not decurrent; **Inf** 6–7 m, paniculate; **Ped** ±15–23 mm; **Fl** 40–50 mm; **Tep** bright yellow, tube conical, 5–6 mm, lobes 14 × 4 mm; **Fil**

scarcely 25 mm, inserted nearly in the tube throat; **Ov** fusiform, 25–30 × 4–5 mm; **Fr** oblong-fusiform, ±35–42 × 8–16 mm, shortly stipitate; **Se** unknown.

An insufficiently known local endemic. In the key of Trelease (1913: 31) it is keyed out with oblong capsules and short pedicels (5–10 mm), albeit that pedicels and fruits were unknown to him; these data were added from *Carabia* 3582 (NY!). It is treated as “Vulnerable” according to IUCN Red List categories (Berazaín & al. 2005: 17).

**A. shawii** Engelmann (Trans. Acad. Sci. St. Louis 3: 314–316, 370, 1875). **Type** [lecto]: USA, California (*Hitchcock* s.n. [MO 3347373]). — **Lit:** Gentry (1982: 639–645, with ill.); Turner & al. (1995: with ill.). **Distr:** USA (S California), Mexico (Baja California).

The protologue cited material of Parry, Parker and Hitchcock, and Palmer. The designation by Trelease (1912a: 47) “Hitchcock, 1875, -the type” represents a lectotypification.

**A. shawii** ssp. **goldmaniana** (Trelease) Gentry (Occas. Pap. Calif. Acad. Sci. 130: 93, 1978). **Type:** Mexico, Baja California (*Nelson & Goldman* 7151 [US, MO]). — **Lit:** Trelease (1912b: 44, 49, tt. 29–31, as *A. goldmaniana*); Berger (1915: 173, as *A. goldmaniana*); Breitung (1963: 49–50, with ill., as *A. goldmaniana*); Gentry (1978: 92–96, with ill. & t. 6); Gentry (1982: 642–644, with ill.); Turner & al. (1995: 63–65); Starr (2012: 245); Webb & Starr (2015: 91–92, 94–95, with ill.); **Distr:** Mexico (C & S Baja California); coastal desert scrub with nocturnal fogs from fall to spring, 5–700 m; flowers December to May. **I:** Ullrich (1990g); Heller (2006: 22, 131); Richter (2011: 75, 98); Pilbeam (2013: 195); Heim (2014: 6, 11–13, as var.); Hochstätter (2015: IV: 30).

≡ *Agave goldmaniana* Trelease (1912) ≡ *Agave shawii* var. *goldmaniana* (Trelease) A. Heim (2014).

[2f] Differs from ssp. *shawii*: **Ros** often larger; **L** lanceolate rather than linear-ovate, more acuminate, longer, 40–70 × 10–18 cm; **Inf** with peduncular **Bra** below lowest part-**Inf** smaller and not closely clustered, fertile part longer than

broad, part-**Inf** mostly 20–30. — **Cytology**:  $2n = 60$  (Pinkava & Baker 1985, Simpson & al. 2011: as *A. goldmaniana*).

Representing the ecotype of the more arid interior habitats (Gentry 1978, Gentry 1982). The coastal ssp. *shawii* differs from the inland ssp. *goldmaniana* in having shorter bright green leaves and inflorescences about as long as broad and large, succulent, red to purple subtending bracts (Gentry 1978, Gentry 1982, Webb & Starr 2015).

**A. shawii** ssp. **shawii** — **Lit**: Engelmann (1878: with ills.); Trelease (1912b: 44, 46–47, tt. 19–21); Berger (1915: 170–171); Breitung (1963: 16–17, with ills.); all as *A. shawii*; Gentry (1978: 86–93, with ills. & t. 5); Gentry (1982: 639–643, with ills.); Turner & al. (1995: 63–65, with ill.); Reveal & Hodgson (2002); Starr (2012: 12, 244–249, with ills.); Vanderplank (2014: conservation California); Webb & Starr (2015: 91–93, with ill.). **Dist**: USA (S-most California), Mexico (N & C Baja California); coastal bluffs with coastal sage scrub and chaparral with frequent fogs and dew, 0–100 m; flowers January to May. **I**: Irish & Irish (2000: t. 39); Heller (2006: 130); Richter (2011: 38, 103); Pilbeam (2013: 194); Heim (2014: 7, 16–18, as var.); Starr & Webb (2015: 93); Hochstätter (2015: IV: 29); Moore (2016: 272, 273); mostly as *A. shawii*.

**Incl.** *Agave orcuttiana* Trelease (1912); **incl.** *Agave pachyacantha* Trelease (1912).

[2f] Stems short to long (2 m), erect to decumbent, frequently branching from leaf axils, forming fragmented clones, or sometimes remaining single; **Ros** compact, 0.8–2 × 1–2.5 m; **L** ovate to linear-ovate, ascending, thick, fleshy, rigid, ± as wide at mid-leaf as at the base, shortly acuminate, flat to slightly hollowed above, slightly asperous, mostly 20–50 × 8–20 cm, glossy light to dark green; **marginal teeth** very variable in size and shape, straight or variously curved, 5–20 mm (at mid-leaf), decreasing in size below, reddish to dark brown or dark grey, usually 10–20 mm apart or rarely confluent; **terminal Sp** acicular, straight or sinuous, broad at the base, openly grooved above, 20–40 mm, dark reddish-brown to grey, decurrent as horny margin for 8–10 cm or along the entire leaf; **Inf** 2–4 m, paniculate, fertile

part ± as long as broad, with closely imbricate, lanceolate to triangular, succulent, persistent, large (10–25 cm), purple **Bra** closely investing the part-**Inf**, part-**Inf** dense, broad, stout, elliptic to oval in cross section, horizontal to ascending, commonly 8–14 per **Inf** in the upper  $\frac{1}{4}$ – $\frac{1}{2}$ , >10 cm, with 35–75 flowers; **Ped** none or short; **Fl** 60–100 mm, densely clustered; **Tep** yellow or reddish, esp. upon withering, frequently purplish or red in bud, tube broadly funnel-shaped, thickly fleshy, knobby at the filament insertions with furrows between, smooth, shiny, sinuses sometimes at unequal levels, 12–19 × 15–22 mm, light yellow, lobes erect, broad and thick at the base, becoming linear-lanceolate, thinner, soon involute and wilting while the stamens extend, unequal, 25–38 mm, the outer longer than the inner, rounded to flat on the outer face, inner with fleshy keel and thin involuting margins, yellow or reddish; **St** long-exserted; **Fil** thick, tapered towards the apex, 43–70 mm, inserted near mid-tube 8–12 mm above its base; **Anth** usually centric, 20–35 mm; **Ov** cylindrical, thick-fleshy, shortly tapered at the base, 30–50 mm, with grooved scarcely constricted neck 6–15 mm long, greenish; **Sty** thick, finally much longer than the filaments; **Sti** capitate; **Fr** variable in shape and size, obovoid or pear-shaped to oblong, slightly attenuate to rounded at the base, thickly succulent when green and drying as a scurfy exocarp, 55–70 × 15–23 mm, with short to long (15 mm) beak; **Se** crescent-shaped to cuneate, 4–7 × 5–6 mm, dull to lustrous black. — **Cytology**:  $2n = 60$  (Pinkava & Baker 1985, Simpson & al. 2011).

*A. shawii* and *A. sebastiana*, making up Sect. *Umbelliflorae*, are unique in the genus by being confined to a Mediterranean-type climate with winter-spring rainfall, supplemented by frequent fogs. Ssp. *shawii* was frequent in S California at the beginning of the twentieth century, but plant collectors and habitat destruction significantly reduced the populations. In the USA, natural populations are at present known only from Border Fields State Park N of Tijuana, although plants have been introduced at other places (Reveal & Hodgson 2002). — Plants may flower at an age of 20–40 years. The flowers are visited by hummingbirds, bats and bees (Turner & al. 1995). The

anthetic flower morphology is described in detail by Engelmann (1878).

**A. shrevei** Gentry (Publ. Carnegie Inst. Washington 527: 95, 1942). **Type:** Mexico, Chihuahua (*Gentry* 2028 [CAS 0000143 [lecto], ARIZ, US]). — **Lit:** Gentry (1972: 111–117); Gentry (1982: 447–455); Klopper & al. (2010: 59–60, 62–63); Starr (2012: 250–253); all with ills. **Distr:** NW Mexico.

Gentry's protologue indicates his collection "2028" as "type and isotypes" (= syntypes). His later designation (Gentry 1972: 112) of "*Gentry* 2028" "deposited in the Dudley herbarium" refers to the specimen CAS 0000143 and represents a lectotypification.

**A. shrevei** ssp. **magna** Gentry (Agaves Cont. North Amer., 451–453, ills., 1982). **Type:** Mexico, Chihuahua (*Gentry & Bye* 23360 [US [4 sheets, status uncertain], ARIZ, ASU, DES, MEXU]). — **Lit:** González-Elizondo & al. (2009: 125–127, with ills.); Klopper & al. (2010: 62–63); Starr (2012: 250–251, 253, with ill.). **Distr:** Mexico (SE Sonora, SW Chihuahua, N Sinaloa, S Durango); rocky slopes in oak woodlands, oak grasslands or oak forests, 1040–1980 m; flowers June to July, October and January. **I:** Richter (2011: 79); Pilbeam (2013: 197); Hochstätter (2015: IV: 13).

[2h] Differs from ssp. *shrevei*: **Ros** larger, 1.4–1.7 × up to 2.5 m, mostly solitary; **L** outcurving, guttered, thickened and broadened towards the base, finely asperous, mature **L** larger, mostly 120–150 × 15–25 cm, margins remotely crenate; **marginal teeth** along most of the lamina, 6–10 (–15) mm, mostly 30–50 mm apart, on pronounced prominences, frequently with small intermittent teeth; **terminal Sp** longer, 35–60 mm; **Inf** larger, 6–7 m, part-**Inf** more numerous, 20–30 per inflorescence; **Fil** longer, 48–70 mm.

The main difference from ssp. *shrevei* is the larger overall size (Gentry 1982: 451). González-Elizondo & al. (2009) provide a new record for Durango.

**A. shrevei** ssp. **matapensis** Gentry (US Dept. Agric. Handb. 399: 115–117, ills., 1972). **Type:**

Mexico, Sonora (*Gentry* 11607 [US 2540344, ARIZ, MEXU, MICH]). — **Lit:** Gentry (1982: 454–455, with ills.); Klopper & al. (2010: 62–63); Starr (2012: 251, 253). **Distr:** Mexico (C Sonora), limestone or granitic slopes in woodlands, 610–1800 m; flowers April to May. **I:** Richter (2011: 78); Pilbeam (2013: 198); Hochstätter (2015: IV: 14).

[2h] Differs from ssp. *shrevei*: **Ros** suckering late and sparingly; larger **marginal teeth** at mid-leaf recurved; **Fil** smaller, ±50 mm; **Tep** tube shorter, 15–20 mm, outer lobes longer and broader, 11–16 × 7 mm; **Fil** longer, 45–55 mm; **Ov** (partly) shorter, 22–41 mm incl. the short unconstricted neck; **Fr** shorter, 35–40 × 20 mm.

Resembling some forms of ssp. *shrevei* (Gentry 1972: 117), but distinguished as detailed above.

**A. shrevei** ssp. **shrevei** — **Lit:** Breitung (1963: 15–17, as *A. shrevei*); Gentry (1972: 111–115); Gentry (1982: 447–450); González-Elizondo & al. (2009: 123–127); Klopper & al. (2010: 60, 62–63); Starr (2012: 250–253); all with ills. **Distr:** Mexico (E & SE Sonora, SW Chihuahua, S Durango); open rocky volcanic or also limestone slopes in oak woodlands and pine-oak forests, 930–1980 m; flowers August, October and February. **I:** Heller (2006: 131); Richter (2011: 78); Pilbeam (2013: 196); Hochstätter (2015: IV: 12). — Fig. 52.

[2h] **Ros** small to medium-sized, closely suckering at maturity; **L** ovate, shortly acuminate, 20–35 × 8–10 cm, or lanceolate, acuminate and 50–60 × 12–18 cm, generally narrowed above the base, firm, thick, flat to conduplicate, straight or outcurving near the tip, light grey, glaucous; **marginal teeth** variable, straight or flexed up- or downwards, larger teeth 5–10 mm (mid-leaf), dark brown to grey, on small to pronounced prominences; **terminal Sp** acicular, stout, with a narrow or open groove from the base to above the middle, mostly 25–50 mm, brown; **Inf** 2.5–5 m, paniculate, with deltoid, long-acuminate **Bra** drying early, fertile part with 8–16 small ascending part-**Inf** in the upper 1/3; **Fil** erect, slender, 60–70 mm, persisting; **Tep** light green to pale yellow, buds at the tips red to purplish, tube cylindrical or urceolate, 18–23 × 10–12 mm, lobes



**Fig. 52** *Agave shrevei* ssp. *shrevei*. (cult.: USA; Arizona, Arizona-Sonora Desert Museum Tucson) (Copyright: J. Thiede)



strictly erect, leathery, unequal, outer 10–12 × 5–7 mm, with red to purplish calloused tips, flat, widely overlapping the shorter keeled inner lobes, pea-green to light yellow; **Fil** flattened, 40–50 mm, inserted unequally at mid-tube, yellow or red; **Anth** large, 22–26 mm, yellow; **Ov** 25–35 mm incl. the constricted neck; **Sty** clearly longer than the tepals; **Sti** capitate; **Fr** oblong, 45–70 × 15–25 mm, shortly stipitate, shortly beaked; **Se** 6–7 × 4.5–5 mm, hilar notch small, marginal wing prominent.

Well distinguished by its broad, light glaucous-grey leaves with margins bearing prominences with well-developed brown teeth, and the leathery perianth with a deep tube, and short, persistently erect tepal lobes, much shorter than the tube (Gentry 1982). Typical and smaller-leaved plants resemble *A. flexispina* in leaf characters, but the latter's flowers appear closer to *A. palmeri* (with a tube and tepals ± equal). A population at Guajaráy (Sonora) with larger leaves in variable shapes shows some characters of *A. palmeri* (Gentry 1972: 115, Gentry 1982: 448). González-Elizondo & al. (2009) provide a new record for Durango. The plants are used as food, for mescal production, and in curing and death ceremonies (Bye & al. 1975: 96, 109, ill.).

**A. sileri** (Verhoek-Williams) Thiede & Eggl (Kakt. and. Sukk. 50(5): 111, 1999). **Type:** USA, Texas (*Siler* s.n. [BH 69–518B]). — **Lit:** Verhoek-Williams (1975: 205–208, as *Manfreda variegata*

var.); Verhoek-Williams (1978a: 168–170, with ills.); Piña Luján (1985: 62); Reveal & Hodgson (2002); Diggs & al. (2006: 410–412, with ills.); Castillejos-Cruz (2009: [282]–[287], with ills.); all as *Manfreda*. **Distr:** USA (S Texas), Mexico (Tamaulipas); open sunny areas on clay soil, in desert scrub and tropical deciduous forests, to 100 m; flowers April to July. **I:** Richardson & King (2011: 19); Hochstätter (2016: I: 42); both as *Manfreda*.

≡ *Manfreda sileri* Verhoek-Williams (1978); **incl.** *Manfreda variegata* var. *sileri* Verhoek-Williams (1975) (*nom. inval.*, ICN Art. 29.1).

[3a1] Plants herbaceous, large (for Subgen. *Manfreda*); corm 5–6 × 4–5 cm, subglobose to subcylindrical, bulb 4–5 × 3.8–4.5 cm, ovoid to subglobose, covered with dry leaf bases 3.8–4.8 cm long, these membranous, not separating into fibres, reproducing vegetatively by buds from the leaf axils of the parent rosette or from the corm; **R** fleshy, thick, with filiform ramifications, contractile; **L** evergreen, 6–8, spreading to slightly ascending, broadly lanceolate to ovate-lanceolate, channelled and undulate or somewhat flattened, long-attenuate towards the tip, tip acute with a soft medium-sized point, succulent, brittle, glabrous on both faces, 15–40 × 2.2–4.8 cm, light green to glaucous, with round to oval, dark green, brown or purple, often confluent spots 1 × 0.5 cm, margins with a conspicuous cartilaginous band, minutely denticulate, teeth in various sizes, irregularly spaced, often some retrorse; **Inf** erect,



2.4–2.6 m, erect, ‘spicate’, green-glaucous, peduncle with 10–15 somewhat inclined **Bra** with truncate base, lower similar to lower leaves, upper smaller and deltoid-acuminate, fertile part dense, 25–42 cm, with 27–46 (–81) flowers; floral **Bra** 0.5–1 × 0.4–0.7 cm; **Fl** 20–36 mm, sessile, erect to ascending, funnel-shaped to broadly campanulate; **Tep** glaucous-green on the outer face, greenish-yellow to golden-yellow on the inner face, tube broadly funnel-shaped to campanulate, (7–) 9–15 (–22) × 6–9 mm, constricted near the tip of the ovary, lobes oblong, reflexed to revolute, keeled on the outer face, tip slightly broadened to acute, with a tuft of short white hairs, (7–) 10–21 mm; **Fil** 43–69 (–100) mm, inserted near the tube base, yellowish-green, with multiple purple dots over the whole surface; **Anth** 9–13 mm, reddish to brownish; **Ov** ellipsoid to slightly obclavate, (10–) 12–20 × 6–7 mm; **Sty** erect, 44–66 (–95) mm, almost reaching the level of the anthers; **Sti** clavate-capitate, 3-lobed, tip papillate; **Fr** cylindrical to subellipsoid, 23–31 × 16–19 mm, apiculate for ±2 mm; **Se** deltoid, flat-concave, 5–6 × 5 mm, black, dull.

Closely related to *A. variegata*, of which it was first classified as a variety (Verhoek-Williams 1975). Both have a similar robust habit and occur in similar habitats (Verhoek-Williams 1978a, Castillejos-Cruz 2009). *A. sileri* differs in its larger size, spreading and only shallowly channelled glaucous leaves spotted with large brown dots, leaf margins with irregularly spaced teeth of different sizes and shapes, and densely many-flowered inflorescences with flowers with yellow-green to golden filaments (Verhoek-Williams 1978a, Castillejos-Cruz 2009). *Manfreda longistaminata* is a related, unpublished new species from Tamaulipas (Castillejos-Cruz 2009).

**A. ×simoni** André (Rev. Hort. (Paris) 76: 297–299, figs. 128–130, 1904). **Type:** not typified. — **Lit:** Berger (1915: 187, as *A. simoni*). **Distr:** Cultivated only.

[2o × 2] This is the garden hybrid “*A. vandervinneni*” (an unplaced name) × *A. potatorum* (as *A. verschaffeltii*). The cross was made in 1877 at the “Jardin Botanique au Parc de la Tête d’Or” in Lyon (France) by its “chef de

culture” M. Gaulain, and a plant raised from the cross flowered in 1903 at Charles Simon at Saint-Ouen (France), and resembled *A. potatorum* (as *A. verschaffeltii*) in habit (Berger 1915: 187). — For *A. simonii* see under *A. ×hybrida*, and for *A. simonis* under *A. pumila*.

**A. singuliflora** (S. Watson) A. Berger (Agaven, 31, 1915). **Type** [syn]: Mexico, Chihuahua (Pringle 1142 [GH, US]). — **Lit:** Rose (1903c: 16–17); Gentry (1972: 151–152); Verhoek-Williams (1975: 259–264); Piña Luján (1985: 87–89); Castillejos-Cruz (2009: [288]–[293], with ill.); all as *Manfreda* except Berger. **Distr:** Mexico (E Sonora, W, SW & S Chihuahua, W Sinaloa, N, W & S Durango, W Zacatecas, N Jalisco); cool slopes in grasslands and in fir, pine, oak, and pine-oak and tropical deciduous forests, 1500–2800 m; flowers late June to early October. **I:** Hochstätter (2016: I: 43); Castro-Castro & al. (2017: 62); Castro-Castro & al. (2018: 499); all as *Manfreda*.

≡ *Bravoa singuliflora* S. Watson (1887) ≡ *Manfreda singuliflora* (S. Watson) Rose (1903) ≡ *Polianthes singuliflora* (S. Watson) Shinnars (1966).

[3a1] Plants herbaceous?, medium-sized (for Subgen. *Manfreda*); corm 1.7–2.4 × 1.2–1.5 cm, cylindrical, bulb 1.8–5 × 1.5–2 cm, cylindrical, completely covered with dry membranous leaf bases 4–8 cm long; **R** fleshy, with filiform ramifications, contractile; **L** evergreen, 3–8, recurved to erect, spreading, linear to linear-lanceolate, channelled, succulent, tip acute, with a medium-sized point, glabrous, 17–30 (–60) × 0.5–1.5 cm, light green to glaucous, occasionally red-speckled at the base, margins bordered by a narrow hyaline band; **Inf** 50–90 (–115) cm, erect, ‘spicate’, glaucous green, peduncle with 5–6 truncate **Bra**, the lower linear-lanceolate, similar to the leaves, the upper lanceolate, decreasing in size upwards, fertile part open, 15–23 (–30) cm, with 5–18 (–26) flowers; floral **Bra** lanceolate, 1.1–1.7 × 0.2–0.4 cm; **Fl** 32–36 mm, usually sessile, reclined to descending; **Tep** green, green with a brown-maroon streak on the lower parts, or yellowish-green, to reddish-green on the outer face, tube narrowly funnel-shaped, arched so that the throat

faces downwards, tapering towards the base near the ovary, 15–25 × 5 mm, lobes oblong, reflexed to revolute, 10–12 × 2–4 mm, apex cucullate, tip soft, with a tuft of short white hairs; **Fil** erect, 17–20 mm, exceeding the tube by 4–6 mm, inserted at mid-tube all at the same level, reddish-green; **Anth** 8–10 mm, yellowish-green to reddish; **Ov** nearly erect, at a narrow angle to the inflorescence axis, cylindrical to ellipsoid, 4–9 × 3–5 mm, apiculate, without a scar near the apex; **Sty** 30–35 mm, exceeding the tube for 5–12 (–15) mm, ± at the anther level, white; **Sti** clavate-capitate, deeply 3-lobed, papillate at the apex; **Fr** globose or cylindrical to subellipsoid, 13–16 × 11–13 mm, apiculate for ±2 mm; **Se** deltoid, flat-concave, 4–5 × 4 mm, black, dull.

Differing from all other members of Sect. *Herbaceae* by the extreme curvature of the downwards-facing perianth (Verhoek-Williams 1975: 263, Castillejos-Cruz 2009). Due to its semisucculent to succulent leaves and its filaments inserted at mid-tube morphologically related to *A. brunnea* and *A. variegata*, but different from both in the strongly recurved perianth tube and the much shorter filaments (Castillejos-Cruz 2009: as *Manfreda*). Martin & al. (1998: 471) provide a new record for Sonora. The lectotypification attempt by Verhoek-Williams (1975: 259) is ineffective because the work was not effectively published.

**A. sisalana** Perrine (Trop. Pl. [U.S. House Representatives Rep. no. 564], 87–88 (8–9, 16, 47, 60, 86), 1838). **Type** [neo]: Mexico, Chiapas (*Gentry* 16434 [US, DES?]). — **Lit**: Berger (1915: 230–232, with ills.); Standley (1930: 233); Standley & Steyermark (1952: 117–118); Breitung (1961: 179, with ills.); Gentry (1982: 628–630, with ills.); Lott & García-Mendoza (1994: online version with ills.); Smith & Mössmer (1996: with ills.); Reveal & Hodgson (2002). **Dist**: Cultivated only; nearly worldwide in tropical and subtropical regions; flowering winter to early spring; naturalized in many places, e.g. RSA. **I**: Irish & Irish (2000: t. 40); Heller (2006: 28, 133); Richter (2011: 13, 139); Pilbeam (2013: 199); Hochstätter (2015: VII: 47).

≡ *Agave rigida* var. *sisalana* (Perrine) Engelm (1875) ≡ *Furcraea sisalana* (Perrine)

Posada-Arango (1909); **incl.** *Agave franceschiana* Trelease ex A. Berger (1912); **incl.** *Agave sisalana* var. *armata* Trelease (1913) ≡ *Agave sisalana* fa. *armata* (Trelease) Trelease (1920); **incl.** *Agave amaniensis* Trelease & Nowell (1933); **incl.** *Agave sisalana* fa. *marginata* Medina (1955); **incl.** *Agave sisalana* fa. *medio-picta* Medina (1955); **incl.** *Agave segurae* D. Guillot & P. Van der Meer (2005).

[2c] Stems 0.4–1 m; **Ros** 1.5–2 × 1.5–2.5 m, commonly suckering with elongate rhizomes; **L** lanceolate, ensiform, spreading, fleshy, firm, slightly convex below, flat above, 60–150 (–180) × (2.5–) 5–12 cm, shiny green, somewhat slightly cross-zoned and glaucous when young, margins straight, finely fibrous, not corneous; **marginal teeth** of young leaves few, minute, 1–2 mm, 20 to >50 mm apart, usually absent on mature leaves; **terminal Sp** conical, subulate, shortly shallowly grooved above, 20–25 mm, dark brown, somewhat lustrous, not decurrent; **Inf** 5–6 m, paniculate, peduncle short, with persistent triangular **Bra** 0.5–2 cm long, fertile part ellipsoid, with 10–15 (–25) ascending part-**Inf** > 10 cm long in the upper ½ of the inflorescence, bulbiferous after flowering; **Fl** erect, 40–65 mm, unpleasantly scented; **Te** greenish-yellow, tube broadly urceolate, 15–18 × 10–12 mm, lobes linear-lanceolate, erect, equal, 17–18 × 5–6 mm, **St** long-exserted; **Fil** erect, 50–60 mm, inserted ± at mid-tube, yellow; **Anth** 20–25 mm, yellow; **Ov** shortly fusiform, 15–25 × 8–9 mm, neck slightly constricted, 2–4 mm; **Fr** and **Se** unknown. — **Cytology**: 2n = 138, 140–149, 147, 149, 150 (5×), 180 (Satô 1935, Doughty 1936, Granick 1944, Castorena Sanchez & al. 1991, Robert & al. 2008); in cultivars 54–65 (2×), 77–99 (3×), 118–128 (4×), 137–151 (5×) (Lv & al. 2009).

Easily recognizable by its green, unarmed mature leaves with a short, dark brown, conical to subulate, non-decurrent terminal spine. The taxon appears to represent a sexually sterile clone that is widely cultivated in fibre plantations and could be of hybrid origin, possibly between *A. angustifolia* of Sect. *Rigidae* (as Group) and *A. kewensis* of Sect. *Sisalanae* (as Group) (Gentry 1982: 630). Ullrich (1990d) consequently removed it from Gentry's Group *Sisalanae* and placed it in

Sect. *Rigidae* (as Group), but this is not followed here. Molecular AFLP data (Gil-Vega & al. 2007) place *A. sisalana* closest to *A. kewensis* and both close to, but separate from species of Sect. *Rigidae* (as Group). The species is not known from the wild, and was probably widely distributed by pre-Columbian people (Reveal & Hodgson 2002). It is naturalized in (sub-)tropical regions, e.g., in the Mediterranean (e.g., Spain: Guillot Ortiz & Meer (2006c) and Guillot Ortiz & Meer (2008b: as *A. amaniensis*), both with ills.) and in RSA (Smith & Mössmer 1996, the plants described appear to be esp. well-nourished individuals and reach much larger size than otherwise reported). Cultivars cultivated in Spain are presented by Guillot Ortiz & Meer (2009a: with ills.). For the synonymous *A. franceschiana*, see also under *A. weberi*.

**A. sobolifera** Houttuyn (Nat. Hist. 2(8): 374, 1777). **Type:** not typified. — **Lit:** Baker (1887: 543, 549, Fig. 165, as *A. morrisii*); Trelease (1913: 32–33, tt. 44–48); Berger (1915: 207); Hummelinck (1927: with ills.); Adams (1972: 81); Hummelinck (1984: 208–212, 226–228, with ills.); Acevedo-Rodríguez & Strong (2012: 85). **Distr:** Jamaica; dry rocky well-drained calcareous hillsides, 30–850 m; flowers February to April. **I:** Richter (2010: 41); Richter (2011: 90, 91, 138); Pilbeam (2013: 200); Hochstätter (2015: VII: 75).

**Incl.** *Agave americana* Lamarck (1783) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave laetevirens* K. Koch (1865); **incl.** *Agave morrisii* Baker (1887); **incl.** *Agave sobolifera* [?] *marginata* hort. ex Trelease (1908); **incl.** *Agave morrisii* Kent (1908) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave sobolifera* fa. *spinidentata* Hummelinck (1984) (*nom. inval.*, ICN Art. 38.1a).

[2p] Acaulescent; **Ros** to 2 × 2.5 m, solitary; **L** 20 or more, variably lanceolate, massive, curved, gradually acute or somewhat subacuminate, often deeply and conduplicately or undulately concave, ±125–200 × 15–24 cm, 9 cm thick near the base, rather light green, somewhat glossy; **marginal teeth** curved or reflexed-triangular (rarely straight), 1–4 mm, glossy dark brown, 5–15 mm apart, often hardened on the tops of green prominences

of the margin, intervening margin ± concave; **terminal Sp** conical, nearly straight, slightly flattened, grooved or slightly involutely channelled below the middle when mature, smooth, somewhat glossy, 15–25 × 3–4 mm, reddish-brown, not decurrent; **Inf** 5–9 m, paniculate, oblong, part **Inf** on rather short spreading branches, above the middle of the inflorescence, freely bulbiferous; **Ped** stout, 8–10 mm; **Fl** ±50 mm; **Tep** golden-yellow to light orange, tube open, 5–7 mm, lobes bluntly triangular-oblong, ±20 × 7 mm; **Fil** ±45 mm, inserted towards mid-tube; **Ov** narrowly fusiform, 15–20 (–25) mm, from slightly shorter to longer than the perianth; **Fr** narrowly oblong, turbinate narrowed at the base, 45–50 × 13–25 mm, shortly beaked at the tip, stipitate; **Se** 7 × 4–5 mm.

Previously ascribed to Salm-Dyck (Hort. Dyck., 307, 1834), but published earlier, as given above (Govaerts 2014+: accessed Oct. 2018). See Trelease (1913: 33) on the difficult interpretation of this name. Plants from the Cayman Islands previously included in *A. sobolifera* were published as a separate species, *A. caymanensis* (see there for differences).

**A. sobria** Brandegee (Proc. Calif. Acad. Sci., ser. 2, 2: 207, 1889). **Type** [syn]: Mexico, Baja California Sur (*Brandegee* 2 [UC, CAS 0000145]). — **Lit:** Gentry (1982: 394–404, with ills.); Turner & al. (1995: 65–67, with ill.). **Distr:** Mexico (Baja California Sur).

The protologue gives “Comondu on the mesas” as type indication, which refers to *Brandegee* 2 (Trelease 1912a: 56); the 2 available sheets represent syntypes.

**A. sobria** ssp. **frailensis** Gentry (Occas. Pap. Calif. Acad. Sci. 130: 54–56, ills., 1978). **Type:** Mexico, Baja California Sur (*Gentry & Cech* 11264 [US 2562946, ARIZ, MEXU, US]). — **Lit:** Gentry (1978: 54–58); Gentry (1982: 401–404); Turner & al. (1995: 66); Webb & Starr (2015); all with ills. **Distr:** Mexico (Baja California Sur: Cape region); on granite hillslopes; flowers May and October. **I:** Richter (2011: 80, 105); Pilbeam (2013: 202); Hochstätter (2015: V: 19).

[2i] Differs from ssp. *sobria*: **Ros** compact, smaller, sparingly caespitose; **L** more numerous, broadly lanceolate, mostly 20–35 × 6–8 cm, glaucous-green to bluish-glaucous, margins with pronounced prominences; **marginal teeth** numerous, smaller, mostly 6–10 mm, chestnut-brown to greying, closely spaced; **terminal Sp** frequently sinuous or contorted, 30–40 mm; **Inf** with 10–15 part-**Inf**; **Fl** slender, 45–63 mm; **Ov** cylindrical, 25–40 mm, lobes 4–6 mm wide.

Ssp. *frailensis* occupies the S part of the total range of *A. sobria*, and is the S-most taxon of Sect. *Deserticolae*. The protologue indicates “Gentry & Cech 11264” at US as “Type”. From the 2 sheets at US, US 2562946 is annotated as “Type” by Gentry (= holotype); US 2540165, annotated as “Type coll.”, is an isotype.

**A. sobria** ssp. **roseana** (Trelease) Gentry (Occas. Pap. Calif. Acad. Sci. 130: 54, 1978). **Type**: Mexico, Baja California Sur (*Rose* 16854 [US, MO, NY]). — **Lit**: Trelease (1912b: 59, tt. 58–60, as *A. roseana*); Berger (1915: 267, as *A. roseana*); Breitung (1963: 173, with ills., as var.); Gentry (1978: 54–56, with ills.); Gentry (1982: 400–403, with ills.); Ullrich (1994b: with ills.); Turner & al. (1995: 66); Webb & Starr (2015: 77, 83, 87, with ill.). **Dist**: Mexico (Baja California Sur: Espíritu Santo Island and adjacent mainland); flowers February to March, May, June and October. **I**: Pilbeam (2013: 203); Hochstätter (2015: V: 20).

≡ *Agave roseana* Trelease (1912) ≡ *Agave sobria* var. *roseana* (Trelease) I. M. Johnston (1924).

[2i] Differs from ssp. *sobria*: **Ros** lax, openly spreading, sparsely surculose; **L** fewer, broadly lanceolate, frequently twisted, acuminate, smaller, 35–50 × 7–10 cm, yellow-green, margins with prominent prominences, tubercles 1–1.5 mm; **marginal teeth** flexuous, few, larger, larger teeth 10–25 mm, remote; **terminal Sp** sinuous to contorted, 50–70 mm; **Inf** with 8–12 part-**Inf**; **Fl** 45–65 mm, lobes 4–5 mm wide.

Ssp. *roseana* occupies the C part of the total range of *A. sobria*.

**A. sobria** ssp. **sobria** — **Lit**: Trelease (1912b: 56, tt. 50–51, as *A. sobria*); Berger (1915: 265, as

*A. sobria*); Breitung (1963: 149, 151, with ills.); Gentry (1978: 48–54, with ills.); Gentry (1982: 396–399, with ills.); Turner & al. (1995: 65–67); Webb & Starr (2014b: 8–11, with ills.). **Dist**: Mexico (Baja California Sur); widely scattered but common on mountain slopes on both sides of the Sierra de la Giganta, 0–1070 m; flowers February to April, and September. **I**: Heller (2006: 134); Richter (2011: 80); Pilbeam (2013: 201); Hochstätter (2015: V: 18).

**Incl.** *Agave affinis* Trelease (1912); **incl.** *Agave carminis* Trelease (1912); **incl.** *Agave slevinii* I. M. Johnston (1924).

[2i] Stems short, or appearing stemless; **Ros** open, 0.5–1.5 × 0.5–1.5 m, usually caespitose; **L** few, linear to lanceolate, straight to curved, sometimes twisted, long-acuminate, thick and convex below towards the base, flat to somewhat concave above, variable, mostly 45–80 × 5–10 cm, bright glaucous-grey, frequently cross-zoned, margins repand to tuberculate; **marginal teeth** variously curved or straight, flattened, base broad, mostly 5–10 mm, grey, reddish towards the tips, mostly 30–40 mm apart; **terminal Sp** acicular, narrowly grooved above, mostly 30–60 mm; **Inf** 2.5–4 m, paniculate, peduncle with small triangular chartaceous **Bra**, fertile part slender, sometimes arching, part-**Inf** compact, nearly globose, 12–20 per inflorescence, on short lateral branches; **Ped** 2–7 mm; **Fl** slender, 45–55 mm; **Tep** pale yellow, tube broadly funnel-shaped, 3–4 × 9–11 mm, lobes very narrow, linear, rather thin, involute at anthesis, rounded at the tip, cucullate, ± equal, 17–22 × 3–4 mm, inner keeled; **Fil** slender, 35–47 mm, inserted at the lobe base on a nectary disc; **Anth** centric, 18–23 mm; **Ov** tapering at the base, 25–35 mm, neck short, scarcely constricted; **Sty** slightly longer than the tepals; **Sti** capitate; **Fr** oblong, thick-walled, 50–65 × 15–18 mm, shortly stipitate, apiculate; **Se** crescent-shaped, 7–8 × 5–6 mm, narrowly winged. — **Cytology**: 2n = 60 (Pinkava & Baker 1985).

*A. sobria* is the S-most species of Sect. *Deserticolae*, occupying the E parts of Baja California Sur, and possibly the most variable species in Baja California (Webb & Starr 2015). Ssp. *sobria* differs from ssp. *roseana* and ssp. *frailensis* by its longer, narrower, very light-glaucous and

long-lanceolate leaves with a straight to repand margin and with remote marginal teeth, and its slender flowers with long, narrower lobes (Gentry 1978, Gentry 1982). Some forms of ssp. *sobria* were misidentified by Gentry (1982) as *A. giganteensis* (Webb & Starr 2014b, Webb & Starr 2015; see under that species).

**A. spicata** Cavanilles (Anales Ci. Nat. 5(15): 261, 1802). **Type:** Ex cult. Madrid (*Cavanilles* s.n. [MA 215275]). — **Lit:** Berger (1915: 43–44, as *A. yuccaefolia*), Breitung (1960: 181–182, with ill., as *A. yuccaefolia*); Gentry (1982: 85–86, with ill., as *A. yuccaefolia*); Ullrich (1995b: with ills.); Ullrich (1996b: with ills.); Guillot Ortiz & Meer (2002b); Alsemgeest & al. (2006a: with ills.). **Distr:** Not known from the wild; flowers September to March (in cultivation). **I:** Redouté (1802–1816: tt. 328–329, as *A. yuccaefolia*, 1811); Curtis’s Bot. Mag. 86: t. 5213, 1860, as *A. yuccaefolia*; Heller (2006: 135); Richter (2011: 61); Hochstätter (2015: VIII: 28).

≡ *Agave yuccifolia* var. *spicata* (Cavanilles) A. Terracciano (1885) (*incorrect name*, ICN Art. 11.4, 25.1); **incl.** *Agave yuccifolia* F. Delaroche (1811); **incl.** *Agave spicata* Gussone (1825) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave guccifolia* Mannetti in F. A. Gera (1834) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave hookeri* K. Koch (1865) (*nomen rejiciendum*, ICN Art. 56.1); **incl.** *Agave cohniiana* Jacobi (1866); **incl.** *Agave yuccifolia* var. *caespitosa* A. Terracciano (1885); **incl.** *Agave yuccifolia* var. *viridis* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

[1b] Stems short or none; **Ros** open, small to medium-sized, suckering, forming dense groups with age; **L** 12–40, linear, recurving at maturity, soft, pliable, scarcely succulent, weakly and finely fibrous, not or hardly narrowed at the base, long and finely acuminate, convex below, concave above, 50–65 × 3–3.5 cm, mostly green with pale midstripe, sometimes reddish- or purple-spotted, margins with red cartilaginous band, finely serrulate with unequal denticles, between the larger mostly a minute one; **terminal Sp** conical to subulate, fine, pungent, 3–8 mm, brown; **Inf** 2–3 m, ‘spicate’, peduncle with triangular-lanceolate long-acuminate erect

**Bra**, fertile part slender, arching, 27–30 cm, part-**Inf** mostly with geminate flowers; **Ped** short; **Fl** 40 mm, unpleasantly scented; **TeP** greenish-yellow, tube narrowly cylindrical, ±8 mm, lobes linear, obtuse, tip revolute, inner ones somewhat narrower, spreading to reflexed, 15–16 mm, inner narrower; **Fil** 40–45 mm, inserted at the orifice of the tube, reddish to reddish-brown; **Anth** 15 mm, yellow; **Ov** roundly 3-angled, 16–18 mm, neck short; **Sty** filiform, finally exceeding the filaments; **Sti** 3-lobed; **Fr** obovate, broadly 3-angled, thinly woody, 20 × 17 mm, shortly beaked, light grey-glaucous; **Se** nearly semicircular, 5 mm, shiny black.

The name *A. yuccifolia* (usually as *A. yuccaefolia*), ascribed to Redouté (1811) and published with two colour plates (reproduced by Ullrich (1995b: 115) and by Smith & Figueiredo (2016: 11)), was widely applied to this species. The herbarium specimen B-W 06789-01 0 labelled “Malmaison Febr. 1811” is probably taken from Redouté’s plant. Hooker (1860) published a colour plate of an “*A. yuccaefolia*” plant flowering at Kew that purportedly was received from Real del Monte (Hidalgo, Mexico). Koch (1865: 104) considered Hooker’s plant to be different from Redouté’s plant and published the new name *A. hookeri* K. Koch 1865 for the former, which antedates the widely applied name *A. hookeri* Jacobi (1866), thus rendering the latter illegitimate. *A. hookeri* K. Koch differs from Redouté’s plant mainly in its distinct stem and much longer inflorescence which may be due to its long cultivation under lush conditions, and the name can be referred to the synonymy of *A. yuccaefolia* (see also under *A. hookeri*). Smith & Figueiredo (2016) established the correct spelling “*yuccifolia*” and author (F. Delaroche).

Ullrich (1995b) and Ullrich (1996b) replaced *A. yuccifolia* by the older name *A. spicata*, which was based on a plant cultivated at Madrid purportedly received from the BG La Habana, Cuba, and established the specimen cited above with the original handwriting of Cavanilles, preserved in 1802, as holotype (Ullrich 1996b: 25). A detailed historical account of both species is provided by Guillot Ortiz & Meer (2002b).



*A. spicata* is a very distinct species without close relatives within Sect. *Inermes* (as Group *Amolae*) (Gentry 1982). This led Ullrich (1996b: 29) to place it in a section of its own (Sect. *Yuccifoliae* (A. Terracciano) Ullrich). Molecular AFLP data place *A. spicata* closest to *A. nizardensis* and close to other members of Sect. *Inermes* (as Group *Amolae*). The spotted leaves, a feature otherwise only known from Sect. *Herbaceae*, might indicate that the species is of hybrid origin involving a species of Sect. *Herbaceae* and one of Subgen. *Littaea* (Ullrich 1996b: 28: the former as *Manfreda*).

**A. stictata** Thiede & Egli (Kakt. and. Sukk. 50(5): 111, 1999). **Type**: not typified. — **Lit**: Rose (1903c: 18–19); Verhoek-Williams (1975: 301–306); Piña Luján (1986: 17, with ill.); Castillejos-Cruz (2009: [204]–[209]); all as *Manfreda maculata*. **Distr**: Mexico (SW México, N Guerrero, C Oaxaca); disturbed places (rocky slopes and moist shady areas) derived from oak and pine-oak forests, 1180–2000 m; flowers mid-July to mid-September. **I**: Rodríguez & Castro-Castro (2007); Hochstätter (2016: I: 29); both as *Manfreda maculata*.

**Incl.** *Polianthes maculata* Martius (1831) ≡ *Manfreda maculata* (Martius) Rose (1903).

[3a2] Plants herbaceous; corm 2–3.5 (–5) × (0.7–) 1.5–2.5 cm, subcylindrical, bulb 2.5–4 (–5.5) cm, ovoid, covered with dried fibrous leaf bases 2–4 cm long; **R** fleshy and thickened, with filiform ramifications, contractile; **L** drought-deciduous, 2–6 (–8), prostrate, lanceolate to narrowly elliptic, narrowed towards the base, canaliculate, densely pubescent on both faces with straight simple hairs 0.6–0.8 mm long, apex acute, 7–22 (–32) × 0.6–2.6 (–4.5) cm, dark green with purple dots, margins entire, slightly wavy and with a hyaline band; **Inf** 30–95 (–120) cm, erect, ‘spicate’, reddish to greenish, pubescent at its base, peduncular **Bra** 3–5, base truncate, lower similar to the leaves, decreasing in size upwards, fertile part (7–) 12–28 cm, lax, with 6–22 flowers; floral **Bra** 3–5 × 3–5 mm; **Fl** 25–32 mm, solitary, sessile, ascending; **Tep** greenish-yellowish to reddish with purplish tinge, semisucculent, forming a tube 12–20 × 4–5 mm, not constricted at the apex

of the ovary, lobes narrowly elliptic to oblong, revolute, 8–12 × 3–4 mm, tip cucullate, with a bundle of short white trichomes; **Fil** 17–22 mm, erect at anthesis, exceeding the tube for 7–14 mm, inserted at mid-tube all on the same level, yellowish-green with cherry-red dots; **Anth** 6–10 mm, yellow; **Ov** cylindrical, (6–) 8–12 × 2–4 mm, greenish, not protruding into the tube, not constricted above; **Sty** 21–37 mm, yellowish-green; **Sti** capitate, 3-lobed, yellowish-green; **Fr** cylindrical to subellipsoid, 11–17 × 9–15 mm, without scar near the apex, tepals persisting; **Se** deltoid, plane-concave, with narrow margin, 3–4 × 2–3 mm, shiny.

Differentiated from most other species of Sect. *Herbaceae* by its ovoid bulbs, and by the pubescent leaves narrowed at the base into a petiolar portion; pubescent leaves are otherwise only found in *A. pubescens* (Verhoek-Williams 1975: 303–304, Castillejos-Cruz 2009: [205]), while *A. guerrerensis* has leaves that are slightly pubescent at the base. When transferring *Manfreda maculata* to the genus *Agave*, a new epithet was necessary because of the earlier name *A. maculata* Regel 1856. The lectotypification attempt (as “Type”) by Verhoek-Williams (1975: 301) is ineffective because the work was not effectively published.

**A. striata** Zuccarini (Flora 15: 2(Beiblatt 2): 98, 1832). **Type** [neo]: Cult. RBG Kew (*Anonymous* s.n. [K]). — **Lit**: Gentry (1982: 242–247, with ills.). **Distr**: Mexico (Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas, San Luis Potosí, Querétaro, Hidalgo); limited to drier valleys and plains with annual rainfall <500 mm.

According to the genetic analysis and bioclimatic modelling of Trejo & al. (2016), both subspecies are genetically separated, coincident with climatic differences along their actual and potential (modelled) distributions, showing overlap in the genetic make-up as well as the potential distribution areas.

**A. striata** ssp. **falcata** (Engelmann) Gentry (Agaves Cont. North Amer., 245, ills. (pp. 236, 245–247), 1982). **Type** [lecto]: Mexico, Coahuila (*Wislizenus* 312 [MO [2 sheets]]). — **Lit**: Engelmann (1875: 304–305, as *A. falcata*); Todaro (1876–92: 77–78, t. 19, as *A. paucifolia*); Berger (1915:

78–80, with ills., as *A. falcata* & *A. californica*); Vázquez-García & al. (2007b: 72–73); González-Elizondo & al. (2009: 130–131, with ill.). **Distr:** Mexico (Coahuila, S Nuevo León, W Durango, NE Zacatecas); sandy coarse rocky soils on bajadas, slopes and plains in desert shrub and succulent deserts, on limestone, 1000–2000 m; flowers May to August. **I:** Irish & Irish (2000: t. 41); Richter (2011: 58, 59); Pilbeam (2013: 205); Hochstätter (2015: VIII: 10).

≡ *Agave falcata* Engelm (1875); **incl.** *Agave californica* Jacobi (1868) ≡ *Agave striata* var. *californica* (Jacobi) A. Terracciano (1885); **incl.** *Agave paucifolia* Todaro (1877); **incl.** *Agave falcata* var. *espadina* A. Berger (1915); **incl.** *Agave falcata* var. *microcarpa* A. Berger (1915).

[1a] Differs from ssp. *striata*: **L** fewer, straight to falcate, rigid, thickly keeled, more xeromorphic, broader, 30–60 × 0.8–1.8 (–2) cm, margins serrulate; **Fr** broader, 12–13 mm wide; **Se** larger, 4–5 × 2.5–3 mm.

Merges gradually into ssp. *striata* (Gentry 1982: 245). In addition to leaf characters given by Gentry (1982: 245), the taxon also differs in fruit and seed characters (González-Elizondo & al. 2009). The occurrence in San Luis Potosí (Gentry 1982: 247) is not supported by specimens and is apparently erroneous. As first noted by Baker (1877a), *A. californica* Jacobi (1868) is closest to *A. striata*, and conspecific with the younger *A. falcata* Engelm (1875), but Gentry's combination

based on the Engelm name has priority at subspecies rank. Engelm (1875), followed by Gentry (1982: 245), assumed that *A. californica* might be identical with *Hesperoyucca whipplei* (as *Yucca*), but that species does not have the curved leaves and finely serrulate leaf margins described in the protologue. Guillot Ortiz & Meer (2002a) interpret a drawing from Sessé & Mociño (1787–1803) labelled *A. angustifolia* as belonging to this taxon. *A. rzedowskiana* resembles this taxon in its leaves, but has a different floral morphology (see there).

**A. striata** ssp. **striata** — **Lit:** Zuccarini (1833: 678); Salm-Dyck (1859: 95); Jacobi (1869: 395–399, incl. *A. recurva*); Baker (1877b: 556–557, fig. 109 & 110, the latter as *A. striata* var. *recurva*); Baker (1888a: 184); Berger (1915: 78–83, incl. synonyms); Gentry (1982: 242–245, with ills.); Vázquez-García & al. (2007b: 72, with ills.); Eguiarte & Scheinvar (2008: 29–34, with ills.); González-Elizondo & al. (2009: 128–130, with ills.); Starr (2012: 254–258, 314–316, with ills., as *A. striata*); **Distr:** Mexico (Coahuila, S Nuevo León, Tamaulipas, SE Zacatecas, San Luis Potosí, Querétaro, Hidalgo); drier limestone valleys, slopes and plains with desert and succulent scrub, 200–2200 m; flowers June to July to September and January. **I:** Curtis's Bot. Mag. 82: t. 4950, 1856; Heller (2006: 38, 136); Richter (2011: 59, 116, 121); Pilbeam (2013: 204). – Fig. 53.

**Fig. 53** *Agave striata* ssp. **striata** (Martinez & Egli 228: Mexico; Hidalgo, Patria Nueva, 1900 m). (Copyright: U. Egli)



**Incl.** *Agave striata* var. *nana* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave recurva* Zuccarini (1845)  $\equiv$  *Agave striata* var. *recurva* (Zuccarini) Baker (1877)  $\equiv$  *Agave striata* fa. *recurva* (Zuccarini) Voss (1895); **incl.** *Bonaparteia hystrix* Pasquale (1867) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Agave hystrix* (Pasquale) Baker (1877) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave ensiformis* hort. ex Baker (1877); **incl.** *Agave richardsii* hort. ex G. Nicholson (1884); **incl.** *Agave striata* [?] *glauca* Franceschi (1900) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Agave striata* var. *mesae* A. Berger (1915).

[1a] Stems short; **Ros** compact, 0.5–1  $\times$  0.5–1.2 m, often forming large dense clusters 2–3 m broad by axillary branching; **L** many, linear, straight to arching, thick, rather turgid, smooth or scabrous along the keels and below, convex above, mostly 25–60  $\times$  0.5–1 (at mid-leaf) cm, pale green to red or purplish, brownish at the tip below the terminal spine, striate, margins cartilaginous,  $\leq$  1 mm wide, pale yellow, scabrous or minutely serrulate; **terminal Sp** subulate, rounded below and above, very pungent, 10–50 mm, reddish-brown to dark grey; **Inf** erect, 1.5–2.5 m, ‘spicate’, peduncle long, **Bra** 5–10 cm, fertile part rather laxly flowered, part-**Inf** with mostly geminate flowers; floral **Bra** shorter than the flowers, deciduous; **Fl** tubular, 30–40 mm; **Tep** greenish-yellow or red to purple, tube shallowly grooved from the tepal sinuses, 14–20  $\times$  8–11 mm, lobes ovate-oblong, spreading with inflexed tips,  $\pm$  equal, 5–7  $\times$  3–5 mm, inner a little wider and with acuminate keel; **Fil** with a high knee, oval in cross section, 30–50 mm, inserted at mid-tube, usually at 2 levels; **Anth** centric, 12–16 mm, bronze or brownish, yellow when dehisced; **Ov** rounded-triangular, grooved, 12–15 mm, neckless, intruding the tepal tube; **Sty** as long as the filaments, below greenish-white, upwards somewhat purplish; **Sti** small, weakly 3-lobed; **Fr** trigonous, 13–16  $\times$  8–10 mm, truncate at the base, apiculate, dark brown; **Se** crescent-shaped, thick, esp. on the curved side, 3.5  $\times$  3 mm. — **Cytology**: 2n = 60 (Granick 1944).

The taxon is represented by extensive populations varying in growth habit, leaf forms, and to a lesser extent in flower structure. Plants with reddish to

reddish-purple leaves may co-occur with typical green-leaved plants and propagate true from seed (Richter 2011: 121, Pilbeam 2013). A small-growing form is sold as “var. *nana*”. *A. echinoides* Jacobi (inflorescence unknown) is a doubtful synonym either of this species or of *A. stricta* (Gentry 1982: 245). *A. tenuifolia* is close to *A. striata* ssp. *striata* (see there for differences). — Used locally for inferior fibres, and as hedge or fence plant (Gentry 1982: 245).

The biology is summarized by Eguiarte & Scheinvar (2008): The flowers are proterandrous, as is common in *Agave*, and last for 5 days. During the male phase on the first day, the anthers open; during the female phase in the last 4 days, the style elongates, the stigma open, and copious nectar is produced during the night. The probability that a flower develops into a fruit is 5–95% (average 50%), and the probability that an ovule develops into a seed is 32%. A plant produces on average  $\pm$ 200 fruits with  $\pm$ 40 seeds each, so an inflorescence produces on average almost 4000 seeds. However, fecundity is highly variable amongst individuals, sites and years. In controlled pollination experiments, much fewer fruits were produced when pollen from the same plant was used, indicating a very strong inbreeding depression (Rocha & al. 2005). Two studies (Rocha & al. 2005, Trejo 2007 [cited in Eguiarte & Scheinvar (2008: 31–32)]) revealed bees, bumblebees, hawkmoths and bats as pollinators, but showed differences in the relative importance of either diurnal bees and bumblebees (Rocha & al. 2005) or nocturnal bats (Trejo 2007 [cited in Eguiarte & Scheinvar (2008: 31–32)]) being most important. The genetic variation is high within populations, which exhibit a relatively high differentiation with geographically distant ones being most distinct, suggesting that gene flow is limited.

**A. stricta** Salm-Dyck (Bonplandia 7(7): 94–95, 1859). **Type** [neo]: Mexico, Puebla (Gentry & al. 20226 [US, MEXU [2 sheets]]). — **Lit**: Berger (1915: 81–82, with ill.); Gentry (1982: 248–249, with ill.); Ullrich (1990c: with ill.); Ullrich (1991d: with ills., as *A. striata* ssp.); García-Mendoza (2011a: 259–263); Starr (2012: 259–263, 314–316, with ills.). **Distr**: Mexico



(Puebla [esp. Tehuacán valley], N Oaxaca); semi-arid open calcareous slopes with sparse desert or succulent scrub, 1500–2060 m; flowers August to October. **I:** Irish & Irish (2000: t. 42); Heller (2006: 137); Richter (2011: 35); Pilbeam (2013: 206); Hochstätter (2015: VIII: 11). – Fig. 54.

≡ *Bonapartea stricta* (Salm-Dyck) Vukotinovic (1871) (*incorrect name*, ICN Art. 11.4) ≡ *Agave striata* var. *stricta* (Salm-Dyck) Baker (1877) ≡ *Agave striata* fa. *stricta* (Salm-Dyck) Voss (1895) ≡ *Agave striata* ssp. *stricta* (Salm-Dyck) B. Ullrich (1990); **incl.** *Agave echinoides* Jacobi (1868) ≡ *Agave striata* var. *echinoides* (Jacobi) Baker (1877); **incl.** *Agave hystrix* Hort. Belg. ex Jacobi (1870).

[1a] Stems elongate and branching, decumbent with age, 1–2 m; **Ros** 0.4–0.7 × 0.6–0.8 m, often densely caespitose; **L** > 100, long-lanceolate, linear, upcurved to straight, rigid, widest near the base, somewhat keeled above and below, rhombic in cross-section, 25–35 (–50) × 0.5–1 cm, glaucous-green, greenish-yellow or purple to

reddish-purple in the upper part, striate, margins thin, whitish or pale yellow to reddish, cartilaginous, scabrous-serrulate; **terminal Sp** acicular, 15–20 (–25) mm, angularly keeled below, flat above, grey, decurrent along the margin for 0.5–1.5 cm, at the base with a grey to blackish projection penetrating into the leaf tissue; **Inf** (1.5–) 2–3 m, ‘spicate’, erect or ascending, sometimes twisted, peduncle with linear or filiform deciduous whitish **Bra** 3–6.5 cm long, fertile part in the upper ½ or a little less, part-**Inf** with geminate flowers; **Ped** 2–3 mm; **Fl** ascending to outcurved, campanulate, 25–30 mm; **Tep** reddish to purplish, tube funnel-shaped, angled, grooved, 6–11 × 7–10 (at the mouth) mm, lobes erect to spreading with incurved tips, deltoid or elliptic, apiculate, equal, 7–10 × 3–6 mm, inner ones broadly keeled; **Fil** 30–37 mm, inserted at 2 levels at mid-tube, reddish; **Anth** centric, 10–13 mm, bronze to brownish-red or purple, opening yellow; **Ov** cylindrical, sharply 6-angled, 8–14 × 2–4 mm, slightly intruding the base of the tepal tube, neckless, wine-red; **Sty** 35 mm, reddish; **Fr** subglobose to pear-shaped, trigonous, 10–14 × 8–10 mm, truncate at the base, apiculate, reddish or purplish; **Se** semicircular, thickly discoid, wing inconspicuous, 3–4 × 2–3 mm, black. — **Cytology:** 2n = 50, 60 (Brandham 1969, Simpson & al. 2011).

Distinguished from the vegetatively very similar *A. striata* by the short flower tube, equalled or exceeded in length by the tepals, and from *A. dasylirioides* by the short, stiff, narrow leaves on elongate stems (Gentry 1982; see also Starr 2012: 314). From *A. petrophila*, *A. stricta* differs esp. in its much smaller rosettes, shorter and narrower leaves, larger and reddish or purple flowers, and its subglobose to pear-shaped, slightly larger fruits (García-Mendoza 2011a).

Plants with reddish-purple leaves co-occur with typical green-leaved plants without intermediates (Pilbeam 2013: 206). Ullrich (1990c) emphasizes vegetative similarities and suggests subspecific rank under *A. striata*, but he was not followed by later authors. Gentry (1982: 248) designated the neotype cited above.

Ullrich (1991d) provided a first record for N Oaxaca based on *Leuenberger* 2747 (B, MEXU), but further collections from Oaxaca are



**Fig. 54** *Agave stricta*. (Copyright: U. Eggli)

meanwhile known (García-Mendoza 2011a). The species is endemic to the Tehuacán-Cuicatlán valley (García-Mendoza 2011a). Photographs from San Luis Potosí labelled *A. stricta* (Pilbeam 2013: 206) most probably belong to *A. striata* ssp. *striata*.

**A. stringens** Trelease (Contr. US Nation. Herb. 23: 114, 1920). **Type:** Mexico, Jalisco (Trelease s. n. (1904) [MO]). — **Lit:** Gentry (1982: 582); McVaugh (1989: 143); Hernández-Vera & al. (2007a: 500); Vázquez-García & al. (2007b: 73, t. GG1, GG2). **Distr:** Mexico (Jalisco: Río Blanco barranca near Guadalajara); on rocks and cliffs. **I:** Pilbeam (2013: 207).

[2g] **Ros** to 1.5–2 m Ø, apparently solitary; **L** ±18–25, narrowly linear, lowermost nearly on the ground, uppermost upright-recurved, those in between ± recurved, concave, thin,  $\geq 60 \times 1\text{--}2$  cm, very glaucous, with bud imprints created by the marginal teeth, margins cartilaginous, narrow, yellowish-white, nearly straight; **marginal teeth** numerous, slightly upcurved, very sharp and slender, 1–2 mm, red or brown,  $\pm 10$  mm apart (Trelease: scarcely 5 mm apart), with small intermittent denticles; **terminal Sp** conical,  $\pm 8 \times 2$  mm, dark; **Inf** 2.5–3.5 m, paniculate, peduncle very long, making up  $\pm 5\%$  of the inflorescence, **part-Inf**  $\pm 10$ , ascending-spreading, lowermost long-stalked; **Tep** yellow but flowers not further described; **Fr** and **Se** not described.

A hardly known and apparently rare but distinctive species, known for long only from the sterile type specimen collected near Guadalajara (Jalisco) and a specimen from a sterile plant grown at Missouri BG, both appearing immature (Gentry 1982). McVaugh (1989) did not know the plant and repeats data from Trelease and Gentry. Hernández-Vera & al. (2007a) could not find the plant at its type locality and assume that it could be a form of *A. angustifolia*. The species was not known from habitat until its rediscovery by Kristen & Etter (Pilbeam 2013: 207; first published photograph). Etter & Kristen (1997+: accessed 2015) provide photographs of a plant with an infructescence and few additional data confirming the placement in Sect. *Rigidae*, following McVaugh (1989). The photograph in Hochstätter (2015: VII: 48) labelled “*Agave*

*stringens*” apparently shows a different plant. Further studies are needed.

**A. subsimplex** Trelease (Annual Rep. Missouri Bot. Gard. 22: 60, tt. 63–64, 1912). **Type:** Mexico, Sonora (Rose 16811 [US, MO, NY]). — **Lit:** Berger (1915: 268); Breitung (1963: 149, 151, with ill., as *A. sobria*); Gentry (1972: 131–134, with ills.); Gentry (1978: 27, 31, 34–35, with ills.); Gentry (1982: 404–407, with ills.); Turner & al. (1995: 67–68); Wilder & al. (2008: 136–137, 140, with ills.). **Distr:** Mexico (Sonora); thinly scattered in small colonies on outwash slopes of granitic and volcanic mountains and the adjacent islands (Tiburón, Dátil, Cholludo), in desert scrub, strictly coastal at low elevations; flowers April to July and October. **I:** Richter (2011: 81); Pilbeam (2013: 208); Hochstätter (2015: V: 13).

[2i] **Ros** low-spreading, 20–35  $\times$  50–70 cm, solitary or caespitose; **L** variable, lanceolate to ovate, thick, rigid, long- to short-acuminate, only a little narrowed towards the base, rounded below, hollowed above, 12–35  $\times$  3–5 cm, grey-glaucous or light yellow-green, or sometimes purple-tinged, margins nearly straight or with strong prominences; **marginal teeth** variable, friable, straight or variously curved, rarely 2-tipped, larger teeth 3–15 mm, brown or more often yellowish-grey; **terminal Sp** subulate, frequently sinuous, shallowly grooved above, 20–40 mm, glaucous-grey, not or only a little decurrent; **Inf** 2–3.5 m, paniculate, slender, narrow, **part-Inf** short and small, 5–8 per inflorescence; **Fl** 40–45 mm; **Tep** yellow to pink, tube shallow, spreading, 3–4  $\times$  10 mm, lobes elliptic, ascending, flat, widest at the middle, apiculate and scarcely hooded, equal, 12–15  $\times$  6–7 mm; **Fil** 25–28 mm, round in cross-section, inserted below the base of the lobes 3 mm above the tube bottom; **Anth** centric, 13–15 mm, yellow; **Ov**  $\pm 25$  mm, with unconstricted neck 5 mm long; **Sty** slightly longer than the tepals; **Sti** capitate; **Fr** variable, (narrowly) oblong, 35–40  $\times$  10–15 mm, bluntly apiculate, narrowly or broadly stipitate, light glaucous; **Se** roughly crescent-shaped, mostly 4.5–5  $\times$  3–4 mm, sooty black, hilum notch narrow, the opposite corner frequently apiculate, margin with a sharp winglike flange.



Closely related to *A. deserti* and *A. cerulata* with which it shares small variable leaves, nearly tubeless flowers, and narrow small panicles, all characteristic for Sect. *Deserticolae* (as Group) (Gentry 1982). *A. subsimplex* may be closest to the polymorphic *A. cerulata* of Baja California, as indicated by the small, variable leaves and the narrow, oblong, waxy capsules, but *A. subsimplex* differs in its more spreading rosettes, wider, less acuminate grey or yellow-green leaves, and filaments inserted below the base of the tepal lobes. The pink to red colour frequently occurring in the style, filaments, and corolla is distinctive for *A. subsimplex*, but not known in *A. deserti* and *A. cerulata* (Gentry 1982). In the population genetic studies of Navarro-Quezada & al. (2003), the three samples of the species form a clade nested within the *A. deserti/A. cerulata*-complex, but none of the latter two species is monophyletic. Diurnal (insects, birds) and nocturnal (insects, bats) pollinators are equally effective (Molina-Freaner & Eguiarte 2003). See also notes under *A. deserti*.

**A. ×taylorii** Hort. B. S. Williams (Gard. Chron., ser. nov. 1: 363, 1874). **Type:** not typified. — **Lit:** Baker (1877a: 620, 621: fig. 125); Baker (1888a: 186); Coulson (1897: with ill.); Trelease (1914: 236, 238); Berger (1915: 71, as *A. taylorii*). **Distr:** Cultivated only.

**Incl.** *Agave ×taylorea* Hort. B. S. Williams ex Rafarin (1877) (*nom. inval.*, ICN Art. 61.1).

[1d × 1d] This is the garden hybrid *A. geminiflora* × *A. filifera* (as *A. filamentosa*), commercially offered by the nursery of B. S. Williams. Baker (1877a) provides a plate of the plant. The second parent was given as *A. densiflora* (= *A. mitis*) in the protologue, but corrected to *A. filamentosa* (= *A. filifera*) by Baker (1888a) in agreement with the very narrow leaves. Coulson (1897) provides a detailed description and photograph of a plant in bloom. J. N. Rose prepared 3 specimens labelled *A. taylorii* from a plant at US: Rose 1132, 1897 (US 302815; leaves), and Rose 4128, 1898 (US 399839 & 399840; leaves, flowers, photographs of a flowering plant; later identified as *A. colimana* by H. S. Gentry in 1977). Trelease (1914) erroneously lists both parentages.

According to Berger (1915), the plant could be identical with *A. wrightii* (= *A. schidigera*) and would antedate that name. Apparently no longer extant in cultivation.

**A. tecta** Trelease (Trans. Acad. Sci. St. Louis 23: 145–146, tt. 26–27, 1915). **Type:** Guatemala (Trelease 17 [ILL [2 sheets, syn]]). — **Lit:** Standley & Steyermark (1952: 118–119); Breitung (1964: 36, with ill.); Gentry (1982: 612–614, with ill.); Lott & García-Mendoza (1994: & online version); Véliz Pérez (2013: 240–242, with ill.). **Distr:** NW Guatemala (region of Quetzaltenango); cultivated only, 1500–2600 m; flowers in April. **I:** Lyons (2002: 162); Hochstätter (2015: II: 9).

[2b] Stems very thick and broad; **Ros** semiglobose, open, 2 × 3–4 m, broad, freely suckering; **L** lanceolate or broadly lanceolate, straightly ascending and often outcurved, very thick, base deeply convex and thick, becoming thinner upwards, acuminate, sigmoidally upcurved at the tip, concave to guttered, smooth, 100–200 × 30–50 cm, greyish or rather dark green, margins almost straight; **marginal teeth** recurved, often lustrous, on triangular often curved prominences often dilated at the base to 15 mm or more, 8–10 (–15) mm (at mid-leaf), dull brown or chestnut-brown becoming grey, 20–70 mm apart, tips flattened, triangular, straight or curved from low bases, dull brown, teeth sometimes on a discontinuous horny band formed by their bases; **terminal Sp** conical or subacicular, subulate, often slightly flexuous, narrowly shortly grooved above to the middle, 40–70 × 5–7 mm, dull brown or chestnut-brown, becoming grey, long decurrent for 10–15 cm, somewhat intruding dorsally into the green leaf tissue; **Inf** 5–7 m, paniculate, thick, with fleshy broadly triangular amplexicaul **Bra**, basal **Bra** sometimes densely imbricate below, sometimes completely covering the peduncle, fertile part ellipsoid, lax, with ±25 slightly ascending part-**Inf**, apparently not bulbiferous; **Ped** thick, to 10 mm; **Fl** 70–95 mm; **Tep** yellow to greenish-yellow, buds tinged red, tube funnel-shaped, deeply grooved, thick-walled, 10–18 × 20 mm, lobes linear-lanceolate, unequal, outer 20–33 × 8–9 mm, thickly apiculate, deeply

cucullate, inner shorter, narrower, thickly keeled; **Fil** broadly flattened, 40–65 mm, inserted at 2 levels 10–13 mm above the tube base; **Ov** 30–43 mm, neck grooved, not constricted; immature **Fr** oblong,  $\pm 60 \times 30$  mm; mature **Fr** and **Se** unknown.

Geographically isolated from other members of Sect. *Salmianae* (as Group); possibly a remnant of former use and now cultivated as a fence plant (Gentry 1982: 614). Cultivated in many miles of hedges around Quetzaltenango (Guatemala), and easily distinguished from other Guatemalan Agaves by its massive leaves of trough-like shape (Standley & Steyermark 1952). The report from oak forests at Tixtla de Guerrero (Guerrero, Mexico; Velázquez & al. 2003: 9) appears doubtful, or might represent the native habitat? The two type specimens at ILL are not cross-labelled and thus represent syntypes (Smith & Figueiredo 2014e: 244).

**A. telegraphica** H. Jekyll (Garden (London, 1871–1927) 1: 51, ill., 1871). **Incorrect name**, ICN Art. Preamble 8. **Type**: not typified. — **Lit**: Anonymous (1872: 172); Cutak (1943: 151); Mitich (1975: 106–107); Nelson (2001: 9–10); all with ill. **Distr**: Printed matter only, and on the verge of extinction.

≡ *Polea telegraphica* (H. Jekyll) E. C. Nelson (2001) (*incorrect name*, ICN Art. Preamble 8).

[2b?] **Ros** open, solitary; **L** 7, broadly lanceolate, older arching over, to  $\pm 200 \times 40$  cm, margins with 4–5 teeth, concave between the teeth; **Inf** paniculate, with 12 regularly horizontal part-**Inf** in the upper  $\frac{2}{3}$  of the inflorescence, part-**Inf** always 2 at the same level, and all in the same plane.

The species, a “rather entertaining bit of English humor” (Cutak 1943), is based on a drawing of a huge *Agave* with an inflorescence representing a telegraph pole and its 12 “part-inflorescences” being the carrying structure for the telegraph wires. In habit, it resembles species of Sect. *Salmianae*.

**A. temacapulinensis** A. Vázquez & Cházaro (Novon 22(2): 236–237, ills., 2012). **Type**: Mexico, Jalisco (*Vázquez-García & Cházaro* 9092

[IBUG, MEXU, MICH, MO]). — **Lit**: Etter & Kristen (2012: 94–95, with ills.); Cházaro Basáñez & al. (2013: with ills.); Vázquez-García & al. (2016: with ill.). **Distr**: Mexico (Jalisco: Río Verde drainage); calcareous outcrops, 1600–1700 m, ecotones between juniper, thorn, and *Taxodium* gallery forests, 1600–1700 m; flowers May to June. **I**: Pilbeam (2013: 209–210); Hochstätter (2015: IV: 15).

[2h] **Ros** open, closed or compact, 0.8–1.15  $\times$  1.72 m, solitary or occasionally surculose; **L** 20–25, ovate to lanceolate, firm and smooth, 55–90  $\times$  (13–) 15–20 (–24) cm, glaucous to light grey, margins crenate; **marginal teeth** variously curved, usually upwards, with broad base, 8–10  $\times$  7 mm, 15–21 mm apart at mid-leaf, 12–29 mm apart towards the tip, 6–10 mm apart towards the base; **terminal Sp** flexuous, channelled, 35–45  $\times$  9 mm, black to bluish-grey, long-decurrent; **Inf** 5–6.5 m, ‘paniculate’, peduncle with reflexed triangular **Bra**, these 20  $\times$  3 cm, fertile part open, part-**Inf** 16–18 in the upper  $\frac{2}{3}$ , 20–22 cm, with 50–70 flowers; **Fl** 60–71 mm; **Tep** yellow, outer face greenish, tube 9–15  $\times$  8–9 mm, equal to or longer than the lobes, lobes dimorphic, outer 10–15  $\times$  5–6 mm, apex red, horny, inner 12–13 mm, white-puberulent, apex galeate, all dorsally with a prominent longitudinal central keel except at the apex, drying leathery, persisting erect; **Fil** inserted unequally at mid-tube, outer inserted 1 mm higher, yellow; **Ov** 17  $\times$  5 mm, neck 7  $\times$  3 mm; **Sty** slender, nearly as long as the filaments, yellow; **Sti** 3-lobed, clavate, glandular; **Fr** oblong to obovoid, 40–51  $\times$  14–18 mm, stipe 2–8 mm; **Se** subcircular to semicircular or triangular, 5–6  $\times$  3–4 mm, black, shiny, wingless.

The light glaucous rosettes, dimorphic tepal lobes, and deep floral tube clearly place the species in Sect. *Ditepalae* where it is most similar morphologically to *A. wocomahi* (with dark green to glaucous leaves with straight to repand margins, longer teeth, shorter inflorescences with a lower number of branches, and larger seeds), and also to *A. durangensis* (with rough-textured leaves, longer teeth, and taller inflorescences with more numerous branches). *A. temacapulinensis* is a locally abundant local endemic, and is threatened

by land degradation and the El Zapotillo dam project, which may flood nearly its entire habitat (Vázquez-García & al. 2016). — According to the protologue, the flowers are visited by hummingbirds during the day and by bats in the evening.

**A. tenuifolia** Zamudio & E. Sánchez (Acta Bot. Mex. 37: 47–52, ills., 1995). **Type:** Mexico, Querétaro (*Carranza* 1905 [IEB, MEXU, TEX]). — **Distr:** Mexico (C Tamaulipas, S Guanajuato, NE Querétaro, Hidalgo, Michoacán); limestone slopes with thin soil, in pine-oak or tropical (sub-)deciduous forests, 450–1500 m; flowers mid-April to July. **I:** Magallán Hernández & al. (2012: 30, as *Agave* sp. 2). Pilbeam (2013: 211); Hochstätter (2015: VIII: 12); Greulich (2018b: 90).

[1a] **Ros** lax, caespitose, forming dense groups by axillary or rhizomatous branching; **L** 30–50 (–90), linear, subcoriaceous, very thin and flexible, young straight, mature recurved, keeled on both faces, (29–) 50–100 (–130) × 0.25–0.5 (middle, to 1.3 at the base) cm, green, striate, margins horny, <1 mm wide, light green or hyaline, shortly serrulate; **terminal Sp** conical-subulate, angulate below, flattened above, 4–10 mm, reddish-coffee-brown; **Inf** (0.9–) 1.5–1.75 (–2.3) m, ‘spicate’, peduncle with triangular long-cuspidate **Bra** (3–) 7–10 (–25) cm long, decreasing in size upwards, fertile part straight, thin, lax, part-**Inf** (19–) 23–25 (–44) per inflorescence, with geminate flowers, in the upper 1/3 of the inflorescence; floral **Bra** triangular, broadly cuspidate, 8–18 mm, generally much shorter than the flowers, caducous; **Fl** tubular, 23–30 mm; **Tep** yellow-greenish, tube sulcate from the sinuses of the lobes, 12–15 × 5–9 mm, lobes ovate-oblong, equal, apex obtuse, slightly cucullate, 4–7 × 3–4 mm; **Fil** 20–35 mm, inserted at 2 levels at mid-tube; **Anth** centric or slightly excentric, 7–13 mm; **Ov** cylindrical, sulcate, (6–) 9–12 mm, neckless, protruding slightly into the tepal tube; **Sty** slightly surpassing the filaments; **Fr** trigonous, 11–18 × 9–13 mm, truncate at the base, shortly apiculate, coffee-brown; **Se** semicircular, flat, 4–5 × 3 mm, thickened in the curved part, with distinct margin, hilum lateral, black, shiny.

According to the protologue close to *A. striata* ssp. *striata* but differing in its lax rosettes, fewer, larger and pliable, recurved leaves and its lax

‘spikes’ with geminate flowers. Molecular AFLP data (Gil-Vega & al. 2006) place *A. tenuifolia* closest to that taxon. For differences from *A. stricta*, see there. *A. tenuifolia* differs from all other members of Sect. *Juncineae* (as Group *Striatae*) in having fewer and longer leaves, lax inflorescences, and short stamens which are only shortly exerted. Pilbeam (2013) provides a new record from near Xichú in Guanajuato (as “Aguascalientes”), Hochstätter (2015) from Metztlán (Hidalgo), and Etter & Kristen (1997+: accessed 2015) from Michoacán.

**A. tequilana** F. A. C. Weber (Bull. Mus. Hist. Nat. (Paris) 8: 220, ills., 1902). **Type:** [lecto — icono]: l.c. fig. 1. — **Lit:** Berger (1915: 251–252); Gentry (1982: 582–585, with ills.); McVaugh (1989: 143–145); Etter & Kristen (2007b: with ills.). **Distr:** Mexico (Sonora, Sinaloa, Jalisco, Michoacán, Oaxaca); cultivated only; flowers July to November. **I:** Irish & Irish (2000: t. 43, variegated form); Heller (2006: 29, 32); Richter (2011: 13); Etter & Kristen (2012: 79–81); Pilbeam (2013: 212–213).

≡ *Agave angustifolia* ssp. *tequilana* (F. A. C. Weber) A. Valenzuela & Nabhan (2004); **incl.** *Agave palmaris* Trelease (1920); **incl.** *Agave pedrosana* Trelease (1920); **incl.** *Agave pes-mulae* Trelease (1920) ≡ *Agave angustifolia* ssp. *rubescens* ‘Pes-mulae’ (Trelease) A. Valenzuela & Nabhan (2003) (*nom. inval.*, ICN Art. 35.1) ≡ *Agave angustifolia* var. *pes-mulae* (Trelease) A. Valenzuela & Nabhan (2003) (*nom. inval.*, ICN Art. 41.4); **incl.** *Agave pseudotequilana* Trelease (1920).

[2g] Stems short, thick, mature 30–50 cm; **Ros** radiately spreading, 1.2–1.8 m, surculose; **L** lanceolate, ascending to horizontal, firmly fibrous, mostly rigidly spreading, narrow and thickened towards the base, widest in the middle, acuminate, concave, 90–120 × 8–12 cm, generally glaucous bluish- to grey-green, sometimes cross-zoned, margins straight to repand; **marginal teeth** generally regular in size and spacing or rarely irregular, mostly 3–6 mm (at mid-leaf), light to dark brown, 10–20 mm apart, with slender tips curved from low pyramidal bases, rarely teeth remote and longer; **terminal Sp** flattened or openly grooved

above, generally 10–20 mm, rarely longer, base broad, dark brown, decurrent or not; **Inf** 5–6 m, paniculate, densely branched, part-**Inf** large, dense, diffusely several times compound, 20–25 per inflorescence; floral bracts small; **Ped** 3–8 mm; **Fl** 68–75 mm; **Tep** green, tube grooved, funnel-shaped, 10 × 12 mm, lobes linear, erect, withering quickly at anthesis, subequal, 25–28 × 4 mm, turning brownish and dry; **Fil** bent inwards against the style, 45–50 mm, inserted at 7 and 5 mm above the tube base; **Anth** 25 mm; **Ov** cylindrical, 6-ridged, slightly tapered at the base, 32–38 mm, neck short, not constricted; **Fr** ovoid, shortly cuspidate, 35–60 × 25–35 mm, sessile or shortly stipitate; **Se** semicircular, hilum subventral. — **Cytology**: 2n = 60; cultivars: 2n = 60 ('Azul'), 90, 120, 150 (Castorena Sanchez & al. 1991, Palomino & al. 2003, Guadalupe & al. 2008, Robert & al. 2008, Simpson & al. 2011).

Distinguished from its close relative *A. angustifolia* by larger leaves, thicker stems, and larger, more diffuse inflorescences with relatively large flowers with rather short tubes, albeit these differences are of degree rather than clear-cut (Gentry 1982: 583). Molecular studies showed that *A. tequilana* is derived from *A. angustifolia*, and that its different cultivars are genetically distinct (Cuevas Figueroa & Flores Berrios 2006). The taxon thus represents a polyphyletic assemblage of cultivars independently derived from within its progenitor species *A. angustifolia* and could consequently be classified at subspecific rank under it. It is here upheld at species rank due to its importance as crop plant. — Gentry (1982: 585) designated the figure cited above as "Type", which represents a lectotypification.

*A. tequilana* is of considerable economical importance as source of the distilled liquor tequila. Under Mexican laws, tequila can only be produced from the cultivar 'Azul' (Gil-Vega & al. 2001), which is cultivated in large plantations, esp. around the town of Tequila (Jalisco) after which it is named. In 2006, this landscape was declared as UNESCO World Heritage "Agave Landscape and Ancient Industrial Facilities of Tequila". The tequila landscape, industry, harvesting and manufacturing is shown and described by

Valenzuela-Zapata (1985) and Etter & Kristen (2012), and in detail by Valenzuela-Zapata & Nabhan (2003).

Molecular studies of *A. tequilana* 'Azul' revealed an extremely low level of genetic diversity, assumed to result from vegetative propagation of a single conserved genotype over many years (Gil-Vega & al. 2001). *A. tequilana* 'Azul' bulbils show genetic differences from the mother plant, while lateral shoots do not show such differences (Cuevas Figueroa & Flores Berrios 2006). In Jalisco, different genotypes exist which were conserved in different regions by asexual propagation (Torres-Morán & al. 2013). Landraces, which are ignored by the tequila industry, show domestication syndromes for fructan content or in the fibres and may be valuable for both ethanol production and genetic resource conservation (Valenzuela 2011). Trejo-Salazar & al. (2016) argue that intensified agriculture to meet the increased demand for *Agave*-derived alcoholic beverages threatens the bat-*Agave* relationship. Bat-friendly procedures should be investigated, and allowing 5% of the plants to flower would be a possible approach. — The embryo sac is of the monosporic *Polygonum*-type and the endosperm formation is helobial (González-Gutiérrez & al. 2014).

**A. thomasiae** Trelease (Trans. Acad. Sci. St. Louis 23: 138, t. 12, 1915). **Type**: Guatemala (*Trelease* 19 [ILL]). — **Lit**: Standley & Steyermark (1952: 119–120); Gentry (1982: 500–501, with ill.); Lott & Garcia-Mendoza (1994: & online version); Véliz Pérez (2013: 241–242, with ill.); Meer & Guillot Ortiz (2016: 188–189, with ill.). **Distr**: W & SW Guatemala; rocky hills in juniper, pine and oak forests, 2000–3080 m; flowers December and April. **I**: Richter (2011: 130); Pilbeam (2013: 214); Hochstätter (2015: VI: 15).

[2o] Acaulescent; **Ros** openly spreading, medium-sized, solitary or sometimes moderately to freely suckering; **L** lanceolate to broadly lanceolate, softly succulent, pliable, narrowed and thickened towards the base, acuminate, flat to mildly guttered, smooth to slightly asperous below, 60–120 × (12–) 15–19 cm, pruinose or light glaucous to pale green; **marginal teeth**



minute, 1–3 mm, 10–20 mm apart or less, reduced to denticles below, with small intermittent teeth; **terminal Sp** subulate to acicular, shallowly grooved above, 30–45 mm, dark brown; **Inf** 4–8 m, paniculate, peduncle short, fertile part narrow, part-**Inf** congested, roundish, 30–60 in the upper  $\frac{1}{2}$ – $\frac{5}{6}$  of the inflorescence; **Fl** 60–70 mm; **Tep** purple to yellow, tube funnel-shaped, knobby, trigonous, rather thin-walled, sulcate, 6–11 mm, lobes erect to incurved, long-linear, bluntly acute, cucullate, unequal, 19–29 mm, inner smaller with a prominent keel; **Fil** 45–60 mm, purple or yellow, inserted near the mouth of the tube; **Anth** regular, excentric, 15–25 mm, yellow; **Ov** strongly trigonous, 30–38 mm, tapering from the tube or with a short grooved neck; **Sty**  $\pm$  as long as the filaments; **Sti** capitate; **Fr** linear-oblong, 43–50  $\times$  20–24 mm, without beak, stipitate for 20 mm; **Se** unknown.

One of the few suckering Agaves in Guatemala. Distinguished by its soft, grey-pruinose leaves with minute teeth and variously coloured flowers with strongly trigonous ovaries (Gentry 1982: 500). The fruit description was added from *Mathiasen* 9921B (DES 00043364!).

Three further Guatemalan *Agave* species with relatively narrow leaves are insufficiently known and here listed as unresolved names on the base of Lott & García-Mendoza (1994): *A. deamiana* (Trelease 1915: 139) with small teeth and few spreading leaves from Fiscal is only known from the sterile type material and is thus of difficult

application; *A. minarum* (Trelease 1915: 139) with moderate, easily detachable teeth from the Sierra de la Minas is of uncertain affinities and could not be located in the field; and *A. kellermaniana* (Trelease 1915: 142) with close, slender-tipped, chestnut-brown teeth from blue bases, likewise from Fiscal. The latter is based on mixed sterile material: Its type (*Deam* 6239) is of uncertain identity, while *Norton* 112 belongs to *A. seemanniana* (Lott & García-Mendoza 1994).

**A. titanota** Gentry (Agaves Cont. North Amer., 176–180, ills., 1982). **Type:** Mexico, Oaxaca (*Gentry & Tejada* 22474 [US  $\dagger$ , syn?: ARIZ [3 sheets], ASU, DES, MEXU [2 sheets], MICH [3 cross-labelled sheets]]). — **Lit:** García-Mendoza (2003: with ill.); Greulich (2005b: with ills.); García-Mendoza (2011a: 63–64); Starr (2012: 264–267, with ills.); Guillot Ortiz & Meer (2014: with ills.). **Distr:** Mexico (S Puebla, NE Oaxaca); limestone canyons and slopes, in desert scrub on brown soils of limestone origin, 500–1420 m; flowers late November to January. **I:** Irish & Irish (2000: t. 44); Heller (2006: 138, 139, 160); Richter (2011: 54, 69, 113); Pilbeam (2013: 215–217); Smith & Figueiredo (2014a: 18); Hochstätter (2015: IX: 43); Moore (2016: 264, 265). — Fig. 55.

**Incl.** *Agave titanota* [?] *minor* hort. ex Heller (2006) (*nom. inval.*, ICN Art. 38.1a).

**Fig. 55** *Agave titanota* (Etter & Kristen 1805: Mexico; Oaxaca, between Tehuacán and Oaxaca, 1800 m). (Copyright: J. Etter & M. Kristen)





[1g] Stems short; **Ros** openly spreading, 0.5–0.8 × 0.8–1.5 m, solitary or rarely sparingly surculose; **L** 20–30, ovate, spatulate, or broadly lanceolate, broad, rigid, thick towards the base, short-acuminate, keeled and convex below, flat or concave above, the apex involute above, finely granular, 30–60 × 12–15 cm, typically alabaster- or glaucous-white, very rarely blue-green, sometimes with lighter mid-stripe, margins horny, wavy to crenate, widest (3–5 mm) towards the leaf tip, continuous to the base or nearly so, brownish or greyish-white; **marginal teeth** deltoid or irregular, variously curved, rough-granular, sometimes with denticles at the base, (10–) 20–40 × (6–) 10–17 mm, white-grey or dark brown, (10–) 30–50 (–85) mm apart at mid-leaf, leaf tip area sometimes toothless for the uppermost 7–12 cm; **terminal Sp** broadly conical, with deep involute groove above, keeled and protruding below for up to 20 mm, 30–65 × 10–20 mm, dark brown to grey or greyish-white, spine and decurrent part forming a horny plate 3–10 × 2–5.5 cm (on the lower face); **Inf** erect, 2.5–3 m, ‘spicate’, peduncle with deltoid, long attenuate, ascending **Bra** 9–20 cm long, fertile part in the upper  $\frac{1}{2}$ – $\frac{1}{3}$ , part-**Inf** with geminate flowers; **Ped** 10–20 mm; **Fl** (30–) 40–47 mm, campanulate; **Tep** yellow, yellowish-green or with lavender flushes, tube broadly funnel-shaped, (1–) 2–4 × 4–6 (at the mouth) mm, lobes ascending, linear, acute, thickly succulent, not clasping the filaments at anthesis, 20–30 × 2–5 mm, outer 1 mm longer, inner with a prominent keel protruding into the apex; **Fil** flattened, finely tapered towards the apex, 45–60 mm, inserted near the tube rim; **Anth** centric, 10–15 mm, yellow or with lavender flushes; **Ov** slenderly cylindrical, (12–) 17–20 (–25) × 3–4 mm, pale greenish, neck slightly constricted for 2–5 mm; **Sty** thick, 55 mm, clearly longer than the tepals; **Fr** ellipsoid or obovoid, acute at the apex, (15–) 25–28 × 10–12 mm, brown; **Se** 3.5–4 × 2–3 mm, wing <1 mm broad, black.

Characterized by ovate, spatulate to broadly lanceolate, glaucous or yellowish-green leaves with large, irregular, whitish-grey teeth, the terminal spine forming a broad robust plate on the lower face, and flowers with a short tube and long and narrow lobes. Known to Gentry (1982) only from its type locality Rancho Tambor where

only plants with alabaster- or glaucous-white leaves occur. Meanwhile, the species is known to be more widespread in NE Oaxaca (Pilbeam 2013), and was also collected in S-most Puebla (García-Mendoza 2011a) and is thus endemic to the Tehuacán-Cuicatlán valley. Illustrations in Greulich (2005b) show the variability in leaf colour and shape. Guillot Ortiz & Meer (2014) give an overview of *A. titanota* cultivars. Var. *minor* is a horticultural name for a small form with short leaves (Heller 2006: 138).

Green-leaved plants collected by F. Otero (Otero 076) in the Sierra Mixteca caused considerable discussions as to their identity. Pilbeam (2013) considers them as a mere form only with deviating leaf colour. Guillot Ortiz & Meer (2014) describe the plant as *Agave* ‘Felipe Otero’. Their speculations that this plant might represent a hybrid of *A. titanota* or *A. horrida* are unfounded, since the green plants appear to occur in pure stands, and the latter is absent from its area. Starr (2019) published the Otero plant as a new species *A. oteroi* which could no more be included in this handbook. For the closely related *A. quiotepecensis*, see there.

The holotype, cited for US in the protologue, is not accessible electronically and was probably never sent: Most probably, Gentry intended the most complete, not cross-labelled specimens (ARIZ 265732–265734) bearing his stamp “Gentry Herbarium” and his hand-writing to be sent to US as “holotype”. The specimens as cited above thus represent 8 syntypes.

**A. toumeyana** Trelease (Contr. US Nation. Herb. 23: 140, 1920). **Type:** USA, Arizona (*Toumey* 442 [MO?, ARIZ, MIN, US]). — **Lit:** Gentry (1982: 208–213, with ill.). **Distr:** USA (C Arizona).

The holotype, cited for MO in the protologue, is not accessible electronically.

**A. toumeyana** ssp. **bella** (Breitung) Gentry (Agaves Cont. North Amer., 211, ill. (pp. 212–213), 1982). **Type:** USA, Arizona (*Breitung & Gibbon* 18153 [CAS 415996]). — **Lit:** Breitung (1960: 80–81, with ill.); Weber (1965:

**Fig. 56** *Agave toumeyana* ssp. *bella* (Etter & Kristen 289: USA; Arizona, Gila County, Indian Coral Mesa, 1400 m). (Copyright: J. Etter & M. Kristen)



with ill.); Hodgson (1999a: 10); Reveal & Hodgson (2002); Starr & Devender (2011: 227, 230–231); Starr (2012: 269–274, 310–311, with ill.); Parker (2017: 262–263, with ill., as var.). **Distr:** USA (C Arizona); open gravelly to rocky limestone or basalt slopes, mostly with desert scrub, chaparral, and pinyon-juniper woodlands, 800–1700 m; flowers May to June. **I:** Heller (2006: 157); Pilbeam (2013: 219); Ettelt (2014: 118); Hochstätter (2015: VIII: 57). – Fig. 56.

≡ *Agave toumeyana* var. *bella* Breitung (1960).

[1e] Differs from ssp. *toumeyana*: **Ros** flat-topped; **L** 100–200, smaller, (3–) 9–20 (–27) × 0.5–1.2 cm, pale green, margins denticulate in the lower ½ of the leaf; **Fl** 16–21 mm; **Fil** 11–13 mm; **Ov** 8–12 mm. — **Cytology:** 2n = 60 (Pinkava & Baker 1985, Baker & al. 2009).

Quite distinct from ssp. *toumeyana* and with a nearly separate, very limited distribution area in C Arizona (Gentry 1982). It hybridizes with *A. chrysantha* (Hodgson 1999a, Reveal & Hodgson 2002).

**A. toumeyana** ssp. *toumeyana* — **Lit:** Breitung (1960: 79–80, with ill.); Weber (1965: with ill.); Gentry (1982: 208–211, with ill.); Hodgson (1999a: 10); Reveal & Hodgson (2002); Starr & Devender (2011: 227, 230–231, with ill.); Starr (2012: 270, 272, 310–311); Parker (2017: 262–263, with ill., as var.). **Distr:** USA (C

Arizona); open gravelly to rocky limestone or basalt slopes, mostly with desert scrub, chaparral, and pinyon-juniper woodlands, 600–1500 m; flowers March to June. **I:** Irish & Irish (2000: t. 45); Heller (2006: 34, 140); Richter (2011: 64); Pilbeam (2013: 218); Ettelt (2014: 117); Hochstätter (2015: VIII: 56). – Fig. 57.

≡ *Agave toumeyana* var. *toumeyana*.

[1e] **Ros** (3–) 10–50 × 15–60 cm, round-topped, freely suckering, densely caespitose; **L** 40–70, linear to linear-lanceolate, ascending to erect, straight or falcate or upcurving, rather rigid, of unequal length, thickly convex towards the base, flat above towards the acute to long-acuminate apex, smooth, 19–46 × 1.2–2 cm, pale green to yellowish, both faces with impressions from the central bud, margins straight, fine, brown with conspicuous curled white fibres, fibres infrequently sparse or absent; **marginal teeth** none, or as minute denticles at the base and apex; **terminal Sp** subulate to filiform, with a short narrow groove above, 6–20 mm, brown to greyish; **Inf** 1.5–3 m, ‘spicate’, peduncle with caducous linear-triangular **Bra** 1–3.5 cm long, fertile part densely or laxly flowered in the upper ½ of the inflorescence, part-**Inf** mostly with geminate flowers, sometimes single; **Ped** to 5 mm, basally pairwise united; **Fl** 21–28 mm, slightly recurved; **Tep** saccate, erect to incurved, green to greenish white, tube campanulate, angled, 3–4.5 × 8–10 mm, lobes lanceolate, thin, erect to

**Fig. 57** *Agave toumeyana* ssp. *toumeyana* (Etter & Kristen 532: USA; Arizona, Gila County, N of Christmas, 1080 m). (Copyright: J. Etter & M. Kristen)



incurved, appressed to the filaments, subequal, 6.5–10 mm, outer closely overlapping the inner, whitish; **Fil** shortly exerted, erect to incurved, 12–17 mm, inserted 1–3.5 mm above the tube base, whitish; **Anth** 7–16 mm, pale yellow; **Ov** 8–16 mm, neck slender, curved, 3–7 mm, slightly constricted; **Sty** thick, slightly longer than the tepals; **Fr** shortly oblong, persistent, 9–15 × 8–10 mm, sessile, short-beaked, walls thin; **Se** thick, 2 × 3 mm. — **Cytology**: 2n = 60, 120 (Zonneveld 2003, Simpson & al. 2011).

The species suggests a large version of *A. parviflora*, but the rosettes are mostly higher, and the leaves are mostly longer and always more long-acuminate, the flowers larger, the filaments are inserted higher up in the tube, and the lobes are more elongate (Gentry 1982: 210, Reveal & Hodgson 2002). Both subspecies hybridize with *A. chrysantha* in Arizona (Hodgson 1999a, Reveal & Hodgson 2002). The rosettes of *A. toumeyana* are denser with more leaves than those of *A. parviflora* and *A. polianthiflora*, and the marginal fibres are thinner and less uniform (Starr & Devender 2011).

**A. triangularis** Jacobi (Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 12: 178, 1869). **Type** [neo]: Mexico, Puebla (Gentry 23399 [US, ARIZ, ASU, DES, MEXU]). — **Lit**: Jacobi (1869: 149–150, incl. *A. rigidissima*); Berger (1915: 101–102; 109–110, with ill., as *A. hanburyi*); Trelease (1920: 137–138); Breitung

(1959: 176–177, with ills.); Gentry (1982: 180–182, with ills.); García-Mendoza (2011a: 64–67). **Distr**: Mexico (S Puebla, N Oaxaca); common in desert scrub on arid limestone soils, 1700–1930 m; flowers June to August. **I**: Heller (2006: 141); Richter (2011: 41, as *A. hanburyi*); Pilbeam (2013: 220); Hochstätter (2015: IX: 44); Moore (2016: 263). – Fig. 58.

≡ *Agave horrida* var. *triangularis* (Jacobi) Baker (1877); **incl.** *Agave rigidissima* Jacobi (1869) ≡ *Agave triangularis* var. *rigidissima* Trelease (1920); **incl.** *Agave kerchovei* var. *inermis* Ortgies ex Baker (1877); **incl.** *Agave hanburyi* Baker (1892); **incl.** *Agave triangularis* var. *subintegra* Trelease (1914).

[lg] Acaulescent; **Ros** slow-growing, lax, 0.6–0.7 × 0.8–1 m, widely surculose, forming open clusters; **L** 30–50, deltoid to deltoid-lanceolate, straight, ascending, rigid, thick at the base, long-acuminate, flat or upper face concave, smooth, 30–55 × 5–8 cm, olive-green to brownish-green or yellowish-brown, finely flecked with brownish-red, margins horny, continuous, straight, 1–2 mm wide, greyish; **marginal teeth** present or mostly absent, straight or variously curved, few, small teeth 1–2 mm and 30–50 mm apart, larger teeth 5–10 mm and 10–20 mm apart, grey; **terminal Sp** conical to subulate, usually straight, somewhat keeled below, grooved above, (20–) 45–60 × 4–5 mm, greyish, sometimes decurrent for ± 1 cm; **Inf** 2.5–3.5 m, ‘spicate’, peduncle green, pruinose, with long triangular or linear chartaceous



**Fig. 58** *Agave triangularis* (Etter & Kristen 1738: Mexico; Puebla, between Tehuacán and Huajuapán de León, 1720 m). (Copyright: J. Etter & M. Kristen)



**Bra** 12–14 cm long, fertile part in the upper  $\frac{1}{3}$ , lax; **Ped** 1–2 mm; **Fl** campanulate, 35–38 mm;  **Tep** yellowish-green with purple or reddish-green tinge, tube 5 × 5–8 mm, lobes oblong, divaricate to slightly recurved, 13–15 × 2–4 mm, pruinose; **Fil** 30–40 (–50) mm, yellow, inserted in the mouth of the tube; **Anth** ±13 mm, yellow; **Ov** cylindrical, 12–15 × 4–5 mm, pruinose, neck 1–3 mm, constricted; **Sty** 40 mm; **Fr** ovate, 20–25 × 15 mm, dark green, pruinose when young; **Se** 4–5 × 3–4 mm, black.

Introduced by K. Besserer from near Tehuacán (Puebla) in 1868 (Jacobi 1869, Berger 1915: 102). *A. triangularis* remained unknown to Berger (1915: 102) who knew only the synonymous *A. hanburyi* published by Baker (1892) from a plant at Hanbury (Berger 1915: 109–110). Known to all authors including Gentry (1982) only in the vegetative state. The generative parts were first described by García-Mendoza (2011a) who also provides a new record from N Oaxaca. The species is recognizable by its open rosettes with thick, rigid, deltoid to deltoid-lanceolate, olive-green to brownish-green or yellowish-brown leaves. Toothless forms are most common (Gentry 1982, García-Mendoza 2011a). The species is partly similar in habit to *A. kerchovei* (Etter & Kristen 1997+: accessed 2015). It is endemic to the Tehuacán-Cuicatlán valley (Gentry 1982, García-Mendoza 2011a). A specimen from Tlaxcala labelled “*Agave cf. triangularis*” (Patrick s.n., ARIZ, DES)

needs verification. — Giant mesquite bugs (“cocopaches”; *Thasus gigas*) feeding on the inflorescences are collected by hand for family consumption as food (Acuña & al. 2011).

**A. tubulata** Trelease (Mem. Nation. Acad. Sci. 11: 45, tt. 99–100, 1913). **Type:** Cuba (Britton & al. 9746 [MO 2148465 & 2148473, NY]). — **Lit:** Berger (1915: 274); León (1946: 317); Álvarez de Zayas (1985: 7–8, 10, 13–15, with ills.); Álvarez de Zayas (1995: 41); Acevedo-Rodríguez & Strong (2012: 87). **Distr:** W Cuba (Pinar del Río, Artemisa, La Habana); calcareous cliffs and karstic dome hills (mogotes), 750–800 m; flowers in March. **I:** Richter (2010: 41); Richter (2011: 93); Pilbeam (2013: 222, as ssp. *brevituba*); Hochstätter (2015: VII: 93); Acuña (2018: 31, 33, as ssp. *brevituba*). — Fig. 59.

**Incl.** *Agave ekmanii* var. *microdonta* Trelease *in sched.* (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave ekmanii* Trelease (1926); **incl.** *Agave tubulata* ssp. *brevituba* A. Álvarez (1985).

[2q] Acaulescent; **Ros** open, ±1 × 1.5 m, single, not surculose; **L** few, broadly lanceolate, gradually acute or subacuminate, sometimes conduplicate, 60–75 (–90) × 15–20 cm, rather glossy green to greyish-green, margins with green prominences or repand between the teeth; **marginal teeth** prevailingly upcurved towards the leaf tip and recurved towards the base, crescent-shaped rather than lenticular at the base, 1–3 mm, 7–20 mm apart, slender-tipped, intervening

**Fig. 59** *Agave tubulata*  
(Etter & Kristen 4127:  
Cuba; Pinar del Río, ±  
10 km N of Viñales, 130 m).  
(Copyright: J. Etter &  
M. Kristen)



margin nearly straight; **terminal Sp** acicularly conical, somewhat upcurved or flexuous, round-grooved or involute below the middle, smooth, 10–20 × 2 mm, brown, dull, decurrent; **Inf** paniculate, narrow, 2–5 m, part-**Inf** ascending, tripartite, 15–30 cm; **Ped** 4–15 mm, slender; **Fl** 25–35 mm; **Tep** yellow, tube narrowly to openly funnel-shaped, 3–8 mm, lobes 10–12 mm; **Fil** 15–25 mm, inserted nearly in the tube throat; **Anth** 10–13 mm; **Ov** oblong, 15 mm; **Sty** much longer than the filaments; **Sti** capitate; **Fr** broadly oblong, 12–40 × 8–18 mm, beaked, shortly but distinctly stipitate; **Se** 5–6 × 3–5 mm.

The “holotype” at MO consists of 2 sheets with a cross-labelling which does not appear to be original; they are therefore considered to be syntypes (Smith & Figueiredo 2014e: 245). Ssp. *brevituba* differs but very slightly, and since material cited for the new taxon was also mentioned in the protologue by Trelease, it was included in the synonymy in the first edition of this handbook and by Acevedo-Rodríguez & Strong (2012: 87) and Govaerts (2014+: accessed April 2014). For differences from *A. jarucoensis*, see there. *A. tubulata* occurs at least sometimes in regions with a predominance of ophiolitic soils (López Almira 2013) and is classified as “Least Concern” in the Cuban Red List (Berzaín & al. 2005: 49).

**A. turneri** R. H. Webb & J. M. Salazar-Ceseña (Brittonia 63(2): 204–206, ills., 2011). **Type:**

Mexico, Baja California (*Salazar-Ceseña* 3740 [MEXU]). — **Lit:** Webb & Starr (2015: 75–76, with ills.). **Distr:** Mexico (Baja California: Sierra Cucupá & Sierra Mayor); on steep slopes or cliffs or steep colluvial slopes in Sonoran desert scrub, only on granodiorite and tonalite soils, 180–400 m; flowering February to April and August. **I:** Hochstätter (2015: V: 26).

[2j] Acaulescent; **Ros** 0.4–1.2 × 0.8–1.9 m, solitary; **L** 10–40, lanceolate, generally not guttered, smooth to scaberrulose on the upper face, and scabridulous to rough on the lower face, 40–90 × 6–13 cm, widest ± ¼ from the base, grey-green to blue-glaucous green, with prominent imprints from the central bud on both faces, occasionally with darker cross-banding, margins straight, with a 1–2 mm wide purple band, aging to white; **marginal teeth** randomly flexed, easily detached, 5–7 mm, purple-black turning to white with age, on average 15 mm apart; **terminal Sp** proximally channelled above, 50–60 mm, purple-black, decurrent; **Inf** 2–4 m, paniculate, with triangular **Bra** 12–13.5 × 4.5–6 cm, part-**Inf** slightly ascending, 5–10, 20–30 cm, ± capitate, subtended by ± triangular purple bracts, in the upper 50–70 cm of the inflorescence; **Ped** 5–20 mm; **Fl** ± erect, densely crowded, 37.5–56 mm; **Tep** yellow-green to yellow, tube crateriform, 2–5.5 × 7–9 mm, lobes ascending, lanceolate, subequal, apex with tufted hairs and beaked tip, occasionally red, 18–24 × 5–9.5 mm,



inner keeled, outer smooth, both gibbous; **Fil** slender, 29–41 mm, subequally inserted, decurrent on the tube inside; **Ov** fusiform, 15–29 × 3–6.5 mm, light glossy green, neck sulcate, 3–6 × 2.5–6 mm, scarcely constricted; **Sty** 15–49 mm; **Sti** bulbous, rugose, vaguely 3-lobed, cream-coloured; **Fr** oblong, smooth, brown when dry, beaked, 36–45 mm, stipitate; **Se** ± crescent-shaped, flat-convex, compressed, 5–8 mm, black, shiny.

According to the protologue already photographed back in 1905, and with affinities to *A. moranii* and *A. deserti* var. *simplex*. Both these taxa share the strictly solitary habit, but differ esp. in having larger inflorescences. In its semi-compact inflorescences and grey leaves, it resembles *A. azurea* and *A. vizcainoensis* (Sect. *Intermediae*), but the flower characteristics are closer to *A. avellanidens*, *A. gigantensis* and *A. moranii* of Sect. *Conicae* where it is placed by Webb & Starr (2015). *A. turneri* is only known from 8 localities and appears critically endangered due to its restricted occurrence on a specific soil type and increasing aridity (annual rainfall possibly <100 mm), but also threatened because of the proximity to the Mexicali metropolitan area (Webb & Salazar-Ceseña 2011, Webb & Starr 2015).

**A. umbrophila** (García-Mendoza) Thiede (Haseltonia 17: 94, 2012). **Type**: Mexico, Oaxaca (García-Mendoza & al. 8524 [MEXU, ENCB, IEB, K, MO, OAX, UAMIZ]). — **Lit**: García-Mendoza (2011b: with ill., as *Manfreda*). **Distr**: Mexico (Guerrero, Oaxaca); at shaded, humid brooksides, in muddy soils of calcareous origin, in pine-oak or montane cloud forests, 1600–2500 m; flowers June to August. **I**: Hochstätter (2016: I: 44, as *Manfreda*).

≡ *Manfreda umbrophila* García-Mendoza (2011).

[3a1] Plants herbaceous; corm 4–8 (–10) × (1.5–) 2–3.5 cm, cylindrical, bulb (4–) 7–12 × 3–4 cm, ovoid, covered with membranous dry leaf bases; **R** fleshy and thickened, with filiform ramifications, contractile; **L** evergreen, 3–8, large, spreading, spatulate or elliptic, brittle, glabrous

on both faces, tip acute, (25–) 35–45 × (5–) 7–10 cm, narrowed at the base to 0.7–1 cm, dark green with large, greenish-red to reddish dots, glabrous on both faces, margins minutely denticulate on a hyaline band, often wavy; **Inf** erect to slightly curved, (1.2–) 1.4–1.8 m, ‘spicate’, peduncle greenish with purple tinge, with 5–7 (–11) **Bra** that are abruptly much shorter than the leaves, fertile part 7–15 (–20) cm, with (8–) 11–20 solitary lax to slightly congested flowers; floral **Bra** 1 × 0.3 cm; **Fl** 25–30 (–35) mm, sessile, ascending, campanulate or sometimes urceolate, slightly zygomorphic, with a lemon-like scent; **Tep** greenish-glaucous to green-brownish, with purple tinge, tube 6–10 (–12) × 6–10 mm, greenish, lobes oblong, revolute, 10–14 (–17) × 3–6 mm, purple to green-brownish; **Fil** (45–) 70–80 (–85) mm, ± curved downwards at anthesis, by far exceeding the tube, inserted ± at mid-tube all on the same level, purple; **Ov** cylindrical, (5–) 10–13 × 3–5 (–7) mm, greenish-glaucous, constricted at the apex; **Sty** 75–85 (–100) mm, greenish with purple dots; **Sti** 3-lobed, papillose; **Fr** subglobose or ellipsoid, 15–20 (–25) × 15–20 mm, slightly rostrate; **Se** crescent-shaped, 6–7 × 4–5 mm, black, shiny.

According to the protologue morphologically most similar to *A. variegata* (as *Manfreda*) and the unpublished *Manfreda huetamensis* (Castillejos-Cruz 2009). *A. variegata* differs in its much shorter corms and bulbs, linear-lanceolate, light green to glaucous leaves with denticulate margins, peduncular bracts similar to the leaves, and a much larger spike with much more flowers. The unpublished *M. huetamensis* differs in its light green leaves with prominent veins and an easily flaking cuticle, and a much larger spike with more flowers with a longer tube (Castillejos-Cruz 2009).

**A. underwoodii** Trelease (Mem. Nation. Acad. Sci. 11: 37, tt. 67–71, 1913). **Type** [syn]: Cuba (*Trelease* 2 & 3 [MO [4 sheets], B]). — **Lit**: Berger (1915: 212); León (1946); Richter (2010: with ill.); Acevedo-Rodríguez & Strong (2012: 87); Greuter & Rankin Rodríguez (2017: 36). **Distr**: SE Cuba; on rocky hills and hillsides in

coastal and near-coastal xerophytic scrub, and on karstic dome hills (mogotes); flowers February to March. **I:** Delanoy (2002: 30); Heller (2006: 142); Richter (2011: 88, 91); Kattermann (2012: 14); Pilbeam (2013: 223); Hochstätter (2015: VII: 63, 76).

**Incl.** *Agave morrisii* Worsley (1895) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave americana* Millspaugh (1900) (*nom. illeg.*, ICN Art. 53.1).

[2p] Acaulescent; **Ros** to 2 × 2 m, solitary; **L** ± narrowly lanceolate, gradually or in the broader forms acuminate pointed, concave, 100–200 × 20–25 cm, green, margins straight or somewhat concave; **marginal teeth** straight or somewhat curved or occasionally hooked (mostly downwards), rather strongly triangular from lenticular bases, 2–5 mm, brown or chestnut-brown, ±10 (–20 or even 30) mm apart, exceptionally on green prominences; **terminal Sp** triquetrously conical or somewhat subulate, straight or slightly upcurved, openly grooved to or beyond the middle or involute, smooth or a little roughened, 15–25 × 4–6 mm, brown, rather dull, decurrent and somewhat dorsally intruded into the green leaf tissue; **Inf** 4–8 m, paniculate, broad, part-**Inf** on sharply recurved to nearly straight **Br** in the upper ¾ or more of the inflorescence, ±40–50, not known to be bulbiferous; **Ped** slender, 15–20 mm; **Fl** 50–55 mm; **Tep** golden-yellow, tube conical, ±8 mm, lobes 15–20 × 5 mm; **Fil** 30–35 mm, inserted somewhat below the tube throat; **Ov** 25–35 mm; **Fr** narrowly oblong, 40–45 × 15 mm, beaked and stipitate; **Se** 5–6 × 3–4 mm.

According to the protologue rather variable (colour of terminal spine and marginal teeth, shape of the groove of the terminal spine, length of the tepal lobes, degree of exertion of the filaments). May form natural hybrids with *A. albescens* (Richter 2010: 41).

**A. undulata** Klotzsch (Allg. Gartenzeitung 8: 274, 1840). **Type:** Cult. BG Berlin (*Anonymous* 3 [B]). — **Lit:** Jacobi (1865: 560); Jacobi (1871: 89–90); Baker (1877b: 808); Rose (1903c: as *Manfreda*); Berger (1915: 37); Verhoek-Williams (1975: 310–312, as *Manfreda*). **Distr:** Known from cultivation only.

≡ *Manfreda undulata* (Klotzsch) Rose (1903); **incl.** *Agave undulata* var. *strictior* Jacobi & C. D. Bouché (1865); **incl.** *Agave drimiifolia* Hort. Petropol. ex Baker (1877) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Agave undulata* [?] *glauca* Hort. Richter (2007) (*nom. illeg.*, ICN Art. 36.1c).

[3a3] Herbaceous; rhizome (corm and bulb) short, thick, covered with dry membranous whitish leaf bases, **L** linear-lanceolate, strongly revolute, flaccid, flat, wavy, acuminate, markedly conduplicate, below with a prominent unarmed mid-rib, scabrous, 15.2–20.3 × 3.18 cm, glaucous dull green, at the base reddish on the lower face, margins minutely toothed, tip a round, convolute point, apex terete, margins entire, narrowly whitish-horny or somewhat reddish, decurrent along the leaf below the apex; **Inf** ±1.2 m, ‘spicate’, dense, tall, bracteate, glaucous; **Ped** short, thick; **Fl** ±40 mm, solitary, curved downwards; **Tep** 30 mm, tube shallowly funnel-shaped, 6-furrowed, 11 × 4 mm, light green, pruinose, with small black dots, lobes lanceolate, erect after anthesis, outer 17 × 4 mm, dorsally convex, with slightly involute margins, 7-veined, papillate, dark reddish-brown, pruinose, tip cucullate, yellowish-brown, inner somewhat broader, keeled; **St** widely exerted; **Fil** subulate, 35 mm, inserted all at the same level, green, densely dotted with reddish-brown, tip light green; **Anth** 11 mm, brownish-green; **Ov** oblong-ovate, inconspicuously 6-angled, 11 × 6 mm, pruinose-green, prolonged into the tube; **Sty** erect, robust, reddish-brown with greenish dots; **Sti** capitate, 3-lobate, papillate; **Fr** and **Se** not known.

An uncertain species, only known from the type specimen at Berlin upon which Klotzsch based his rather brief description. A plant labelled *A. undulata* flowered at the BG Berlin in 1869, from which Jacobi (1871) added, from memory, the description of its flowers. All descriptions from Jacobi to Berger indicate similarities with *A. guttata* (Verhoek-Williams 1975: 311). The erose leaf margins of the type specimen and the undulate leaves with minutely toothed margins of the protologue point towards *A. guttata* or *A. debilis*, but it cannot be assigned with confidence to either, and thus remains of uncertain

**Fig. 60** *Agave utahensis* ssp. *kaibabensis* (Etter & Kristen 295: USA; Arizona, Coconino County, Grand Canyon East Rim Drive, 2280 m). (Copyright: J. Etter & M. Kristen)



application (Verhoek-Williams 1975: 312; as *Manfreda guttata* and *M. pringlei*).

Cultivated plants labelled as “*Manfreda undulata*” have narrow, conduplicate green leaves without dots and slightly wavy erose margins (Richter 2007: 43–44, with ill.), and merit further study. *Manfreda undulata* ‘Chocolate Chips’, ‘Mint Chocolate Chip’ and ‘Cherry Chocolate Chip’, all refer to cultivars with conduplicate leaves with strongly wavy margins and large purplish to reddish dots, and are therefore misplaced in *M. undulata*, which has plain green leaves; they might represent selections or hybrids of *A. maculosa*, *A. guttata* or *A. variegata* (all Subgen. *Manfreda*).

**A. utahensis** Engelmann (in S. Watson, Bot. US Geol. Expl. 40. Parallel 5: 497, 1871). **Type** [lecto]: USA, Utah (*Palmer* s.n. [MO, US]). — **Lit**: Gentry (1982: 257–262, with ills.); Reveal & Hodgson (2002); Janeba (2010: ill. synopsis). **Distr**: USA (California, Utah, Nevada, Arizona).

≡ *Agave haynaldii* var. *utahensis* (Engelmann) A. Terracciano (1885) (*incorrect name*, ICN Art. 11.4, 25.1).

Plants from N and/or high altitude populations of ssp. *utahensis*, ssp. *kaibabensis* and var. *eborispina* may tolerate temperatures down to  $-21\text{ }^{\circ}\text{C}$  to  $-29\text{ }^{\circ}\text{C}$  and may survive outdoors in C Europe nearly without rain protection (Boeuf 2007: 134).

**A. utahensis** ssp. *kaibabensis* (McKelvey) Gentry (Agaves Cont. North Amer., 259, ill. (p. 260), 1982). **Type**: USA, Arizona (McKelvey 4381 [A]). — **Lit**: Breitung (1960: 21–22); Reveal (1977: 537–538); both with ills., as var.; Gentry (1982: 259–260, with ills.); Hodgson (1999a: 11); Reveal & Hodgson (2002); Janeba (2010: 14–17, with ills.); Starr (2012: 274, 276, 279). **Distr**: USA (N Arizona); calcareous or sandstone outcrops in desert scrub, pinyon-juniper, or conifer woodlands, 700–2500 m; flowers May to July and December. **I**: Heller (2006: 143); Pilbeam (2013: 225); Hochstätter (2015: IX: 17, as *A. utahensis*). — Fig. 60.

≡ *Agave kaibabensis* McKelvey (1949) ≡ *Agave utahensis* var. *kaibabensis* (McKelvey) Breitung (1960).

[1h] Differs from ssp. *utahensis*: **Ros** solitary or sparingly caespitose, larger, (20–) 30–60 × 40–100 cm; **L** larger, lanceolate, (25–) 27–50 × 3–5.5 cm; **marginal teeth** shorter, (2–) 3–5 mm, more distant, 20–40 mm apart; **terminal Sp** shorter, stout, subulate, 20–40 mm; **Inf** larger, 3.5–5 m, narrowly paniculate, longer part-**Inf** (1–) 4–10 cm long, with 4–12 flowers; **Fl** larger, (26–) 29–43 mm; **Ov** larger, 15–29 mm. — **Cytology**: n = 30 (Baker & al. 2009: as var.).

Distributed along the N Grand Canyon rim. Habitat temperatures may drop down to  $-18\text{ }^{\circ}\text{C}$ .

**A. utahensis** ssp. *utahensis* — **Lit**: Breitung (1960: 21–22, with ills.); Reveal (1977: 537–538,

with illis.); Gentry (1982: 257–260, with illis.); Hodgson (1999a: 10–11); Reveal & Hodgson (2002); Janeba (2010: 9–13, with illis.); Starr (2012: 274–279); Parker (2017: 262, 264–265, with illis.). **Distr:** USA (SE California, SW Nevada, S Utah, NW Arizona); calcareous outcrops with desert scrub, 600–1400 m; flowers late winter to early summer. **I:** Heller (2006: 143); Janeba (2008: 302, as *A. utahensis*); Richter (2011: 126); Pilbeam (2013: 224); Hochstätter (2015: IX: 16, as *A. utahensis*).

≡ *Agave utahensis* var. *utahensis*; **incl.** *Agave newberryi* Engelmann (1875); **incl.** *Agave scaphoidea* Greenman & Roush (1929) ≡ *Agave utahensis* var. *scaphoidea* (Greenman & Roush) M. E. Jones (1930); **incl.** *Agave utahensis* var. *discreta* M. E. Jones (1930); **incl.** *Agave utahensis* fa. *nuda* hort. ex E. & B. Lamb (1978) (*nom. inval.*, ICN Art. 39.1).

[1h] Acaulescent; **Ros** rather compact, 15–30 × (15–)25–40 cm Ø, caespitose; **L** 70–80, linear-lanceolate, stiff, straight or falcate or upcurving, convex below, flat to concave above, mostly (12–)15–30 × 1.5–3 cm, light greyish- to yellow-green, in dwarf forms also bluish-grey-glaucous; **marginal teeth** blunt, thick, detachable, larger teeth mostly 2–4 (–15) mm, brown-ringed around the bases, light grey, 10–25 mm apart; **terminal Sp** acicular, openly grooved above, 20–40 mm (to 200 mm in extreme forms), light grey or ivory-white, decurrent for 1–3 cm; **Inf** 1.7–4 m, ‘spicate’, racemose, or narrowly racemose-paniculate (then with short lateral branches 0.5–5 cm long), peduncle with caducous narrowly triangular **Bra** 4–8 cm long, fertile part lax or congested, part-**Inf** with 2–8 clustered flowers; **Ped** very short; **Fl** urceolate, 23–32 mm; **Tep** yellow, tube broadly funnel-shaped, bulging at the lobe bases, very short, 2.5–4 × 9–12 mm, lobes connivent around the filaments, persisting erect, nearly equal, 9–12 mm, outer thin, deeply concave and overlapping the inner, these strongly keeled; **Fil** 18–20 mm, inserted near the tube bottom; **Anth** small, 9–12 mm; **Ov** 12–22 mm, neck 4–6 mm, constricted; **Fr** ovoid to oblong, 10–25 × 10–12 mm, shortly beaked; **Se** crescent-shaped, thick, variable in size, 2–4 × 3–4 mm, dull or shiny black, hilar notch usually conspicuous. — **Cytology:** 2n = 60,

120 (Granick 1944 (identity uncertain), Zonneveld 2003, Simpson & al. 2011).

Ssp. *utahensis* differs from ssp. *kaibabensis* esp. in its smaller rosettes, narrower leaves and smaller flowers (Reveal & Hodgson 2002). The localities in S Utah are the second-most N *Agave* localities (only *A. virginica* of Subgen. *Manfreda* extends further N-wards).

**A. utahensis** var. **eborispina** (Hester) Breitung (Cact. Succ. J. (US) 32: 22, 1960). **Type:** USA, Nevada (Hester s.n. [CAS, G, NY, US [8 sheets]]). — **Lit:** Hester (1943: with illis.); Breitung (1960: 22–23, with illis.); Gentry (1982: 262); Reveal & Hodgson (2002); Janeba (2010: 18–21, with illis.); Starr (2012: 274–279, with illis.). **Distr:** USA (SE California, S Nevada); calcareous outcrops with desert scrub, 1100–1900 m; flowers May to July. **I:** Heller (2006: 144); Janeba (2008: 300–301, as *A. eborispina*); Pilbeam (2013: 227); Hochstätter (2015: IX: 16, as ssp.).

≡ *Agave eborispina* Hester (1943) ≡ *Agave utahensis* ssp. *eborispina* (Hester) Hochstätter (2015).

[1h] Differs from var. *utahensis*: **marginal teeth** larger, 6–12 (–15) mm; **terminal Sp** ivory-white, stout, very long, 100–200 mm.

A montane endemic in the S Mohave Desert (Gentry 1982). Specimens with esp. long terminal spines are highly attractive. The protologue illustrates rare part-inflorescences to 10 cm long and with up to 14 flowers. See also the comment for var. *nevadensis*.

**A. utahensis** var. **nevadensis** Engelmann ex Greenman & Roush (Ann. Missouri Bot. Gard. 16: 390, 1929). **Type:** USA, California (*Parish* 414 [MO, CAS]). — **Lit:** Hester (1943: with illis.); Breitung (1960: 22–23, with illis.); Gentry (1982: 261); Reveal & Hodgson (2002); Janeba (2010: 22–24, with illis.); Starr (2012: 273–276, 279, with illis.). **Distr:** USA (SE California, S Nevada); calcareous outcrops with desert scrub, 1200–1900 m; flowers May to July. **I:** Irish & Irish (2000: t. 46); Heller (2006: 144); Janeba (2008: 299, as *A. nevadensis*); Pilbeam (2013: 227).

≡ *Agave nevadensis* (Engelmann ex Greenman & Roush) Hester (1943) ≡ *Agave utahensis* ssp.



*nevadensis* (Engelmann *ex* Greenman & Roush) Hochstätter (2015).

[1h] Differs from var. *utahensis*: **marginal teeth** longer, 4–6 mm; **terminal Sp** slender, longer, 40–80 mm, brown to whitish. — **Cytology**:  $2n = 60$  (Reveal & Hodgson 2002, Zonneveld 2003).

A montane endemic in the S Mohave Desert (Gentry 1982). *A. utahensis* var. *nevadensis* and var. *eborisipina*, both accepted by Gentry (1982), were included in the synonymy of ssp. *utahensis* by Little (1981) and McKinney (1993). Gentry (1982: 261) mentions ‘transitional forms’, but since typical plants of both taxa are clearly distinct and are largely geographically separated, they are upheld here at varietal level under ssp. *utahensis* following Reveal & Hodgson (2002).

**A. valenciana** Cházaro & A. Vázquez (Novon 15(4): 525–527, ills., 2005). **Type**: Mexico, Jalisco (*Vargas-Rodríguez & al.* 436 [IEB, ENCB, GUADA, IBUG, MEXU, MO, WIS, XAL]). — **Lit**: Cházaro Basáñez & al. (2005b: with ills.); Cházaro Basáñez & al. (2006b: with ills.); Vázquez-García & al. (2007b: 74–77, t. II); Cházaro Basáñez & al. (2008a: with ills.). **Distr**: Mexico (W Jalisco); steep slopes of basaltic rock in canyons, 900–1250 m, in the ecotone of tropical deciduous forests with oak forests; flowers March to May. **I**: Richter (2011: 57); Etter & Kristen (2012: 89–90); Pilbeam (2013: 228); Hochstätter (2015: VI: 1, 24); Moore (2016: 239).

[2n] Stems short; **Ros** 1.7–2.2 × 2.7–3.3 (–4.1) m, solitary, not suckering; **L** 7–15, broadly lanceolate, ± straight or variously curved, thick, firmly concave, smooth on both faces, 150–230 × 37–46 (–53) (at mid-leaf) cm, up to 30 cm wide and up to 15 cm thick at the base, dark green, slightly glaucous, cross-banded on both faces, margins frequently repand, distinctly crenate in the middle to closely dentate at the ends, with prominences 4–6 × 5–19 mm; **marginal teeth** flattened, mostly straight, some curved towards the base, mostly 2–5 (–7) mm, 5–17 (–22) mm apart, dark brown to red-brown, tips from very broad bases 5–9 (–12) mm, intermittent teeth few or none; **terminal Sp** usually short and conical, robust, 10–15 (–20) mm, dark to red-brown, rarely shortly

decurrent; **Inf** 5–6 (–7) m, paniculate, peduncle very thick, 12–35 cm Ø at the base, with scarious triangular **Bra** variable in size, ±15 cm apart, fertile part with 25–40 part-**Inf**, straight, diffuse, flat-topped, in the upper ½ of the inflorescence; **Ped** 5–10 mm; **Fl** 50–60 (–70) mm; **Tep** brilliant yellow, tube somewhat funnel-shaped, 5–7 × 10 mm, lobes linear, fleshy, erect, 10–13 × 4–5 mm, yellow, apex galeate; **Fil** slender, 34–38 mm, yellow, inserted 2–4 mm above the tube base; **Ov** proper 18–27 × 4–5 mm, light green, neck 3–5 mm, strongly constricted; **Sty** finally longer than the filaments; **Sti** capitate; **Fr** oblong, 23–29 × 10–13 mm, slenderly stipitate, beak short; **Se** triangular, but curved to one side, flat, membranous, 3–4.5 × 2–3 mm, black.

A “gigantic” species placed in Sect. *Marmoratae*, with which it shares most of its distinctive characteristics, except the much larger size. It may be closest to *A. marmorata*, which shares a robust habit, leaves much wider in the middle than towards the tip, cross-banded on both faces, and marginal teeth >15 mm apart, but differs from the latter in its much larger size with fewer but longer and wider leaves, and smaller spines, teeth, and fruits. The authors consider *A. valenciana* to possibly have potential for the production of “raicilla” (an alcoholic tequila-like beverage), and mature “heads” (stems) of the species weigh > 350 kg, which is at least 3 × heavier than for *A. tequilana*. Magaña-González & al. (2007) found 3 species of hummingbirds and 3 perching birds as diurnal and 4 bats (3 nectarivorous, 1 insectivorous) as nocturnal flower visitors and argue that the hummingbirds are the main pollinators.

**A. variegata** Jacobi (Hamburg. Gart.- & Blumenzeit. 21: 459–462, 1865). **Type**: not typified. — **Lit**: Rose (1903c: 20–21); Small (1903: 288); Berger (1915: 34–35, with ills.); Verhoek-Williams (1975: 192–205); Piña Luján (1985: 61–62); Reveal & Hodgson (2002); Castillejos-Cruz (2009: [294]–[299], with ills.); all as *Manfreda* except Berger. **Distr**: USA (S Texas), Mexico (Nuevo León, Tamaulipas, E San Luis Potosí, N Hidalgo, C Veracruz, Puebla); dry chaparral sites, on slopes, or between rocks, and in moist oak, thorn and tropical deciduous and (semi-)



evergreen rain forests and desert scrub, 10–2000 m; flowers February to June. **I:** Refug. Bot. t. 326, 1872; Addisonia 17: t. 569, 1932; Rodríguez & Castro-Castro (2007: 7, 9); Richardson & King (2011: 19); Hochstätter (2016: I: 45); the last 4 as *Manfreda*.

≡ *Manfreda variegata* (Jacobi) Rose (1903)  
 ≡ *Polianthes variegata* (Jacobi) Shinnery (1966);  
**incl.** *Manfreda tamazunchalensis* Matuda (1966);  
**incl.** *Manfreda xilitlensis* Matuda (1966).

[3a1] Herbaceous; corm 3–6.2 (–7) × 2–3 cm, subglobose to subcylindrical, bulb (1–) 1.5–3.5 × 3–3.2 cm, subcylindrical to ovoid, apically covered with dried membranous leaf bases 6–8 cm long; **R** fleshy and thickened, with filiform ramifications, contractile; **L** drought-deciduous, 6–8 (–16), spreading to slightly ascending, lanceolate to linear-lanceolate, long-attenuate towards the apex, succulent, canaliculate, somewhat wavy, glabrous on both faces, apex acute, soft, 15–45 × 2.2–3.5 cm, light green to glaucous, with many dark green or purple round to oval dots to 1 × 0.5 cm, margins conspicuously denticulate on a cartilaginous hyaline band, denticles of various sizes, irregularly spaced, some retrorse; **Inf** 50–110 (–170) cm, erect, green-glaucous, ‘spicate’, peduncle robust, **Bra** 10–13, base truncate, lower ones similar to the leaves, decreasing in size abruptly in the fertile part, fertile part 15–20 (–30) cm, lax, with 7–40 flowers; floral **Bra** 0.6–1 × 0.4–0.6 cm; **Fl** 25–35 mm, solitary, sessile, ascending to spreading; **Tep** green-glaucous on the outer face, reddish-green to brown on the inner face, perianth as a whole broadly funnel-shaped to campanulate, tube 7–11 × 6–9 mm, constricted near the apex of the ovary, lobes oblong, reflexed to revolute, keeled on the outer face, (7–) 10–13 (–16) mm, tip slightly broadened to acute, with a bundle of short white trichomes; **Fil** 35–70 (–90) mm, ± spreading at anthesis, exceeding the tube for 30–65 (–85) mm, inserted 2–3 mm below the mouth of the tube all on the same level, greenish-red, with multiple purple dots all over the surface; **Anth** 8–12 mm, reddish to brownish; **Ov** ellipsoid to slightly obclavate, (9–) 12–15 × 4–5 mm, greenish, constricted above for ±3 mm; **Sty** 44–66 (–95) mm, elongating during anthesis, reaching the level of the anthers,

green or mahogany-brown; **Sti** capitate, 3-lobed, papillate; **Fr** cylindrical to subellipsoid, 17–26 × 13–18 mm, apiculate for 2 mm, tepals persisting; **Se** deltoid, plane-concave, 4–6 × 4 mm, dull.

Notable within Sect. *Herbaceae* for its succulent, minutely toothed and often spotted leaves, its tall inflorescence stalks, and flowers with short campanulate tubes and long-exserted stamens and styles (Verhoek-Williams 1975: 194). *A. variegata* is close to *A. sileri*, which was first treated as a variety of it (Verhoek-Williams 1975: 205), and morphologically similar to the recently published *A. umbrophila* (see there). The species is cultivated as ornamental in Yucatán (Castillejos-Cruz 2009), but previous records of the species from Yucatán may also relate to either *A. petskinil* or *A. paniculata* (see there). In Texas used against snakebites (Piña Luján 1985, Castillejos-Cruz 2009). Plants from the Cañon del Sumidero (Chiapas) referred here (Espinosa-Jimenez & al. 2011: 46) may be misidentified or represent a new record. ‘Macho Mocha’ is a hybrid with *A. mitis* (as *A. celsii*; Klein (2010), as ×*Mangave*).

**A. vazquezgarciae** Cházaro & J. A. Lomeli (Novon 16: 459–460, ills., 2006). **Type:** Mexico, Jalisco (*Cházaro-Basáñez & Vázquez-García* 8172 [IBUG, GUADA, IEB, MEXU, MO, WIS, XAL, ZEA]). — **Lit:** Hernández-Vera & al. (2007a); Cházaro Basáñez & al. (2008a: with ills.); Cuevas Guzmán & al. (2012). **Dist:** Mexico (W Jalisco: N slopes of the Sierra de Manantlán and adjacent mountain chains, N Colima); on cliffs and slopes, in pine-oak forests mixed with mesophytic elements (ecotone to cloud forests), 1550–2100 m; flowers November to February. **I:** Richter (2011: 57); Etter & Kristen (2012: 88–89); Pilbeam (2013: 229); Hochstätter (2015: VIII: 26).

[1b] Acaulescent; **Ros** open, symmetrical, (0.9–) 1.7–1.8 × (0.6–) 1–1.2 m, solitary; **L** 70–80, lanceolate or narrowly elliptic, indurate, base gradually narrowed, acuminate, with a sigmoid shape 8–9 cm below the apex, 40–91 × 9.5–16.8 cm, pale green to glaucous, margins straight; **marginal teeth** 0.5–3 × 3.5–4 (at the base) mm, brown, 2 teeth per cm; **terminal Sp** subulate, stout, 40–65 mm, reddish to dark brown or

blackened; **Inf** erect, 5–7 m, ‘spicate’, peduncle with linear coriaceous **Bra** 4.4–10.5 × 0.2 (at the base) cm, fertile part in the upper  $\frac{2}{3}$  of the inflorescence, 25–30 cm Ø; **Ped** 5–14 mm; **Fl** geminate, 52–94 mm; **Tep** greenish-yellow, tube funnel-shaped, 6–10 × 3–6 mm, lobes erect or ascending, 16–22 × 5–6 mm; **Fil** 40–72 mm, inserted at the tube apex; **Ov** 13–27 × 5–7 mm, neck slightly constricted; **Sty** 49–77 mm, equal to or longer than the stamens; **Fr** geminate or towards the inflorescence tip solitary by abortion, oblong-obovoid, 18–24 × 10–13 mm, pale brown, slightly apiculate; **Se** crescent-shaped, 3–4 × 2–3 mm.

Placed in Sect. *Inermes* (as Group *Amolae*) in the protologue due to its densely flowered ‘spike’, ascending to partly outcurving tepal lobes, and the shallow tepal tube much shorter than the lobes. It is closely related to *A. attenuata* ssp. *dentata* with which it shares the acaulescent habit and shallow tepal tube, and the repeated flowering with so-called “lateral” inflorescences which are actually likely terminal on rudimentary rosettes. Some of the material now assigned to *A. vazquezgarciae* was previously referred to *A. attenuata* ssp. *dentata* (as *A. pedunculifera*) by Gentry (1982), McVaugh (1989) and Vázquez-García & al. (1995). According to the protologue, its vernacular names are “cola de zorra” or “lechuguilla”. Fried flower buds are eaten as “bayusas” (Etter & Kristen 2012: fig. 20). Padilla Velarde & al. (2008: 68) provide a new record for N-most Colima.

**A. venustuliflora** (E. Solano & al.) Thiede & Gideon F. Smith (Bradleya 37: 263, 2019). **Type:** Mexico, Michoacán (*Solano & Ríos Gómez* 1793 [MEXU, CHAPA, FEZA, IEB, MO, UAMIZ]). — **Distr:** Mexico (N Michoacán); in disturbed pastures, farmlands or their margins, and in desert scrub, 1785–2080 m; flowers July to August; only known from 2 localities.

≡ *Polianthes venustuliflora* E. Solano & al. (2019).

[3b1] Herbaceous; corm 1.4–3 × 0.7–1.2 cm, oblong, bulb 2–4 × 1–2 cm, ovoid, covered with dried fibrous leaf bases; **R** fleshy, thickened, contractile; **L** drought-deciduous, 3–7 (–9), ±

ascending, linear, glabrous, apex acute, 12–35 (–40) × 0.2–0.4 cm, green, usually with purple dots at the base, margins papillose to regularly denticulate; **Inf** 24–65 (–68) cm, erect, ‘spicate’, greenish, peduncle with ±3 **Bra**, lowest 7–22 cm, bracts and internodes decreasing in size distally, fertile part ±2.5 cm, lax, with 3–7 remote floral nodes; floral **Bra** ovate, apex long acuminate; **Ped** none; **Fl** geminate, fragrant, 19–28 mm, ascending to diffuse; **Tep** white, pink after anthesis, the base ascending, forming a tube curved ± in the middle, narrowly infundibuliform, distal portion campanulate, tube ±15–24 × 2–4 mm at the base of the lobes, mouth irregular, lobes equal, elliptic or oblong, recurved, 4–7 × 1.5–3 mm, apex rounded or obtuse, with a bundle of inconspicuous white trichomes; **Fil** filiform, 1–3 (–7) mm, included, inserted 10 mm above the base of the tube, white; **Anth** oblong, 4–6 mm, slightly surpassing the tube; **Ov** ±5 × 2 mm; **Sty** filiform, 15–27 mm, included; **Sti** 3-lobed; **Fr** semiglobose, 11–18 × 6–10 mm, tepals persisting; **Se** semicircular, flat, 3.5–4 × 2.5–3 mm, shiny.

According to the protologue related morphologically to *A. rosei* (as *Polianthes montana*) and *A. platyphylla* (as *Polianthes*), but differing from the former esp. in having more and narrower leaves, with shorter inflorescences and ascending to diffuse flowers with smaller, reflexed lobes and shorter filaments, and larger fruits, and from the latter in its longer and narrower leaves with papillose to denticulate margins, inflorescences with fewer floral nodes, flowers with larger lobes, and longer styles. The inflorescences are locally sold on markets for ornamental and ceremonial purposes. — Classified in the IUCN Red List Category “Critically Endangered”. For the ecological niche modeling, see Solano & Feria (2007).

**A. verdensis** W. C. Hodgson & Salywon (Brittonia 65(1): 6–9, ills., 2013). **Type:** USA, Arizona (*Hodgson & Salywon* 25495 [DES, ASC, ASU, MO, NY]). — **Lit:** Parker (2018a: 22, 26, with ills.). **Distr:** USA (C Arizona); on rocky, limestone, sandstone or clayey-loamy igneous derived soils, in semi-arid desert grassland to

pinyon-juniper woodland, 1050–1350 m; flowers late June to mid-July. **I:** Hochstätter (2015: III: 8); Parker (2018b: 105).

[2h] **Ros** 50–60 × 50–60 cm, open, freely offsetting via rhizomes, forming clones of few to many rosettes; **L** numerous, short-lanceolate to short-oblongate, erect-spreading, firm, acuminate, guttered, broadest at, just below, or just above the middle, 28–42 (–47) × 5.5–10 (–13) cm, glaucous-grey, tinged with maroon distally; **marginal teeth** strongly deflexed, occasionally porrect, recurved, or upturned, esp. along the distal 1/3 of the leaf, firmly attached, grey, brown, dark mahogany to brown-black, closely set, intermittent teeth (0–) 2–8 along the distal 2/3 of the leaf; **terminal Sp** 18–34 mm, grey to dark grey-mahogany-brown, decurrent; **Inf** 4.5–6 m, narrowly paniculate, peduncle maroon-green-glaucous, part-**Inf** 17–20, horizontally spreading to ascending, 13.5–17 cm, maroon-glaucous to purplish, in the upper 2/3 of the inflorescence, with 15–49 flowers; **Fl** 42–57 mm, with a sweet-musky fragrance at anthesis; **Tep** tube thick, bulging at the base of the tepal lobes, 13–15 × 12–15 mm, light green to cream, lobes persistently erect, leathery with age, slightly unequal to subequal; **OTep** 7.8–11.5 mm, light cream-light yellow, with conspicuous brown papillose cucullate tips; **ITep** 7–10.2 mm, light cream with less cucullate and lighter tip, strongly keeled, with white ciliate hairs within the tips; **Fil** 31–49 mm, (light green-) cream to cream-yellow, subequally inserted 5.7–8.7 mm above the tube base; **Ov** 18–28 × 4–7.5 (–10) mm, light green, neck 4.5–7 mm, light green-cream; **Sty** 32–47 mm, longer than the tepals, (light green) cream-yellow; **Sti** capitate; **Fr** only produced on the uppermost part-inflorescences, linear-oblong to obovoid, (26–) 32–39 × 14–22 mm, with short beak, stipe 1–4.5 mm; **Se** only few viable per fruit, crescent-shaped, rugose, 6.5 × 5 mm, dull black, with narrow marginal wing. — **Cytology:** 2n = 60 (protologue).

According to the protologue, the species represents a pre-Columbian cultivar showing affinities with *A. chrysantha*, *A. shrevei* and *A. delamateri*, the latter representing another such cultivar.

Leaf shape and colour of *A. verdensis* suggests a small *A. delamateri*, which is difficult to distinguish as a young plant, but the latter differs in rosette and flower characters and ploidy level, and both also hybridize (Parker 2018a: 26). According to the protologue, *A. verdensis* occurs sympatrically with *A. delamateri*, *A. phillipsiana*, *A. parryi* and *A. chrysantha* and may represent a specialized, regionally domesticated plant developed by prehistoric Verde Valley farmers.

**A. verhoekiae** (García-Mendoza) Thiede (Haseltonia 17: 94, 2012). **Type:** Mexico, Oaxaca (García-Mendoza & Mérida 2551 [MEXU]). — **Lit:** García-Mendoza (2011a: 79–82); García-Mendoza (2011b: 754–756); both with ill., as *Manfreda*. **Distr:** Mexico (Oaxaca, C Veracruz); open spots in pine-oak forests and desert scrub, 2200–2400 m; flowers July to September. **I:** Hochstätter (2016: I: 46, as *Manfreda*).

≡ *Manfreda verhoekiae* García-Mendoza (2011).

[3a3] Herbaceous; corm 9–25 × 2–3 cm, cylindrical, bulb 7–12 × 4–6 cm, cylindrical, covered with fibrous dry leaf bases; **R** fleshy and thickened, contractile; **L** drought-deciduous, 4–6, erect or diffuse, linear-lanceolate, narrowing at the base, semisucculent, cartilaginous, leaf veins on the upper part of the lower face papillate, tip acute, (30–) 40–55 × 2.5–4 cm, glaucous or green-yellowish, margins minutely denticulate on a hyaline band, with papillae between the denticles; **Inf** (1.5–) 2–2.5 m, erect, ‘spicate’, peduncle greenish, with 7–10 **Bra**, the lower ones similar to the leaves, the upper deltoid, fertile part with 12–20 solitary densely arranged flowers in the uppermost 6–9 cm of the inflorescence; floral **Bra** 0.5–1 × 0.2–0.5 cm; **Fl** 30–35 mm, sessile, ascending; **Tep** greenish or green-yellowish, sometimes with purple tinge, forming a tube 13–16 × 9–10 mm, yellowish-green, lobes oblong, revolute, 7–10 × 2–4 mm; **Fil** 30–38 mm, erect or ± spreading at anthesis, exceeding the tube by far, inserted at mid-tube all on the same level, yellowish-green with purple dots; **Ov** cylindrical, 8–10 × 2–3 mm, glaucous, not constricted, apex prolonged into the tepal tube; **Sty** 50–60 mm, surpassing the filaments; **Sti** 3-lobed; **Fr** ellipsoid to oblong, 20–25 × 13–15 mm, tepals persisting;

**Se** crescent-shaped, plane-concave, 4–5 × 4–5 mm, black.

According to the protologue, the species belongs to Ser. *Guttatae* of Sect. *Herbaceae* (as *Manfreda guttata*-Group) and is morphologically most similar to *A. debilis*, which differs in much shorter corms, narrower, linear-lanceolate, dark brown and glabrous leaves without prominent veins, a shorter inflorescence with green-yellowish to purple flowers, and its stoloniferous growth. Rivera-Hernández & al. (2019, as *Manfreda*) provide a new record from C Veracruz.

**A. vicina** Trelease (Mem. Nation. Acad. Sci. 11: 19, tt. 4, 10, 1913). **Type** [syn]: Aruba (*Boldingh* 3&5 [MO]). — **Lit**: Boldingh (1913: 150–151); Boldingh (1914: 18); Hummelinck (1936: 231–236, 247–248, tt. 1–2, as *A. vivipara*); Hummelinck (1938: 16–19, tt. 2–3, as *A. vivipara*); Hummelinck (1993: 6–10, 219, 223, with ills., as *A. vivipara*); **Dist**: Leeward Antilles (Aruba, Bonaire, Curaçao); coral rocks and debris of it, limestone and igneous rocky hillsides, to 350 m; flowers March to May. **I**: Richter (2011: 97); Pilbeam (2013: 230); Thomson (2014: 176–177); Hochstätter (2016: VII: 49).

**Incl.** *Agave vivipara* var. *cabaiensis* Hummelinck (1936); **incl.** *Agave vivipara* var. *cuebensis* Hummelinck (1936).

[2u] Nearly acaulescent; **Ros** ±1–1.2 m Ø, suckering; **L** very broadly lanceolate, sub-acuminate, flatly concave, (17–) 40–80 (–100) × (5–) 12–20 cm, somewhat transiently glaucous, with age rather glossy green, margins a little concave between the teeth; **marginal teeth** commonly upcurved in the upper ½ of the lamina and recurved in the lower ½, slender from crescent-shaped bases, (2–) 4–8 (–12) mm, (4–) 10–20 mm apart, often on green prominences; **terminal Sp** triquetrously acicular, somewhat flexuous, narrowly round-grooved to the middle and involute below, smooth, polished towards the tip, (12–) 15–25 (–36) × 2–6 mm, red-brown, shortly decurrent; **Inf** (2–) 2.5–4 (–6) m, paniculate, narrowly oblong, with broadly triangular imbricate **Bra**, fertile part with part-**Inf** on ascending branches in the upper ½–½ of the inflorescence, freely bulbiferous; **Ped** 3–8 mm; **Fl**

40–60 mm; **Tep** yellow, tube open, 3–6.5 mm, greenish-yellow, lobes 12–22 × 4–6 mm; **Fil** 23–37 mm, greenish-yellow, inserted 1 mm above to 1 mm below the tube throat; **Anth** 12–21 mm, yellow; **Ov** oblong, (20–) 23–27 (–37) × 6.5–7 mm, yellowish-green; **Sty** 38–48 mm; **Fr** broadly oblong, 25–45 × 14–19 mm, usually slightly stipitate, slightly or not beaked; **Se** unknown.

Hummelinck (1936) wrongly used the name *A. vivipara* L., the earliest name for a Caribbean species in the genus, for this plant. According to Wijnands (1983: 35), *A. vivipara* represents the oldest name for the widespread continental taxon previously referred to as *A. angustifolia*, and this view was followed in the first edition of this handbook. However, García-Mendoza & Chiang (2003) showed that *A. angustifolia* and *A. vivipara* are two distinct species and re-established the former in the sense used by Gentry (1982), and the latter for the Caribbean species previously known under that name. *A. vicina* is the oldest available binomial that clearly refers to the Caribbean plants in question here. See also the note for *A. cocui*.

According to Hummelinck (1936: 243), only one (*Boldingh* 3) of the two syntypes cited in the protologue belongs here (and the other, *Boldingh* 5, is probably *A. ruteniae*). The varieties that Hummelinck published 1936 were later synonymized with the species as mere “extreme forms in the range of variability” by Hummelinck (1938: 17). Plants from Isla Margarita (Venezuela) placed here need verification as to their identity (Hummelinck 1993: 10).

**A. victoriae-reginae** T. Moore (Gard. Chron., ser. nov. 4(94): 484–485, fig. 101, 1875). **Type**: [lecto — icono] l.c. fig. 101. — **Lit**: Gentry (1982: 183–185); Ullrich (1991g); García-Mendoza (2003); Aalsemgeest & al. (2007a); González-Elizondo & al. (2011); Martínez-Palacios & Eguiarte (2011); Thiede (2011); Roosbroeck (2012); Starr (2012: 280–285); all with ills. except García-Mendoza (ill. is of *A. nickelsiae*). **Dist**: Mexico (S Coahuila, NW & W-C Nuevo León, NE Durango). **I**: Ettl (2014: 121); Hochstätter (2015: IX: 52, 53, 56, 57); Walker (2017).

**Incl.** *Agave victoriae-reginae* var. *candida* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave victoriae-reginae* var. *dentata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave victoriae-reginae* var. *elongata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave victoriae-reginae* var. *latifolia* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave victoriae-reginae* var. *punctata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave victoriae-reginae* var. *striata* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave victoriae-reginae* var. *viridis* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a).

The lectotype cited above was designated by Ullrich (1991e) and supersedes the neotype designated by Gentry (1982: 184), which belongs to *A. nickelsiae* and thus would have changed the application of the name. For the population genetics of the *A. victoriae-reginae*-complex, see Martínez-Palacios & al. (1999). The history and horticultural importance was summarized by Thiede (2011).

**A. victoriae-reginae** ssp. *swobodae* Halda (Acta Mus. Richnov. Sect. Nat. 7(2): 71, 2000). **Type:** Mexico, Coahuila (*Halda* 8504315 [PR]). — **Lit:** González-Elizondo & al. (2009: 132–136, as *A. victoriae-reginae* [NE Durango]); González-Elizondo & al. (2011: 76–78, figs. 1b, 2, 3b); Thiede (2011: 149–150); all with ills. **Distr:** Mexico (S Coahuila, NE Durango); calcareous slopes, rarely on plateaus, in desert scrub, 865–1550 m. **I:** Alsemgeest & al. (2007a: 63, as *A. victoriae-reginae* compacte vorm); Roosbroeck (2012: 163); Hochstätter (2015: IX: 53).

**Incl.** *Agave victoriae-reginae* ‘Compacta’ hort. (s.a.); **incl.** *Agave victoriae-reginae* fa. *compacta* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave victoriae-reginae* var. *compacta* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1).

[lg] Differs from ssp. *victoriae-reginae*: **Ros** 20–35 × up to 35 cm, compact, oblong-globose to subcylindrical when mature; **L** 70 to ±180,

narrowly oblong to narrowly triangular, 6–12 × 1.5–4.5 cm, flat above to concave at the base, margin often separating distally in dried leaves; **Tip** inside rosy-white or reddish, tube greenish-white; **Fil** pale rose-purple; **Anth** pale yellow; **Sty** pale rose-purple; **Fr** narrowly oblong, 17–19 × 7–9 mm; **Se** 3 × 2 mm.

Plants belonging here are apparently known since Trelease (1920) indicated occurrences of “*A. victoriae-reginae*” in Nuevo León, Coahuila and Durango (see Thiede (2011)). The first specimen was not collected until 1985 by J. J. Halda who subsequently published the subspecies based on material from Parras de la Fuente, Coahuila. The protologue erroneously indicates that flowers and seeds are larger than in ssp. *victoriae-reginae*, but the flowers fall within the range of the latter and the seeds are much smaller (González-Elizondo & al. 2011: 77). Alsemgeest & al. (2007a) also recognized the plants as a distinct “compact form from Coahuila and Durango”. Plants traded as *A. victoriae-reginae* var./fa. *compacta* or ‘Compacta’ appear to belong here.

**A. victoriae-reginae** ssp. *victoriae-reginae* — **Lit:** Breitung (1960: 35–38); Gentry (1982: 183–185); Ullrich (1991g); García-Mendoza (2003); Alsemgeest & al. (2007a: as ‘vierde vorm Huasteca Canyon’); González-Elizondo & al. (2011: 73–76, figs. 1a, 2, 3a); Martínez-Palacios & Eguiarte (2011); Thiede (2011); Roosbroeck (2012); Starr (2012: 280–285); all with ills. **Distr:** Mexico (NW & W-C Nuevo León), on much inclined, often vertical, calcareous slopes, in desert and submontane scrub, 565–1685 m. **I:** Irish & Irish (2000: tt. 47, 48); Heller (2006: 145, 163); González (2008); Pilbeam (2013: 231–232, as fa. *victoriae-reginae*); Ettelt (2014: 121); Hochstätter (2015: IX: 52, 56, 57); Walker (2017). – Fig. 61.

**Incl.** *Agave victoriae-reginae* fa. *variegata* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave victoriae-reginae* var. *stolonifera* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave considerantii* Carruel (1875); **incl.** *Agave victoriae-reginae* fa. *dentata* Breitung (1960); **incl.** *Agave victoriae-reginae* fa. *latifolia* Breitung (1960); **incl.** *Agave victoriae-reginae* fa. *longifolia*



**Fig. 61** *Agave victoriae-reginae* ssp. *victoriae-reginae* (Etter & Kristen 2762: Mexico: Nuevo León, Huasteca Canyon, 1550 m). (Copyright: J. Etter & M. Kristen)



Breitung (1960); **incl.** *Agave victoriae-reginae* fa. *longispina* Breitung (1960); **incl.** *Agave victoriae-reginae* fa. *ornata* Breitung (1960) (*nom. inval.*, ICN Art. 40.1); **incl.** *Agave victoriae-reginae* fa. *stolonifera* H. Jacobsen (1960) (*nom. inval.*, ICN Art. 40.1).

[lg] Acaulescent or with short invisible stem; **Ros** (20–) 30–65 × 60 cm, compact, globose or depressed-globose, solitary, sometimes caespitose, rarely surculose; **L** (150–) 280 to ±500, lanceolate or narrowly oblong, rigid or rarely flexible, densely imbricate, tip truncate or rounded, rarely acute, keeled or rarely rounded below, sometimes nearly triangular in cross-section, conduplicate or concave above except at the thickened base, (7–) 10–22 × 3.6–4.8 cm, green to lemon-green with conspicuous narrow white bands on both faces and along the margins, margins horny, white or grey, entire, continuous over the whole length, 1–3 mm wide; **marginal teeth** none; **terminal Sp** 1, straight or curved, from very short and mucroniform to subulate and acicular, rarely lanceolate, at the base broadened or narrow, 4–18 mm, furrowed or channelled above, coffee-brown, dark grey or nearly black, often accompanied by 1–3 small denticles; **Inf** ascending or erect, 1.6–4.3 m, ‘spicate’, with several chartaceous deltoid **Bra**, densely flowered in the upper ½, part-**Inf** with (2–) 3 flowers; **Ped** short, thick; **Fl** 39–53 mm; **Te** 26–36 mm, cream-white or greenish-white,

sometimes tinged reddish, tube funnel-shaped, 3–5 × 7–9 mm, lobes erect, subequal, broadly linear, 10–19 × 3–4 mm; **Fil** 20–48 mm, inserted above the throat of the tube; **Ov** thickly fusiform, 13–17 mm, neck short; **Fr** oblong to narrowly oblong, (13–) 17–21 × 7–11 mm, shortly beaked; **Se** 4 × 2–3.5 mm, black, dull or shiny. — **Cytology**: 2n = 60, 120 (Simpson & al. 2011).

A recent study of the *A. victoriae-reginae* complex by González-Elizondo & al. (2011) recognized 4 taxa: *A. victoriae-reginae* with 2 subspecies, the re-established *A. nickelsiae* (better known as *A. ferdinandi-regis*), and the completely new *A. pintilla*. *A. victoriae-reginae* has compact rosettes with densely imbricate, green to lemon-green leaves and a small terminal spine. In contrast, *A. nickelsiae* and *A. pintilla* both have open to subcompact rosettes with greyish-green to pale green or bluish-green leaves and larger flowers. *A. nickelsiae* is characterized by 80–170 grey-green to dull green, puberulent, oblong leaves with a strong, decurrent terminal spine, in contrast to the similar, but smaller *A. pintilla* with 60–180 green to bluish-grey-green, narrowly triangular, not puberulent leaves with a not or hardly decurrent terminal spine.

Earlier authors such as Ortgies, Engelmann, Baker, and Berger knew only the “classical” localities of ssp. *victoriae-reginae* near Monterrey, esp. at Huasteca Canyon (Thiede 2011), but the subspecies is more widespread in NW and W-C Nuevo León (González-Elizondo & al. 2011).

Previous reports of natural hybrids of *A. victoriae-reginae* relate in fact to hybrids of *A. nickelsiae* (see there). Thiede (2011) provided the first report of a putative natural hybrid of *A. victoriae-reginae* ssp. *victoriae-reginae* with *A. lechuguilla*. — ‘Kazo Bana’, ‘Snowburst’, and ‘White Rhino’ are variegated cultivars (Starr 2012: 285), and ‘Himesanoyuki’ is a miniature cultivar (Starr 2014: 221, with ill.).

**A. ×villarum** André (Rev. Hort. (Paris) 58: 465–466, 1886). **Type**: not typified. — **Lit**: Berger (1912: 365, as *A. villarum*); Trelease (1914: 237–238); Berger (1915: 74, as *A. villarum*). **Distr**: Cultivated only.

**Incl.** *Agave ×villae* Pirotti ex Baker (1892) (*nom. inval.*, ICN Art. 61.1).

[1d × 1g] According to the protologue a garden hybrid *A. filifera* × *A. xylonacantha* raised by the Villa brothers, nurserymen at Cornigliano (Italy). Apparently no longer extant in cultivation. “*A. villae* Pirotti” is placed in *A. kerchovei* by Baker (1892: 2), but is placed here by Gentry (1972: 74).

**A. vilmoriniana** A. Berger (Repert. Spec. Nov. Regni Veg. 12: 503, 1913). **Type** [neo]: Mexico, Guadalajara (*Rose & Hough* 4833 [US]). — **Lit**: Berger (1915: 127); Gentry (1942: 94–95, t. 14, as *A. mayoensis*); Gentry (1972: 62–69, with ill.); Gentry (1982: 67, 83–85, with ill.); McVaugh (1989: 145); Turner & al. (1995); Hernández-Vera & al. (2007a); Vázquez-García & al. (2007b: 41–42, t. B); González-Elizondo & al. (2009: 137–139, with ill.); Starr (2012: 286–291, with ill.). **Distr**: Mexico (S Sonora, Chihuahua, Sinaloa, Durango, Zacatecas, Aguascalientes, Jalisco); on volcanic barranca cliffs in tropical deciduous or pine-oak forests, 600–1850 m; flowers March to July. **I**: Irish & Irish (2000: t. 49); Etter & Kristen (2001: 180–183); Etter & Kristen (2003a: 3, 6); Heller (2006: 146); Richter (2011: 49); Etter & Kristen (2012: 92–93); Pilbeam (2013: 234); Hochstätter (2015: VIII: 17, 27); Moore (2016: 240–241).

**Incl.** *Agave edwardii* Trelease ms. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Agave eduardii* Trelease (1920); **incl.** *Agave houghii* hort. ex

Trelease (1920); **incl.** *Agave mayoensis* Gentry (1942).

[1b] Stems short; **Ros** ±1 × 2 (–2.6) m, solitary; **L** linear-lanceolate, arching, pliable, deeply guttered, broadest at the base, heavily thickened towards the base, long acuminate, concave to conduplicate above, smooth, 90–180 × 6–10 cm, light green to yellowish-green, margins with a fine brown continuous border ±1 mm wide, scaly with age; **marginal teeth** none; **terminal Sp** acicular, 3–20 mm, brown to greyish-brown; **Inf** 3–5 (–6) m, ‘spicate’, peduncle 1–2 m, with scarious acicular **Bra**, lower **Bra** 10–20 cm, brownish towards the brittle tip, fertile part densely flowered, bulbiferous or not, part-**Inf** with 2–4 (–8) flowers; floral **Bra** deltoid, 2–3 mm; **Ped** 1–2 (–4) × forked, 8–20 mm; **Fl** 35–40 mm; **Tep** yellow, tube open, shallow, 4 × 8–9 mm, lobes ascending to spreading, nearly flat, clasping the filaments when drying, equal, 14–17 × 4–5 mm; **Fil** 30–40 mm, inserted at the upper edge of the tube; **Anth** 16 mm; **Ov** 15–20 mm incl. the 3–4 mm long neck; **Sty** somewhat longer than the tepals but much shorter than the filaments; **Sti** capitate; **Fr** 18–25 × 7–13 mm, beaked for 1–2 mm, somewhat glaucous; **Se** crescent-shaped, 3–4 × 2–3 mm, dull.

A cliff-dweller which may form extensive vertical colonies, distinguished by the unarmed, large, gracefully arching, deeply guttered leaves (“Octopus Agave”). The “lectotype” of Gentry (1982: 82) is in fact a neotype. Gentry (1982) and McVaugh (1989) cite a line drawing most certainly prepared by Berger from the original plant cultivated by Vilmorin and collected by Diguet (US 1023581!). The sheet is listed as “apparently genuine original material” in the US database, but the drawing, dated 20.II.1914, was prepared later than the protologue.

Related to *A. chryso glossa* and *A. ocahui* (see there). Wild populations at higher altitudes experience occasional sharp frosts (Gentry 1982), and cultivated plants may tolerate temperatures down to –9 °C (Turner & al. 1995). The species exhibits substantial diurnal CO<sub>2</sub> assimilation esp. at lower temperatures, unlike other agaves studied (Turner & al. 1995). The flowers are visited by bees, hummingbirds (documented with photographs

by Etter & Kristen (2003a) and Etter & Kristen (2012)) and perhaps bats (Turner & al. 1995). Crushed leaves are used as detergent (bath, shampoo, laundry) and also to stupefy fishes (Turner & al. 1995). — ‘Stained Glass’ is a variegated cultivar (Starr 2012: 289–291); Moore (2016: 241) illustrates an unnamed variegated form.

**A. virginica** Linné (Spec. Pl. [ed. 1], 1: 323, 1753). **Type** [neo]: USA, Virginia (*Clayton* 498 [LINN, BM]). — **Lit**: Verhoek-Williams (1975: 133–181); Diggs & al. (1999: 1079–1081, with ills.); Reveal & Hodgson (2002); Castillejos-Cruz (2009: [300]–[308]); all as *Manfreda*. **Distr**: S and E USA (from Missouri and Texas to the Atlantic), Mexico (Nuevo León, Tamaulipas); flowers June to August.

≡ *Aloe virginica* (Linné) Crantz (1766) ≡ *Manfreda virginica* (Linné) Salisbury ex Rose (1899) ≡ *Polianthes virginica* (Linné) Shinners (1966); ≡ *Agave pallida* Salisbury (1796) (*nom. illeg.*, ICN Art. 52.1).

The species is aberrant in being the only member of Subgen. *Manfreda* occurring in temperate regions, and it is the N-most species in the genus *Agave*. In addition to its distribution, the taxon is easily recognized by its slender green flowers with erect lobes and the style that is shorter than the stamens (Verhoek-Williams 1975: 170, 172). For the typification, see Reveal & Jarvis (2009: 977).

**A. virginica** ssp. **lata** (Shinners) Thiede & Eggl (Kakt. and. Sukk. 52(6): 167, 2001). **Type**: USA, Texas (*Daly* 61 [BRIT/SMU]). — **Lit**: Diggs & al. (1999: 1079–1080, 98 & 1081 ills.); Diggs & al. (2006: 412, 292 & 417: ills.); both as *Manfreda*. **Distr**: USA (S Oklahoma, N-C Texas); mainly in clay soils in the Blackland Prairie (Texas); flowers mid-June to mid-July.

≡ *Agave lata* Shinners (1951) ≡ *Polianthes lata* (Shinners) Shinners (1966) ≡ *Manfreda virginica* ssp. *lata* (Shinners) O’Kennon & al. (1999).

[3a4] Differs from ssp. *virginica*: **L** 4–10, 12–18 × (2–) 3–8 (–10) cm, 3–6 × as long as broad; **Inf** peduncle near the base 6–10 mm Ø, 3–5 mm Ø at the base of the fertile part; **Fl** 26–35 mm; **Tep** lobes 2.5–3 mm wide at the base; **Anth** 13–17 (–20) mm.

Verhoek-Williams (1975), and later Reveal & Hodgson (2002) and Castillejos-Cruz (2009: [300]) included this taxon in the synonymy of the widespread and variable *Manfreda virginica*. Diggs & al. (1999) re-emphasized the clear, albeit overlapping differences between *A. lata* and *A. virginica*, and recognized the former at subspecies rank (as *Manfreda*).

**A. virginica** ssp. **virginica** — **Lit**: Mulford (1896: 68–70, t. 26); Rose (1903c: 19); Small (1903: 287); Berger (1915: 32–33); Verhoek-Williams (1975: 133–181); Piña Luján (1985: 57–58); Diggs & al. (1999: 1079–1080, 1081, ills.); Reveal & Hodgson (2002); Diggs & al. (2006: 412–413, 417: ills.); Castillejos-Cruz (2009: [300]–[308]); all as *Manfreda* except Mulford and Berger. **Distr**: S and E USA (Missouri, Illinois, Indiana, Ohio, Kentucky, West Virginia, Virginia, Oklahoma, Arkansas, Tennessee, North Carolina, Texas, Louisiana, Mississippi, Alabama, Georgia, South Carolina, Florida), Mexico (Nuevo León, Tamaulipas); open wooded areas, on rocky and sandy soils (USA), in pine-oak, oak, and tropical (sub-)deciduous forests, desert scrub and grasslands (Mexico), 100–600 m; flowers mid-July to mid-August. **I**: Curtis’s Bot. Mag. 29: t. 1157, 1809; Hochstätter (2016: I: 6, 47, as *Manfreda*).

**Incl.** *Aloe caroliniana* Hill (1768); **incl.** *Agave conduplicata* Jacobi & C. D. Bouché (1865) ≡ *Agave virginica* var. *conduplicata* (Jacobi & C. D. Bouché) A. Terracciano (1885) ≡ *Manfreda conduplicata* (Jacobi & C. D. Bouché) Rose (1903); **incl.** *Agave virginica* var. *polyantha* Engelm. (1875); **incl.** *Agave virginica* var. *tigrina* Engelm. (1875) ≡ *Manfreda tigrina* (Engelm.) Small (1903) ≡ *Manfreda virginica* var. *tigrina* (Engelm.) Rose (1903) ≡ *Agave virginica* fa. *tigrina* (Engelm.) E. J. Palmer & Steyermark (1935) (*nom. inval.*, ICN Art. 35.1) ≡ *Agave tigrina* (Engelm.) Cory (1936) ≡ *Polianthes virginica* fa. *tigrina* (Engelm.) Shinners (1966); **incl.** *Allibertia intermedia* Marion (1882); **incl.** *Agave alibertii* Baker (1883) ≡ *Manfreda alibertii* (Baker) Rose (1903); **incl.** *Agave virginica* Baker (1883) (*nom. illeg.*, ICN Art. 53.1).

[3a4] Herbaceous; corm 3–5 × 2–2.5 cm, cylindrical, bulb 1.5–2.3 × 1.3–2 cm, ovoid, covered with dried membranous leaf bases 1.8–4.5 cm long; **R** fleshy and thickened, with filiform ramifications, contractile; **L** drought-deciduous, 8–10, spreading to slightly ascending, lanceolate to oblanceolate, somewhat wavy, succulent to semi-succulent, canaliculate, glabrous on both faces, apex acute with a soft tip, (12–) 15–45 × 1.2–4.5 (–6.5) cm, 7–15× as long as wide, light green, sometimes with reddish to purple dots, conspicuously denticulate on a hyaline cartilaginous band, denticles of various sizes and irregularly spaced; **Inf** (50–) 90–150 (–180) cm, erect, glaucous green, ‘spicate’, peduncle 4–7 mm Ø at the base, 1.5–3.5 mm Ø at the base of the fertile part, with 8–10 **Bra**, **Bra** base truncate, lower similar to leaves, the upper decreasing in size abruptly in the fertile part, fertile part 15–68 cm, lax, with 10–60 flowers; floral **Bra** 0.7–1.2 × 0.3–0.5 cm; **Fl** (17–) 22–23 mm, solitary, sessile, ascending to spreading; **Tep** glaucous-green to yellowish-green, forming a tube 11–15 × 3–4 mm, constricted near the apex of the ovary, lobes deltoid, erect, 4–8 × 1.5 mm, tip obtuse, with a bundle of short white trichomes; **Fil** 27–35 (–40) mm, erect at anthesis, exceeding the tube for 18–30 mm, inserted near the base of the tube on slightly different levels, yellowish-green, with multiple purple dots on the entire surface; **Anth** 8–12 mm, yellow with reddish to brownish dots; **Ov** ellipsoid to cylindrical, 6–10 (–12) × 3–4 mm, greenish, prolonging slightly into the tube, slightly constricted above; **Sty** 27–33 mm, elongating during anthesis, almost reaching the level of the anthers; **Sti** capitate, 3-lobed; **Fr** globose to ellipsoid, 10–14 (–17) × 10–13 (–16) mm, apiculate, tepals persisting; **Se** deltoid, plane-concave, 3–4 × 3 mm, dull. — **Cytology**: n = 30 (McKelvey & Sax 1933, Verhoek-Williams 1975).

Due to its wide distribution, the species presents great morphological variation which is mainly manifested in the shape and size of the leaves. Its most distinctive feature are the erect and short tepal lobes only 4–8 mm long, but it can also be distinguished by its fragrant banana-scented flowers (very reminiscent of the scent of

*A. singuliflora*). In addition, its perianth is tubular, thin, green and shorter than stamens and stigma (Castillejos-Cruz 2009).

Nectar and pollen production patterns indicate the species to be primarily adapted to nocturnal pollinators. Nocturnal moths and hawkmoths contribute to most of the seed set, large diurnal bees contribute much less (Groman & Pellmyr 1999). Infusions of the corms were used against snakebites by the native Americans, as is alluded by its vernacular name “rattlesnake master” (Diggs & al. 2006, Castillejos-Cruz 2009). — For the seedling establishment and outdoor cultivation in C Europe (Germany), see Richter (2011) and Werner (2016), both with ills. Lindstrom (2006) raised hybrids with *A. amica* (as *Polianthes tuberosa*) hardy down to –25 °C, subsequently published as ×*Polifreda* ‘Lindstrom’ (Ritchie & Lindstrom 2014).

**A. vivipara** Linné (Spec. Pl. [ed. 1], 1: 323, 1753). **Type**: [lecto — icono]: Commelin, Prael. Bot. 65: t. 15, 1703. — **Lit**: Trelease (1913: 18–19, tt. 1–3); Boldingh (1914: 18); Berger (1915: 223–224); Hummelinck (1936: 244); Hummelinck (1938: 21–23); Hummelinck (1993: 214–217, 223, with ills.); the last 3 all as *A. cocui*; Álvarez de Zayas (1995: 3, figs. 1, 3, 5). **Distr**: Leeward Antilles (Aruba, Bonaire, Curaçao); in secondary formations, often cultivated or naturalized, probably introduced. **I**: Pilbeam (2013: 235).

≡ *Aloe vivipara* (Linné) Crantz (1766) (*nom. illeg.*, ICN Art. 53.1).

[2u] Nearly acaulescent; **Ros** suckering; **L** very broadly lanceolate, subacuminate, flatly concave, 40–60 × 12–20 cm, somewhat transiently glaucous, with age rather glossy green; **marginal teeth** commonly upcurved in the upper ½ of the leaf and recurved in the lower ½, slender from crescent-shaped bases, 3–7 mm, 10–15 mm apart, often on green prominences, intervening margin a little concave; **terminal Sp** triquetrously acicular, somewhat flexuous, narrowly round-grooved to the middle and involute below, smooth, polished towards the tip, 15–30 × 3–5 mm, red-brown, shortly decurrent; **Inf** scarcely 3 m, paniculate, narrowly oblong,



peduncle with broadly triangular imbricate **Bra**, fertile part with part-**Inf** on ascending branches in the upper  $\frac{1}{2}$  or more of the inflorescence, freely bulbiferous; **Ped** scarcely 5 mm; **Fl** 40–45 mm; **Tep** yellow, tube open,  $\pm 4$  mm, lobes  $15\text{--}25 \times 4\text{--}7.7$  mm; **Fil** 30–43 mm, inserted usually 0.5–1 mm below the tube throat; **Ov** oblong, 20–25 mm; **Fr** broadly oblong,  $30 \times 25$  mm, beaked, very shortly stipitate; **Se** unknown. — **Cytology**:  $2n = 58, 60, 120, 180$  (Satô 1935, Simpson & al. 2011).

The concept of *A. vivipara* Linné, the earliest-named *Agave* from the Caribbean, was subject to change over time. Trelease (1913) equated it with naturally occurring plants from Curaçao with small rosettes and flowers and glaucous leaves with slender teeth on small crescent-shaped bases, separating it from his two new species *A. vicina* from Aruba (with small rosettes and flowers and dull green leaves with heavily triangular teeth on small crescent-shaped bases) and *A. cocui* from the Venezuelan coast (with rather large rosettes and flowers). Hummelinck (1936), Hummelinck (1938) and Hummelinck (1993) applied the name *A. vivipara* to Trelease's *A. vicina*, and included Trelease's *A. vivipara* in *A. cocui*, thus extending the area of the latter to Curaçao and neighbouring islands. Wijnands (1983: 35) established *A. vivipara* as oldest name for the widespread continental taxon previously referred to as *A. angustifolia*, which for reasons of priority was renamed as *A. vivipara*, and designated the lectotype cited above. However, García-Mendoza & Chiang (2003) showed that *A. angustifolia* and *A. vivipara* are two distinct species and re-established *A. angustifolia* in the sense of Gentry (1982) and *A. vivipara* in the sense of Trelease (1913). This is followed here. In this sense, *A. vivipara* includes plants from Curaçao and neighbouring islands, which can be differentiated from *A. vicina* as given above. Naturalized in RSA (Smith & al. 2008: 38–39).

**A. vizcainoensis** Gentry (Occas. Pap. Calif. Acad. Sci. 130: 67–69, ill., 1978). **Type**: Mexico, Baja California Sur (Gentry 7469 [UC, ARIZ, CAS 373726, DES, MEXU?, MICH]). — **Lit**: Gentry

(1982: 407–408, with ill.); García-Mendoza (2003); Webb & Starr (2014a: 93–95, with ill.); Webb & Starr (2015: 89–90, with ill.). **Distr**: Mexico (Baja California Sur: Vizcaino Desert); in the mountains and on alluvial fans, in succulent desert and desert scrub, 120–240 m; flowers March to April, also August. **I**: Richter (2011: 79); Pilbeam (2013: 236); Hochstätter (2015: V: 22).

[2k] **Ros** open,  $30\text{--}50 \times 50\text{--}90$  cm, surculose or solitary; **L** 16–20, linear-lanceolate to obovate-lanceolate, thickly fleshy, rather rigid, narrowed above the base, broadest in the middle, acute to attenuate,  $25\text{--}40 \times 6\text{--}10$  cm, glaucous-grey to green, sometimes reddish, with imprints from the central bud, margins repand, horny above; **marginal teeth** nearly straight or curved, slender or broadly flattened, 5–10 mm (middle of the lamina), dark brown to greyish, 10–30 mm apart, on small to distinct prominences; **terminal Sp** stoutly subulate, mostly rather straight, shallowly grooved above, 25–40 mm, brown to greyish, long-decurrent; **Inf** 1.8–3.5 m, paniculate, part-**Inf** spreading, 8–15 in the upper  $\frac{1}{2}$  of the inflorescence; **Ped** stout, 8–12 mm, with small bracteoles; **Fl** 65–75 mm; **Tep** yellow, tube funnel-shaped, bulging at the filament insertions,  $8\text{--}12 \times 15$  mm, lobes linear-lanceolate, obtuse, cucullate, strictly erect at anthesis, involute above the spreading base,  $21\text{--}26 \times 4\text{--}5$  mm; **Fil** 55–70 mm, inserted somewhat unequally 7–9 mm above the tube base; **Fil** 21–26 mm; **Anth** excentric; **Ov** 36–41 mm, green, neck 6–8 mm, in fresh flowers scarcely constricted but drying very narrow; **Sty** to 70–85 mm; **Sti** broad, lobed; **Fr** oblong, striate,  $50\text{--}70 \times 20$  mm, stipitate, rostrate, brown; **Se** drop-shaped,  $6\text{--}7 \times 4.5$  mm, black, marginal wing narrow.

The comparatively long flower tubes suggest an affinity with *A. margaritae* from the same general region, which differs in its small size and short, broad, long-toothed leaves. According to Gentry (1978) and Gentry (1982), the two species do not show close relations to other members of Sect. *Deserticolae* (as Group), but are assigned to this group for convenience only. Webb & Starr (2015) finally placed both in a separate Sect. *Intermediae*, intermediate between Sect. *Deserticolae* and Sect.



*Umbelliflorae* (Webb & Starr 2014b). Plants from Bahia Tortugas and Cerro Prieto now placed here were previously misidentified as *A. sebastiana* (Webb & Starr 2014b, Webb & Starr 2015). Plants from the region of the Pichachos de Santa Clara are more robust and less surculose than those in the Sierra Vizcaino proper, and resemble *A. giganteensis* (Gentry 1982: 407); Webb & Starr (2014a) finally published these plants as a new species, *A. azurea* (see there).

**A. wallisii** Jacobi (Nachtr. Versuch syst. Glied. Agaveen 2: 162, 1870). **Type:** Colombia (*Wallis* s.n. [not known to have been preserved]). — **Lit:** Berger (1915: 222); Bernal & al. (2015: 794); Giraldo-Cañas (2017: 47). **Distr:** Colombia (mountains of the Río Cauca region); no data on the ecology available.

[2v] Acaulescent; **L** relatively few, broadly lanceolate, at first erect, somewhat recurved, older spreading to all sides, recurved towards the tip, base thickly fleshy, becoming thin-fleshy and fibrous upwards, from the 4 cm broad base continuously broadened to 6.7 cm somewhat above the middle, lanceolate-acuminate in the upper part, below with broad rounded keel, keel more flattish in the upper part, above in the lower ½ flat or flatly convex, in the upper ½ flatly guttered, tip with several grooves, fresh green, dull, slightly glaucous, margins somewhat undulate and recurved; **marginal teeth** as very small denticles, triangular, slightly curved upwards, at first pergamentaceous with brownish tip, later horny, chestnut-brown, on flat fleshy basis; **terminal Sp** thin, corneous, subulate, on a fleshy base, horny, 6–8 mm, chestnut-brown; **Inf, Fl** and **Fr** unknown.

According to the protologue based on an undeveloped young plant 45 cm in diameter imported by Linden in Belgium in 1867 through the botanical collector Wallis from mountains of the Río Cauca region in Colombia. Trelease (1920: 135), based on the description alone, considered the species as “closely related” and “evidently allied” to *A. micracantha*, now a synonym of *A. mitis*. Munter (1981: 74) reports that the species “only rarely offsets in the wild” and must consequently have seen it in habitat. Hochstätter (2015) published a photograph of a young plant

labelled “*Agave wallisii*”, cultivated in Spain by P. van der Meer, but the plant originates from Santa Marta at the Caribbean coast of Colombia and does not belong here (P. van der Meer, pers. comm. Nov. 2018). The area in the Cauca valley is heavily urbanized now, and a search by G. Xhonneux was unsuccessful (P. van der Meer, pers. comm. Feb. 2019). See also under *A. cundinamarcensis*.

**A. warelliana** De Smet ex T. Moore & Masters (Gard. Chron., ser. nov. 5: 603, 1876). **Type:** [neo — icono]; Gard. Chron. ser. nov. 8: 265, fig. 53, 1877. — **Lit:** Berger (1915: 46–47); Gentry (1982: 230–232, with ill.); Lott & García-Mendoza (1994: online version with ills.); Cházaro Basáñez & al. (2008b: with ills.); Smith & Figueiredo (2014c: 27–29, with ills.). **Distr:** Mexico (C Veracruz, N-C Oaxaca, Chiapas), Guatemala (Huehuetenango); steep rocky limestone slopes with black soil, in pine forests, 1400–2420 m; flowers in May. **I:** Curtis’s Bot. Mag. 139: t. 8501, 1913; Richter (2011: 48); Hochstätter (2015: IX: 10).

[1f] Stems short or to 1 m; **Ros** rather robust,  $\pm 1 \times 1.7$  m, sparsely surculose, branching axillary; **L** dense, lanceolate to lanceolate-spatulate, erect or spreading, thickly fleshy, slightly constricted above the base, long acuminate, lower face convex, upper face flat, 50–70  $\times$  8–15 (6–7 at the base) cm, light pale green or shiny glaucous, margins finely serrulate, straight, brown; **marginal teeth** deltoid denticles, slightly curved, on a thin horny band not always continuous and formed by the base of the denticles, 1–2 mm, 1–3 mm apart; **terminal Sp** straight, rigid, broadly grooved above, 18–25  $\times$  3–4 mm, brown, decurrent for 5–10 cm; **Inf** erect, 4–6 m, ‘spicate’, peduncle 2–2.5 m, densely bracteate with deltoid long-acuminate appressed **Bra** 3.5 cm long (lower); floral **Bra** small, pale, lanceolate, 35 mm; **Fl** 45–55 mm, in groups of 2–4; **Te** reddish-yellow within, brownish outside, tube funnel-shaped, 6-grooved, 8–13 mm, light green, lobes linear-lanceolate, revolute,  $\pm 14$ –15  $\times$  4–6 mm, yellow within, spotted violet-brown on the back, inner 10–11 mm broad, slightly concave, with a broad thick keel; **Fil** 45–60 mm,

reddish; **Anth** 20–25 mm, reddish; **Ov** trigonous, narrowed at the base and apex, smooth, 25–30 mm, greenish-brown; **Sty** 140 mm, reddish; **Sti** 3-lobed; **Fr** somewhat obovoid, 3-grooved, narrowed at the base, 40 × 15 mm, beaked, green with some reddish dots; **Se** 5–6 × 3–5 mm, shiny black. — **Cytology**: 2n = 90, 100 (= 3×) (Simpson & al. 2011).

According to Gentry (1982), *A. warelliana* is the largest species in Sect. *Micracanthae* (as Group *Polycephalae*), esp. notable by its large flowers. Gentry relied exclusively on Baker's and Berger's descriptions and Berger's specimens at K and US; living plants or native localities were unknown to him. Lott & García-Mendoza (1994) provided the first report from nature from Mexico (Chiapas) and Guatemala (Huehuetenango) and give a description based on this new material; the later internet version (accessed Feb. 2015) omits the record from Guatemala. *A. warelliana* is now known from C Veracruz (near Pico de Orizaba, habitat photographs in Cházaro Basáñez & al. (2008b), Santos Valencia (2009: 4), Richter (2011) and Smith & Figueiredo (2014c)), from N-C Oaxaca (map in Cházaro Basáñez & Vázquez-García (2013: 59)), and from Chiapas (Pijijiapan, Motozintla, La Trinitaria, and El Triunfo, Lott & García-Mendoza (1994), Martínez-Meléndez & al. (2008: 29), Pérez-Farrera & al. (2012: 123), Portal Datos Abiertos UNAM (2018+: accessed 2018)), and from Guatemala (Huehuetenango) (specimen *Steyermark* 50940, IS 44130!, identified by A. García-Mendoza, label 2002).

According to Lott & García-Mendoza (1994) *A. warelliana* is very similar to *A. chiapensis* and differs in the size and shape of the leaves, its margins with a dark brown, almost continuous band, its decurrent terminal spine, much shorter bracts, and a much larger inflorescence. The flowers have been found to be smaller than those of *A. chiapensis*, which contrasts the data provided by Gentry (1982) and earlier authors.

Baker (1877a: 264, fig. 53), previously regarded as publication of the protologue, is antedated by the reference given above. Smith & Figueiredo (2014c) designated Fig. 53 from the former as lectotype, which thus represents a neotype. For

the in vitro-propagation, see Santos Valencia (2009). The triploid chromosome count from Simpson & al. (2011) may have been taken from a natural hybrid between *A. warelliana* and a further species with the parents being di- and tetraploid; the plant depicted by Smith & Figueiredo (2014c: fig. 7) with much broader leaves and stronger marginal teeth may be such a hybrid.

**A. weberi** J. F. Cels ex Poisson (Bull. Mus. Hist. Nat. (Paris) 7: 230–232, 1901). **Type** [neo]: USA, Texas (Gentry & al. 20003 [US [2 sheets], DES [?], MEXU [2 sheets]]). — **Lit**: Berger (1915: 259); Gentry (1982: 631–633, with ills.); Reveal & Hodgson (2002); Guillot Ortiz & al. (2008: 79–80, with ill.); Guillot Ortiz & Meer (2008b: 26–27, 31, with ill.); González-Elizondo & al. (2009: 149, with ill.); Smith & Figueiredo (2015: with ills.). **Distr**: Known from cultivation only (NE and C Mexico, introduced to Texas); flowers May to June. **I**: Irish & Irish (2000: t. 50); Heller (2006: 148); Richter (2011: 71, 117); Hochstätter (2015: VII: 21); Moore (2016: 234, 235).

**Incl.** *Agave neglecta* Small (1903).

[2a] Stems short, 0.4–1 m; **Ros** open, 1.2–1.4 × 2–3 m, freely suckering, without rhizomes; **L** lanceolate, rather softly fleshy, pliable, erect and straight to recurving, widest in the middle, narrowed below, slightly convex below, concave or guttered above at least towards the apex, 110–160 × 12–18 cm, green to greyish- or yellowish-green, or pruinose-greyish esp. when young, not cross-zoned, margins straight, finely fibrous; **marginal teeth** 1–2 mm, to 10 mm apart, usually absent along the upper 1/3–1/2 of the leaf, or completely absent; **terminal Sp** subulate, openly shallowly grooved above in the upper 1/2, 30–45 mm, brown to greyish, decurrent for several cm; **Inf** 6.5–8 m, paniculate, fertile part open, with 20–25 horizontal to slightly ascending diffuse part-**Inf** several times compound, in the upper 1/2–1/3 of the inflorescence, with 15–27 flowers, longer than 10 cm, sometimes bulbiferous; **Fl** 70–80 mm; **Te** bright yellow, tube rather urceolate, deeply grooved, 15–20 × 14–19 mm, lobes erect, involute, obtusely cucullate, subequal, 20–24 mm, inner narrower, more strongly folded; **Fil** long-

tapering, 55–60 mm, long exserted, yellow to yellow-green, inserted at mid-tube; **Anth** centric or excentric, 30–31 mm, yellow; **Ov** cylindrical, 33–40 mm, pale green, neck short, grooved, 2–4 mm, not constricted; **Sty** finally longer than the filaments; **Sti** capitate; **Fr** 55 × 30 mm, shortly stipitate but scarcely beaked; **Se** unknown.

A huge, highly attractive ornamental with gracefully arching leaves, but of unknown origin. Gentry (1982) assigned several related horticultural forms to this species which share green or glaucous-grey leaves that usually have small teeth or denticles. More distinctly grey-coloured variants might superficially be mistaken for *A. americana*, but the smooth or nearly unarmed leaf margins distinguish *A. weberi* immediately. Ullrich (1990d: 106) placed the species in Sect. *Agave* (as Group *Americanae*), which is followed here, in contrast to Gentry's placement in Group *Sisalanae*. It is perhaps a cultivar derived from *A. angustifolia* (of Sect. *Rigidae*; Govaerts (2014+)), but might also have arisen as a hybrid between *A. americana* s.l. and *A. angustifolia* s.l. The neotype at US designated by Gentry (1982: 633) consists of 2 sheets which were cross-labelled afterwards by R. Franck in 2012. *A. weberi* is cultivated for pulque and fibre and is locally naturalized in S Texas (Reveal & Hodgson 2002), Spain (Sáez & Guillot Ortiz 2015) and RSA (Smith & Figueiredo 2015). Further plants naturalized in Spain assigned here (Guillot Ortiz & al. 2008: 79–80, Guillot Ortiz & Meer 2008b: 26–27, 31) differ clearly and may represent *A. sisalana* or a relative. For a photoseries of the inflorescence development and flowering, see Bernhard (2012: accessed Dec. 2018). 'Reiner's Selection' is a cultivar with grey-green leaves, and 'Arizona Star' is a variegated cultivar with pale yellow margins.

*A. neglecta*, a local cultivate from Florida (Gentry 1982: 627–628, Reveal & Hodgson 2002), is treated as synonym by Franck (2012: 10–13). *A. franceschiana* (Berger 1912: 358, Berger 1915: 234) was related to *A. sisalana* by Berger (1915) or considered as a form of it (Ullrich 1993b: 25, 30), with which it coincides in its size and its cross-zoned leaves; this is followed here, while Gentry (1982), Smith & Figueiredo (2015: 165) and Govaerts (2014+: accessed Oct. 2018) placed

it in the synonymy of *A. weberi*, which is a much larger plant without cross-zoning of the leaves.

**A. wendtii** Cházaro (Cact. Suc. Mex. 42(4): 95, ill., 1997). **Type:** Mexico [ex cult.], Veracruz (Cházaro & Flores Macías 6645 [XAL, CHAPA, ENB, MEXU, WIS]). — **Lit:** Cházaro Basáñez (1995); Cházaro Basáñez (1997); Jimeno-Sevilla (2010: 100–102); Meer (2016a); all with ill. **Distr:** Mexico (Veracruz, Tabasco); rock faces in tropical evergreen forests with ±3000 mm rainfall, 80–350 m; flowers April to May; known only from 3 localities. **I:** Trager (2005: 93); Pilbeam (2013: 237–238); Hochstätter (2015: IX: 11, 14).

[1f] Acaulescent; **Ros** lax, to 45–60 cm Ø; **L** 25–50, lanceolate-oblong, fleshy, soft, brittle when bent, 10–25 × 1.8–3.5 cm, glaucous when young, later turning light green; **marginal teeth** small denticles, ±1–2 mm, green to coffee-brown; **terminal Sp** 8–10 mm, dark; **Inf** erect, 1–2 m, 'spicate', peduncle with narrowly-elongate **Bra**, fertile part dense, part-**Inf** with 2–3 flowers, subtended by triangular **Bra**, in the upper ½–¾ of the inflorescence, bulbiferous (in cultivation); **Fl** 20–29 mm, self-fertile; **Tep** pale yellow to yellowish-green, pale rose inside, free to the base, oblong, ±20 mm, tip roundish-acuminate; **St** 46 mm, pale yellow, long-exserted; **Anth** 11 mm, yellowish; **Ov** narrowly fusiform, ±10 × 3 mm; **Sty** ±29 mm, exserted, pale green; **Fr** nearly globose, small; **Se** not known.

According to the incomplete protologue only known from the Río Uxpanapa Gorge (Veracruz) and closely related to *A. pendula*, from which it differs in its greenish-glaucous leaves without lighter median stripe and with yellow marginal teeth, and its shorter, strictly erect inflorescence fertile in its upper half. Jimeno-Sevilla (2010) provides additional morphological data and a second locality from Veracruz at the Río Chalchijapan. *Morales Damián* 40 (MEXU 1355269!) from S Tabasco, Ejido Niños Heroes de Chapultepec, is a new state record. The record by Wendt from the Chimalapas region in Oaxaca mentioned by Cházaro Basáñez (1997: 14) needs confirmation.

**A. wercklei** F. A. C. Weber *ex* Wercklé (Monatsschr. Kakt.-kunde 17(5): 71–72, 1907).

**Type** [neo]: Cult. La Mórtoia (*Berger* s.n. [US 1023816]). — **Lit**: *Berger* (1915: 201–202); *Horich* (1973: with ill.); *Gentry* (1982: 500–502, with ill.); *Ullrich* (1992d: with ill.); *Lott & García-Mendoza* (1994: online version with ill.); *Smith & Steyn* (2002a: with ill.); *Smith & Steyn* (2003); *Grayum* (2003: 29, 30, 32, with ill.); *Walters & al.* (2011: 55–58, with ill.). **Distr**: Costa Rica (Valle del Río Grande de Candelaria/Caraigres); Pacific slopes, hot regions in sparse grasslands, 500–1700 m; flowers January to March; naturalized in South Africa. **I**: *Heller* (2006: 149); *Smith & al.* (2008: 39); *Richter* (2011: 84); *Pilbeam* (2013: 239); *Trager* (2018: 87–88).

**Incl.** *Agave costaricensis* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1).

[2o] Acaulescent; **Ros** compact, 0.8–1 × 1–2 m, solitary, very rarely offsetting from rhizomes; **L** variable, ovate to lanceolate, rigidly spreading, upper ½ outcurved and deeply channelled, thick and robust, broad, thickly fleshy, narrowed towards the enlarged overlapping bases, clasping the stem, short-acuminate, tip inrolled, flat to concave in the upper ½, smooth, rough when young or rough below with age, (35–) 70–150 × 10–22 (–30) (at mid-leaf) cm, light glaucous-green to white-glaucous, with impressions from the central bud, margins smoothly rounded, straight to repand; **marginal teeth** deltoid or sinuous, slender, straight or variously curved, (1–) 3–4 mm, black to dark purplish- or greyish-brown, irregularly spaced 5–20 mm at mid-leaf, on low green prominences, smaller intermittent teeth absent or extremely rare; **terminal Sp** conical at the base tapering into an acicular point, narrowly grooved above, 16–30 mm, shiny dark purplish-brown or black, shortly decurrent; **Inf** (1–) 3–8 m, paniculate, peduncle short, surpassing the leaves, with deltoid **Bra**, fertile part large, broad, profuse, with up to 40–45 horizontally spreading, branched, dense, ‘umbellate’ part **Inf** in the upper ½ of the inflorescence, 13–20 cm long, often bulbiferous; **Ped** 4–5 mm; **Fl** 35–60 (–65 (–80)) mm, unscented to faintly fruit-scented, copiously nectariferous; **Tep** bright golden-yellow or greenish-yellow below and orange above, greenish-yellow to greenish-cream in

bud, 42–47 mm, tube openly funnel-shaped, succulent, 3–4 (–9) × 10 (at filament insertion) mm, lobes elliptic or oblong, slightly succulent, finely grooved dorsally, equal, 10–17 × 4 mm, wilting and turning brown before the female phase of anthesis; **St** 90 mm, exerted for 5–15 mm, light yellowish-green; **Fil** 28–40 mm, stout, tapered towards the apex, greenish-yellow, inserted above mid-tube; **Anth** linear, centric, 9–18 mm, golden-yellow to orange; **Ov** elongate, narrowed at both ends, terete to indistinctly grooved distally, 15–20 (–40) × 6–7 mm, light green, neck slightly constricted; **Sty** 35–40 mm, stout, terete, longer than the filaments, light yellowish-green; **Fr** ovoid-angular, chartaceous, 22–35 × 15–18 mm, dark brown mottled with light brown dots, slightly beaked; **Se** semicircular, flat, 3.5–6 × 3–4 mm, shiny.

The large, thick leaves and the flowers point towards a relationship with *A. parvidentata* (*Gentry* 1982). According to *Smith & Steyn* (2002a) similar to the Venezuelan *A. cocui*, which has a longer peduncle, somewhat longer part-inflorescences with more densely clustered flowers, and is suckering. *A. wercklei* is endemic to the region of the Valle del Río Grande de Candelaria W of San Ignacio de Acosta (*Horich* 1973, *Ullrich* 1992d, *Grayum* 2003). Populations from calcareous rocks at 1700 m near Cerro Caraigres have very dense ‘umbels’ and may represent a separate taxon (*Grayum* 2003: 32). *Smith & Steyn* (2002a) provided a detailed description and illustrations, and established the correct author citation and date and place of publication, correcting an earlier attempt by *Ullrich* (1992d). The lectotype designated by *Gentry* (1982: 501) represents in fact a neotype. The flowers on the specimen ARIZ 0004877 might represent an isoneotype. — *A. wercklei* *Trelease* (1920: 132) (*nom. illeg.*, ICN Art. 53.1) is a different species, of Sect. *Agave* (as Group *Americanae*), with more slender, white-glaucous leaves, cultivated in Costa Rica (*Gentry* 1982: 502).

**A. willdingii** *Todaro* (*Hort. Bot. Panorm.* 2: 36, t. 32, 1878). **Type**: not typified. — **Lit**: *Trelease* (1913: 42–43, tt. 93, 94); *Berger* (1915: 272); *León* (1946: 319); *Álvarez de Zayas* (1981:

37); Álvarez de Zayas (1985: 6–7); Álvarez de Zayas (1995: 41); Acevedo-Rodríguez & Strong (2012: 87); Greuter & Rankin Rodríguez (2017: 35). **Distr:** Only known from cultivation; probably originating from Hispaniola. **I:** Hochstätter (2015: VII: 94).

[2q] Acaulescent; **Ros** solitary; **L** rather few,  $\pm 15$ –30, oblanceolate or oblong-spatulate, erect-spreading, at the base flat and thick, gradually acute, upwards becoming thin and broadly guttered by the upcurved margins,  $50$ – $80 \times 12$ – $16$  cm ( $5$ – $9$  cm at the base), light green or slightly glaucous; **marginal teeth** variously curved, acuminate triangular or somewhat lenticular at the base and on green prominences,  $1$ – $4$  mm, upwards becoming smaller, at first red-brown, absent in the uppermost  $50$ – $70$  mm,  $10$ – $15$  mm apart, intervening margin slightly concave or more rarely straight; **terminal Sp** conical, slit-grooved below the middle, smooth,  $10$ – $15 \times 2$ – $3$  mm, brown, dull, becoming grey, scarcely decurrent; **Inf**  $3$ – $4$  m, paniculate, peduncle slender, with remote appressed **Bra**, fertile part in the upper  $\frac{1}{2}$ , axis slightly arching in the upper part, slightly zig-zag between the branches, **part-Inf** few, very lax, on ascending slender branches, with  $\pm$  densely congested flowers; **Ped** slender,  $5$ – $10$  mm; **Fl**  $30$  to  $<40$  mm; **Tep** yellow-orange to orange-yellow, tube openly conical,  $4 \times 12$  mm, lobes linear,  $10$ – $16 \times 4$  mm, soon fading; **Fil**  $25$ – $30$  mm, inserted nearly in the tube throat; **Anth**  $11$  mm, yellow; **Ov** cylindrical, slender,  $15$  mm, greenish; **Fr** and **Se** unknown.

Todaro's protologue is based on a plant cultivated at BG Palermo (Italy) probably originating from Mexico. According to Berger (1901), who studied the plant at Palermo, it appears to be a form of *A. kewensis*. Trelease (1913) placed it in Sect. *Antillares*, gives its origin as possibly from W Cuba, as indicated by the small, orange-yellow flowers, and on t. 94 depicts specimens from Palermo and from La Mortola where *A. willdingii* was cultivated since long (Berger 1915). *A. willdingii* specimens of Berger are extant (US 1023521 & 1023522; MO 2056808 & 2056809). Álvarez de Zayas (1981) and Álvarez de Zayas (1985) dismiss the Cuban origin of *A. willdingii* and its placement in Sect. *Antillares* due to its

“orange” flowers and the branching pattern of the inflorescence. However, the protologue and Berger (1915) give the flower colour as yellow-orange (“giallo aranciato”) and orange-yellow, respectively; such colours are also found in Sect. *Antillares*. According to Álvarez de Zayas (1995: 41), *A. willdingii* can possibly be included in the species of Sect. *Antillanae* from Hispaniola such as *A. antillarum*, which it indeed resembles. — The species is named after G. Willding, but the epithet is often misspelled ‘*wildingii*’ etc.

**A.  $\times$ winteriana** A. Berger (Agaven, 160, fig. 55 (p. 159), 1915). **Type:** not typified. — **Lit:** Guillot Ortiz & Meer (2012: with ill.); López-Pujol & al. (2015a: 58, with ill.). **Distr:** Cultivated only; naturalized in Spain.

[2a  $\times$  2c?] This is the garden hybrid *A. americana*  $\times$  *A. franzosinii*, which originated in the garden of L. Winter at Bordighera (Italy) (Berger 1915). It is still found in cultivation in Spain (Guillot Ortiz & Meer 2012, López-Pujol & al. 2015a). The involvement of *A. americana* as parent is doubtful: The hybrid is similar to *A. franzosinii*, but much smaller than both stated parents, and the first parent must have been a species which contributed the smaller habit, smaller teeth and cross-zoning to the hybrid; Guillot Ortiz & Meer (2012) suggest *A. sisalana* as possible parent. Some of the plants cultivated in the USA as *A. franzosinii* appear to belong here (see also there). Locally naturalized in Spain (López-Pujol & al. 2015a).

**A. wocomahi** Gentry (Publ. Carnegie Inst. Washington 527: 96–97, t. 17, 1942). **Type** [syn]: Mexico, Chihuahua (Gentry 1989 [CAS [2 sheets], ARIZ [2 sheets], US [2 sheets]]). — **Lit:** Breitung (1962: 142–143, with ill.); Gentry (1972: 105–109, with ills.); Gentry (1982: 456–458, with ills.); McVaugh (1989: 147); Vázquez-García & al. (2007b: 79–80, tt. O6–O7); González-Elizondo & al. (2009: 140–143, with ills.); Klopper & al. (2010: 62); Starr (2012: 292–296, with ills.). **Distr:** Mexico (SE Sonora, SW Chihuahua, N Sinaloa, S Durango, E Jalisco: Sierra Madre Occidental); rocky limestone mountain slopes in pine-oak and thorn forests,  $1350$ – $2500$  m;



flowers July to September. **I:** Bye & al. (1975: 110); Richter (2011: 54); Pilbeam (2013: 240); Hochstätter (2015: IV: 16).

[2h] **Ros** 0.8–1.3 × 1.5–2 m, eventually depressed and open at maturity, single, not suckering; **L** mostly lanceolate to linear-lanceolate, rarely ovate, ascending to depressed with age, thick-fleshy, rather rigid, somewhat narrowed towards the base, flat, smooth, 30–90 × 9–25 cm, dark to glaucous-green, margins straight to repand; **marginal teeth** large, variously curved, below the middle of the lamina frequently down-curved, with smaller irregular intermittent teeth, larger teeth 10–20 mm, dark brown to glaucous-brown; **terminal Sp** stout, usually sinuous, flattened or with a broad groove, 30–60 mm, black to bluish-grey, short- or long-decurrent; **Inf** 3–5 m, paniculate, peduncle with scarious appressed or reflexed **Bra** 15–20 (in the middle) cm long, fertile part open, part-**Inf** small, 8–15 in the upper 1/3 of the inflorescence; **Fl** erect, 65–85 mm; **Tep** yellow, tube deeply funnel-shaped, narrowly grooved below the lobe sinuses, 18–22 × 15 mm, light yellow, lobes erect, thick, linear, conduplicate, rounded and deeply hooded at the tip, dimorphic, 15–23 × 5 mm, outer with papillate pubescence well below the apex and sometimes red-tipped, inner shorter and prominently keeled, yellow; **Fil** 60–65 mm, inserted unequally 9–14 mm above the tube base; **Anth** excentric, 26–34 mm, yellow; **Ov** cylindrical, 34–40 mm incl. a 2–5 mm long neck, light green; **Sty** longer than the tepals; **Sti** capitate; **Fr** oblong, 50–60 × ≥ 15 mm, shortly stipitate; **Se** oblique, flattened on the end opposite the hilar notch, 7 × 4.5–5 mm, finely punctulate, wavy-corrugate, with a narrow margin partly upcurved, shiny black.

In the protologue, Gentry designated his collection “1989” as “type”. His later designation of a lectotype (as “holotype CAS”; Gentry 1982: 456) consists of 2 sheets which were apparently cross-labelled later.

A montane mesophyte, uncommon and with populations consisting of small colonies with widely scattered individuals. The dimorphic tepal lobes place *A. wocomahi* in Sect. *Ditepalae*. It is sometimes sympatric with the habitually similar *A. shrevei* from the same section, from which it is

usually easily distinguished by its dark green leaves and more remote teeth, and the different flowers. It is easily confused with *A. bovicornuta* (Sect. *Crenatae* (as Group)) with lighter yellowish-green leaves conspicuously narrowed just above the base, and with different flowers (Gentry 1982). Morphologically also similar to the recently published *A. temacapulinensis*. Hernández-Vera & al. (2007a) provide a new record from Jalisco. The flowers are visited by hummingbirds (photo in Starr (2012)). Baked “hearts” are used to produce mescal bread (“mesagoli”) and a fermented alcoholic beverage (“sugui”) (Bye & al. 1975: 96).

**A. xylonacantha** Salm-Dyck (Bonplandia 7: 92, 1859). **Type:** [neo — icono]: Curtis’s Bot. Mag. 93: t. 5660, 1867. — **Lit:** Berger (1915: 112–114); Breitung (1959: 116, with ill.); Gentry (1982: 186–188, with ill.); Alsemgeest & al. (2007b: with ill.); Eguiarte & Scheinvar (2008: 40–43, with ill.); Starr (2012: 297–301, with ill.). **Dist:** Mexico (Tamaulipas, San Luis Potosí, Guanajuato, Querétaro, Hidalgo); dry limestone slopes and valleys, on the desert side of the Sierra Madre Oriental, 90–1900 m; flowers February to July. **I:** Irish & Irish (2000: t. 51); Etter & Kristen (2006: 258); Heller (2006: 23, 150, 151); Spracklin (2007: 150); Zuijlen (2008: 76, 82); Pilbeam (2013: 241); Hochstätter (2015: IX: 45); Moore (2016: 276); Greulich (2016c: 152).

**Incl.** *Agave xylonacantha* var. *latifolia* Jacobi (s.a.) (*nom. inval.*, ICN Art. 29.1?); **incl.** *Agave xylonacantha* var. *macracantha* Jacobi (s.a.) (*nom. inval.*, ICN Art. 29.1?); **incl.** *Agave xylonacantha* var. *torta* Jacobi (s.a.) (*nom. inval.*, ICN Art. 29.1?); **incl.** *Agave amurensis* Jacobi (1864); **incl.** *Agave kochii* Jacobi (1866); **incl.** *Agave splendens* Jacobi (1870) ≡ *Agave heteracantha* var. *splendens* (Jacobi) A. Terracciano (1885); **incl.** *Agave vanderdonckii* hort. ex Baker (1877); **incl.** *Agave xylacantha* hort. (1877) (*nom. inval.*, ICN Art. 61.1); **incl.** *Agave carchariodonta* Pampanini (1907) ≡ *Agave univittata* var. *carchariodonta* (Pampanini) Breitung (1959); **incl.** *Agave xylonacantha* [?] *mediopicta* Trelease (1908); **incl.** *Agave xylonacantha* var. *horizontalis* hort. ex A. Berger (1915); **incl.** *Agave cornuta* Hort. Besauccèle ex A. Berger (1915) (*nom. inval.*,

ICN Art. 36.1c/38.1a); **incl.** *Agave maximiliana* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave vanderdonckii* var. *horizontalis* Hort. Besaucèle ex A. Berger (1915) (*nom. inval.*, ICN Art. 36.1c/38.1a); **incl.** *Agave xylonacantha* [?] *minor* Heller (2006) (*nom. inval.*, ICN Art. 38.1a).

[1g] Stems short; **Ros** openly spreading, to  $0.9 \times 1.2$  m, solitary or occasionally caespitose; **L** ensiform-lanceolate, rather rigid, broadest in the middle, long-acuminate, rounded below, flat to concave above,  $45\text{--}90 \times 5\text{--}10$  cm, green to yellowish-green, sometimes glaucous, with or without a pale mid-stripe, margins horny, continuous, straight between the remote conspicuous prominences but looping over the prominences; **marginal teeth** broadly flattened, thickly terminating the broad prominences, frequently 3- to 5-tipped, 8–15 mm, light grey, commonly 20–50 mm apart; **terminal Sp** trigonous-subulate, stout, flat to slightly grooved above, keeled below, 25–50 mm, light grey; **Inf** erect, 3–6 m, ‘spicate’, peduncle with very narrow chartaceous **Bra**, fertile part long-tapering, in the upper  $\frac{1}{2}\text{--}\frac{2}{3}$  of the inflorescence, part-**Inf** with 2–3 flowers; **Fl** 40–50 mm; **Tep** greenish to pale yellow, tube 3–5 mm, lobes  $3\text{--}5 \times 8\text{--}10$  mm, erect, narrowing and clasping the filaments at anthesis,  $\pm$  equal,  $15\text{--}20 \times 4\text{--}5$  mm; **Fil** slender, 38–42 mm, sometimes red or purple; **Anth** excentric, 17–22 mm; **Ov** fusiform, 4-angulate, 20–27 mm; **Sty** slender, much shorter than the filaments, yellowish-green; **Sti** small, capitate; **Fr** linear-oblong,  $20 \times 10$  mm, beak very short, shortly stipitate, brownish, pruinose; **Se** crescent-shaped,  $6 \times 3$  mm. — **Cytology**:  $2n = 60$  (Granick 1944, Simpson & al. 2011).

Related to *A. lophantha*. The highly convoluted leaf margins with large, flattened, several-tipped teeth are like an exaggeration of the forms known from *A. lophantha* (Gentry 1982: 188). Var. “*minor*” Heller (2006: 150) is a horticultural name for a small form with shorter leaves. Plants from Ezequiel Montes (Querétaro) with exceptionally strong and wildly curved horny teeth (Richter 2011: 121) may belong here. For the closely related *A. megalodonta*, see there. Gentry (1982: 188) designated the neotype cited above.

The flowers produce nectar between 22:00 and 6:00 and are mainly visited by bats and bees, also by sphingids, bumblebees and hummingbirds. The fruit and seed set belongs to the highest among the studied agaves. Populations show a moderate genetic variation. Variation is higher in the Barranca de Metztlán than outside of the barranca, suggesting that the species may have originated there. Compared to other agaves, genetic diversity and structure is low, possibly associated with a very recent origin and/or a high efficiency of its pollinators, mainly bats (Eguiarte & Scheinvar 2008). — ‘Frostbite’ is a variegated cultivar (Starr 2012).

**A. yavapaiensis** W. C. Hodgson & Salywon (Brittonia 65(1): 10, ills. (pp. 8–9), 2013). **Type**: USA, Arizona (Hodgson & Salywon 25496 [DES, ASC, ASU, MO, NY]). — **Lit**: Parker (2018a: 22, 27, with ills.). **Distr**: USA (C Arizona); rocky, clayey-loamy soils derived from igneous rocks, less frequently on limestone soils, in semi-arid desert grassland to pinyon-juniper woodland, 915–1220 m; flowers late June to early August. **I**: Hochstätter (2015: III: 10).

[2h] **Ros**  $\pm 60\text{--}70 \times 60\text{--}70$  cm, open, freely offsetting via rhizomes, forming clones of few to several rosettes; **L** numerous, narrowly elliptic to linear-oblong, erect-spreading, firm, deeply guttered, abruptly acuminate, broadest at or just above or below the middle,  $33.5\text{--}50 \times 4.2\text{--}8$  cm, blue-green, usually without maroon flush distally; **marginal teeth** porrect, upturned or recurved, firmly attached, grey, red-brown to dark mahogany, close-set, intermittent teeth 3–7 along the distal  $\frac{2}{3}$  of the leaf margin; **terminal Sp** 16–31 mm, grey to dark brown-grey, decurrent; **Inf** to 4–6 m, narrowly paniculate, peduncle dark green-maroon, glaucous, part-**Inf** 16–18, slightly ascending, 13–18 cm, in the upper  $\frac{2}{3}$  of the inflorescence; **Fl** 42–57 mm, with a sweet-musky fragrance at anthesis; **Tep** thickish, bulging at the lobe bases, tube  $13\text{--}16 \times 11\text{--}15.5$  mm, dark chartreuse-green, lobes persistently erect, leathery with age, unequal, outer 11–12 mm, cream to cream-yellow, with brown papillose-pubescent cucullate tips, inner 9–10.5 mm, cream to cream-yellow, strongly keeled, with white hairs within the

tips; **Fil** 33–43 mm, cream-yellow, subequally inserted 5–10.5 mm above the tube base; **Ov** 20–26 × 5–8.5 mm, green to dark chartreuse-green, neck 2–4 mm; **Sty** 28–39 mm, longer than the tepals, light cream; **Sti** capitate; **Fr** produced only on the uppermost part-inflorescences, linear to linear-oblong, 34–42 × 11–17 mm, apiculate, stipe 4–6 mm; **Se** only few per capsule, 5 × 4 mm, dull black. — **Cytology**: 2n = 60 (protologue).

According to the protologue a pre-Columbian cultivar species most similar to *A. verdensis*, another pre-Columbian cultivar, from which it differs in its leaf shape and colour, the orientation of the marginal teeth, the colour of the tepal lobe apices and the ovary, and its conspicuously stipitate, narrower fruits. It also shows similarities with *A. chrysantha* and *A. shrevei*. For further pre-Columbian cultivar species in Arizona, see under *A. verdensis*.

**A. zapopanensis** (E. Solano & Ríos-Gómez) Thiede (Haseltonia 17: 95, 2012). **Type**: Mexico, Jalisco (*Castillejos C. & Solano C.* 1564 [MEXU, CHAPA, ENCB, FEZA, IBUG, IEB, NY, UAMIZ]). — **Lit**: Solano & Ríos-Gómez (2011: with ill., as *Polianthes*). **Distr**: Mexico (C Jalisco); in oak forests and ecotones with tropical deciduous and pine-oak forests, 1235–1950 m; flowers July to September. **I**: Castro-Castro & al. (2015: 145); Hochstätter (2016: II: 25); Castro-Castro & al. (2016: 721); all as *Polianthes*.

≡ *Polianthes zapopanensis* E. Solano & Ríos-Gómez (2011).

[3b2] Herbaceous; corm cylindrical, 0.5–2.5 (–3) × 0.9–2 cm, with renewal buds, bulb ovoid, 3.5–5.7 × 1.7–2.5 (–4.2) cm, covered with dried leaf bases; **R** fleshy, thickened, contractile, 5–13 cm long; **L** drought-deciduous, 3–5 in sterile plants, ascending, arching over, linear, cartilaginous, lower face with lines of prominent papillae on the veins, upper face glabrous, apex acute, thickened, 43–61 × (0.17–) 0.3–0.7 (–1) cm, green, margins denticulate or papillose, scaberulous, papillae smaller than those on the veins, irregularly distributed; **Inf** (0.6–) 1–1.9 m, erect, ‘spicate’, peduncle with ±8–9 **Bra**, these similar to the leaves, base truncate, bracts and

internodes decreasing in size upwards, fertile part 41–98 cm, lax, with (12–) 16–44 floral nodes, usually with 1–2 branches 6–24 cm long, between the 5. and the 8. node; floral **Bra** 5–15 × 1–2.5 mm; **Ped** 6–19 mm, ± ascending; **Fl** geminate, 18–27 mm, diffuse to divaricate at anthesis, zygomorphic, funnel-shaped, unscented; **Tep** orange or pink, succulent, slightly curved, tube 14–20 × 2–3 mm at the base of the lobes, dorsally papillate, lobes subequal, erect, broadly ovate or transversally elliptic, succulent, papillose on both faces, much shorter than the tube, 1–3 × 1–3 mm, apex cucullate, obtuse to rounded, papillose, margin hyaline, rarely green; **Fil** filiform, 5.5–10 mm, included, inserted 5–7 mm above the ovary apex, yellow; **Anth** linear, 5–8 mm, yellow, at anthesis at the mouth of the tube; **Ov** cylindrical, 3–4 × 2–3 mm; **Sty** filiform, 10–18 mm, yellow, included; **Sti** 3-lobed, papillose; **Fr** globose, 10 × 12 mm, tepals persisting; **Se** deltoid, flat, 4–5 × 2.8–3.8 mm, dull or shiny.

Belonging to Ser. *Bravoa* (as Group) of Sect. *Polianthes* according to the protologue, and differing from the other species in its thick infundibuliform flowers and its usually branched inflorescences. The species shows morphological similarities with *A. coetocapnia*, *A. graminifolia* and *A. oaxacana*.

**A. zebra** Gentry (US Dept. Agric. Handb. 399: 126–130, ill., 1972). **Type**: Mexico, Sonora (*Gentry* 21984 [US [2 syn], ARIZ, MEXU, MICH]). — **Lit**: Gentry (1982: 516–518, with ill.); Turner & al. (1995); Velazco Macías & Alanís Flores (2002); Starr & al. (2008: 172–175, with ill.); Starr (2012: 302–307, 320–321, with ill.). **Distr**: Mexico (Sonora: Sierra del Viejo, Cerro Quituni); arid limestone slopes with desert scrub, 700–1000 m; flowers late June to August. **I**: Irish & Irish (2000: t. 52); Etter & Kristen (2001: 168); Richter (2011: 82, 129); Pilbeam (2013: 242–243); Hochstätter (2015: VI: 23); Greulich (2017a: 47). – Fig. 62.

[2n] **Ros** rather open, low-spreading, 0.4–0.6 × 1–1.6 m, solitary (in cultivation also offsetting); **L** lanceolate, arcuate, thick, rigid, narrowed above the base, broadest near the middle, deeply guttered, scabrous, 50–80 × 12–17 cm, light grey-glaucous,

**Fig. 62** *Agave zebra*  
(Etter & Kristen 539:  
Mexico; Sonora,  $\pm$  30 km S  
of Caborca, 500 m).  
(Copyright: J. Etter &  
M. Kristen)



conspicuously cross-zoned, margins strongly repand; **marginal teeth** variously curved, strong, flattened, large, mostly 10–20 mm (at mid-leaf), grey with chestnut-brown tips, 10–30 mm apart, bases broad, low, scabrous, 25–40 on each margin, on conspicuous prominences; **terminal Sp** acicular, mostly very narrowly grooved above, 35–75 mm, yellowish-brown to light grey, scabrously decurrent for 5–10 cm to the uppermost teeth; **Inf** 6–8 m, paniculate, with large **Bra** towards the base, fertile part narrow, part-**Inf** small, 7–14 in the upper  $\frac{1}{5}$ – $\frac{1}{4}$  of the inflorescence; **Ped** angled, very short; **Fl** 40–55 mm; **Tep** yellow, tube funnel-shaped, bulging, deeply sulcate, 6–7 mm, lobes lanceolate, erect to ascending, revolute, cucullate,  $\pm$  equal, 12–15  $\times$  5–6 mm, inner prominently keeled; **Fil** broad, 35–40 mm, inserted at mid-tube; **Anth** 15–18 mm; **Ov** cylindrical-angulate, slender, straight, 25–32 mm, neck slightly constricted, 6-sulcate; **Sty** longer than the tepals; **Sti** capitate; **Fr** oblong to obovate, with strong and conspicuously lined walls, mostly 40–50  $\times$  12–15 mm, stipitate, apex round, apiculate; **Se** obliquely rounded, concave on one side or both faces, 4.5–5  $\times$  4–4.5 mm, marginal wing very low, hilar notch shallow.

The attractive cross-striping of the leaves appears to be accentuated in plants exposed to full sunshine; seedlings show the banding already from a very early age (Pilbeam 2013). Velazco

Macías & Alanís Flores (2002) list it as endemic to the Sierra el Viejo, but it also occurs on nearby Cerro Quituni (Aquituni) as given by Gentry (1972), Gentry (1982) and Turner & al. (1995). The “holotype” at US consists of 2 sheets which are not cross-labelled (but both have the same identical label) and thus represent syntypes.

## References

- Acebes Ginovés, J. R. [& al. 2010], León Arencibia, M. C., Rodríguez-Navarro, M. L., Aguilar, M. del A., García Gallo, A., Pérez de Paz, P. L., Delgado, O. R., Martín Osorio, V. M. & Wildpret de la Torre, W. (2010) Pteridophyta, Spermatophyta. In: Arechavaleta, M. & al. (eds.): Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres), Ed. 2; pp. 119–172. La Laguna (ES): Gobierno de Canarias.
- Acevedo-Rodríguez, P. & Strong, M. T. (2012) Catalogue of seed plants of the West Indies. Smithsonian Contr. Bot. 98: i–xxv, 1–1192, maps. <https://doi.org/10.5479/si.0081024X.98.1>.
- Acuña, A. M. [& al. 2011], Caso, L., Aliphath, M. M. & Vergara, C. H. (2011) Edible insects as part of the traditional food system of the Popoloca town of Los Reyes Metzontla, Mexico. J. Ethnobiol. 31(1): 150–169. <https://doi.org/10.2993/0278-0771-31.1.150>.
- Acuña, J. M. (2018) The genus *Leptocereus* in Cuba. Part 1: Populations in Pinar del Río, the most western region of the island. Xerophilia 7(1): 27–42, ill.
- Adams, C. D. (1972) Flowering plants of Jamaica. Mona (JM): University of the West Indies.
- Adams, C. D. & Baksh-Comeau, Y. S. (2005) Checklist of the vascular plants of Chacachacare Island, Trinidad



- and Tobago. Living World J. Trinidad & Tobago Field Natural. Club 2005: 1–10.
- Adams, K. R. & Adams, R. K. (1998) How does our agave grow? Reproductive history of a suspected ancient Arizona cultivar, *Agave murpheyi* Gibson. Desert Pl. 14(2): 11–20. <http://repository.arizona.edu/handle/10150/554320>
- Aguirre-Dugua, X. & Eguiarte, L. E. (2013) Genetic diversity, conservation and sustainable use of wild *Agave cupreata* and *Agave potatorum* extracted for mezcal production in Mexico. J. Arid Environm. 90: 36–44, map, ills. <https://doi.org/10.1016/j.jaridenv.2012.10.018>.
- Alarcón, R. [& al. 2010], Riffell, J. A., Davidowitz, G., Hildebrand, J. G. & Bronstein, J. L. (2010) Sex-dependent variation in the floral preferences of the hawkmoth *Manduca sexta*. Animal Behav. 80(2): 289–296. <https://doi.org/10.1016/j.anbehav.2010.05.007>.
- Alfaro Rojas, G. [& al. 2007], Legaria Solano, J. P. & Rodríguez Pérez, J. E. (2007) Diversidad genética en poblaciones de Agaves pulqueros (*Agave sp.*) del nororiente del estado de México. Revista Fitotec. Mex. 30(1): 1–12. <http://www.redalyc.org/comocitar.oa?id=61030101>
- Almaraz-Abarca, N. [& al. 2009], Delgado-Alvarado, E. A., Hernández-Vargas, V., Ortega-Chávez, M., Orea-Lara, G., Cifuentes-Díaz de León, A., Ávila-Reyes, J. A. & Muñiz-Martínez, R. (2009) Profiling of phenolic compounds of somatic and reproductive tissues of *Agave durangensis* Gentry (*Agavaceae*). Amer. J. Appl. Sci. 6(6): 1076–1085. <https://doi.org/10.3844/ajassp.2009.1076.1085>.
- Almaraz-Abarca, N. [& al. 2013a], Delgado-Alvarado, E. A., Ávila-Reyes, J. A., Uribe-Soto, J. B. & González-Valdez, L. S. (2013) The phenols of the genus *Agave* (*Agavaceae*). J. Biomater. Nanobiotechnol. 4(3A): 9–16. <https://doi.org/10.4236/jbnb.2013.43A002>.
- Almaraz-Abarca, N. [& al. 2013b], Delgado-Alvarado, E. A., Torres-Morán, M. I., Herrera-Corral, J., Ávila-Reyes, J. A., Naranjo-Jiménez, N. & Uribe-Soto, J. N. (2013) Genetic variability in natural populations of *Agave durangensis* (*Agavaceae*) revealed by morphological and molecular traits. Southw. Naturalist 58(3): 314–324. <https://doi.org/10.1894/0038-4909-58.3.314>.
- Almaraz-Abarca, N. [& al. 2013c], González-Elizondo, M. del S., Campos, M. da G., Ávila-Sevilla, Z. E., Delgado-Alvarado, E. M. & Ávila-Reyes, J. A. (2013) Variability of the foliar phenol profiles of the *Agave victoriae-reginae* complex (*Agavaceae*). Bot. Sci. 91(3): 295–306. <https://doi.org/10.3844/ajassp.2009.1076.1085>.
- Alsemgeest, W. (2004) De geschiedenis rond *Agave ellemeetiana* Jac., een plant genoemd naar een Nederlander. Succulenta 83(3): 105–118, ills.
- Alsemgeest, W. (2006) Ervaringen met Agaven in cultuur. 3. Succulenta 85(1): 18–25, ills.
- Alsemgeest, W. (2013) *Agave albopilosa*. Succulenta 92(2): 58–63, ills.
- Alsemgeest, W. & Roosbroeck, J. van (2010) De vormen rond *Agave parryi*—deel 1/2/3/4. Succulenta 89(1): 33–40, (2): 68–74, (3): 178–182, (4): 276–281, ills.
- Alsemgeest, W. & Roosbroeck, J. van (2012?) De vormen rond *Agave parryi*—deel 9. sine loco (NL): Digitally published by the authors.
- Alsemgeest, W. [& al. 2005], Roosbroeck, J. van & Walderveen, T. van 't (2005) *Agave applanata*, de metamorfose van een Agavesoort... Succulenta 84(6): 246–250, ills.
- Alsemgeest, W. [& al. 2006a], Roosbroeck, J. van & Walderveen, T. van 't (2006) Agaven en bloei. 1. *Agave spicata* Cavanilles. Succulenta 85(4): 167–171, ills.
- Alsemgeest, W. [& al. 2006b], Roosbroeck, J. van & Walderveen, T. van 't (2006) Agaven en bloei. 2. *Agave obscura*. Succulenta 85(5): 211–216, ills.
- Alsemgeest, W. [& al. 2007a], Roosbroeck, J. van & Walderveen, T. van 't (2007) *Agave victoriae-reginae*. Succulenta 86(2): 63–69, ills.
- Alsemgeest, W. [& al. 2007b], Roosbroeck, J. van & Walderveen, T. van 't (2007) *Agave xylonacantha* en *Agave heteracantha*. Succulenta 86(5): 225–235, ills.
- Álvarez de Zayas, A. (1981) *Agave cajalbanensis*: Una nueva especie de Cuba occidental. Revista Jard. Bot. Nac. Univ. Habana 1(2–3): 33–39, ills. <http://www.jstor.org/stable/42596598>
- Álvarez de Zayas, A. (1985) Los Agaves de Cuba occidental. Revista Jard. Bot. Nac. Univ. Habana 5(3): 3–16, ills. <http://www.jstor.org/stable/42596752>
- Álvarez de Zayas, A. (1995) Los Agaves de las Antillas. Bol. Soc. Bot. México 57: 37–48, ills., map.
- Álvarez de Zayas, A. (1996) Los Agaves de Cuba central. Fontqueria 44: 117–128, ills., key, maps. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=3135>
- André, E. (1903) Les plantes nouvelles à l'exposition quinquennale de Gand. Rev. Hort. (Paris) 75: 224–227. <http://biodiversitylibrary.org/page/49711930>
- André, E. (1904) Chronique horticole. Floraisons d'Agaves. Rev. Hort. (Paris) 76: 325–326. <http://biodiversitylibrary.org/page/49737192>
- Anonymous (1872) Melanges. Un échantillon de “fun” anglais. Ill. Hort., n.s. [= sér. 3] 19(6): 172. <http://biodiversitylibrary.org/page/15848721>
- Anonymous (1874) Royal Botanic. Gard. Chron., ser. nov. 1: 545. <http://biodiversitylibrary.org/page/26045863>
- Anonymous (1892) *Agave engelmanni* [sic!]. Wiener Ill. Gart.-Zeitung 17: 398.
- Anonymous (1910) Hybrids raised at Kew. Bull. Misc. Inform. Kew 1910(9): 321.
- Anonymous (1913) *Agave leopoldii*. Gard. Chron., ser. 3, 53: 10–11. <http://biodiversitylibrary.org/page/25915772>
- Anonymous (1940) *Manfreda guttata*. Desert Pl. Life 12: 174–175, ills.
- Applequist, W. L. (2014) Report of the Nomenclature Committee for Vascular Plants: 66. Taxon 63(6): 1358–1371. <https://doi.org/10.12705/636.20>.
- Applequist, W. L. (2016) Report of the Nomenclature Committee for Vascular Plants: 68. Taxon 65(5): 1153–1165. <https://doi.org/10.12705/655.16>.
- Archibald, J. K. [& al. 2015], Kephart, S. R., Theiss, K. E., Petrosky, A. L. & Culley, T. M. (2015) Multilocus



- phylogenetic inference in subfamily *Chlorogaloideae* and related genera of *Agavaceae*—Informing questions in taxonomy at multiple ranks. *Molec. Phylogen. Evol.* 84: 266–283, ills., map. <https://doi.org/10.1016/j.ympev.2014.12.014>.
- Arévalo, J. R. [& al. 2015], Fernández-Lugo, S., Mellado, M. & Concepción, T. de la (2015) Experimental management control of *Opuntia dillenii* Haw. and *Agave americana* L. in Teno Rural Park, Canary Islands. *Pl. Spec. Biol.* 30(2): 137–146. <https://doi.org/10.1111/1442-1984.12049>.
- Arias Toledo, A. A. [& al. 2000], Valverde Valdés, M. T. & Reyes Santiago, J. (2000) Las plantas de la región de Zapotitlán Salinas, Puebla. México D.F. (MX): Instituto Nacional de Ecología. [http://centro.paot.mx/documentos/ine/plantas\\_zapo.pdf](http://centro.paot.mx/documentos/ine/plantas_zapo.pdf)
- Arizaga, S. & Ezcurra, E. (1995) Insurance against reproductive failure in a semelparous plant: Bulbil formation in *Agave macroacantha* flowering stalks. *Oecologia* 101(3): 329–334. <https://doi.org/10.1007/BF00328819>.
- Arizaga, S. & Ezcurra, E. (2002) Propagation mechanisms in *Agave macroacantha* (*Agavaceae*), a tropical aridland succulent rosette. *Amer. J. Bot.* 89(4): 632–641, ills. <https://doi.org/10.3732/ajb.89.4.632>.
- Arizaga, S. [& al. 2000a], Ezcurra, E., Peters, E., Arellano, F. R. de & Vega, E. (2000) Pollination ecology of *Agave macroacantha* (*Agavaceae*) in a Mexican tropical desert. I. Floral biology and pollination mechanisms. *Amer. J. Bot.* 87(7): 1004–1010. <https://doi.org/10.2307/2657000>.
- Arizaga, S. [& al. 2000b], Ezcurra, E., Peters, E., Arellano, F. R. de & Vega, E. (2000) Pollination ecology of *Agave macroacantha* (*Agavaceae*) in a Mexican tropical desert. II. The role of pollinators. *Amer. J. Bot.* 87(7): 1011–1017. <https://doi.org/10.2307/2657001>.
- Arzate García, K. M. (2009) Distribución de cinco especies de *Agave* y su relación con algunos parámetros ambientales en Metztlitlán, Hidalgo. México D.F. (MX): UNAM, Posgrado en Ciencias Biológicas, Instituto de Ecología; thesis.
- Asensi, A. [& al. 2016], Díez-Garretas, B. & Pereña, J. (2016) Alien plants of coastal dune habitats in southern Spain. *Pl. Biosystems* 150(3): 477–483, map. <https://doi.org/10.1080/11263504.2014.973463>.
- Avendaño-Arrazate, C. [& al. 2015], Iracheta-Donjuan, L., Gódinez-Aguilar, J. C., López-Gómez, P. & Barrios-Ayala, A. (2015) Caracterización morfológica de *Agave cupreata*, especie endémica de México. *Phyton* (Buenos Aires) 84: 148–162, ills. <http://ppct.caicyt.gov.ar/index.php/phyton/article/view/8121>
- Ávila-Akerberg, V. [& al. 2008], González-Hidalgo, B., Nava-López, M. & Almeida-Leñero, L. (2008) Refugio de fitodiversidad en la ciudad de México, el caso de la cuenca del Río Magdalena. *J. Bot. Res. Inst. Texas* 2 (1): 605–619. <http://biodiversitylibrary.org/page/41650613>
- Aymerich, P. (2015) Nuevos datos sobre plantas suculentas alóctonas en Cataluña. *Bouteloua* 22: 99–116, ills.
- Aymerich, P. (2016) Notas sobre plantas alóctonas de origen ornamental en el litoral septentrional de Cataluña. *Bouteloua* 26: 78–91, ills.
- Aymerich, P. & Gustamante, L. (2016) Nuevas citas de plantas alóctonas de origen ornamental en el litoral meridional de Cataluña, II. *Bouteloua* 24: 93–112, ills.
- Baker, J. G. (1877a) The genus *Agave*. *Gard. Chron.*, ser. nov. 7: 171, 303, 368–369, 527, 620, 717, ills., key. <http://www.biodiversitylibrary.org/item/84215#page/185/>
- Baker, J. G. (1877b) The genus *Agave*. *Gard. Chron.*, ser. nov. 8: 40, 136, 200, 264, 396, 490, 556–558, 620, 682, 717, 748, 780, 807–808, ills. <http://biodiversitylibrary.org/page/27984874>
- Baker, J. G. (1887) *Agave* (*Eu-Agave*) *morrisii* Baker n.sp. *Gard. Chron.*, ser. 3, 1: 543, fig. 105 (p. 549). <https://biodiversitylibrary.org/page/33039215>
- Baker, J. G. (1888a) Handbook of the *Amaryllideae*, including the *Alstroemerieae* and *Agaveae*. London (UK): G. Bell & Sons. <https://doi.org/10.5962/bhl.title.15516>.
- Baker, J. G. (1888b) *Agave ellemeetiana*. *Curtis's Bot. Mag.* 114: t. 7027 + 2 pp. text. <https://biodiversitylibrary.org/page/437475>
- Baker, J. G. (1892) Agaves and arborescent *Liliaceae* on the Riviera. *Bull. Misc. Inform. Kew* 1892(61): 1–10. <http://www.jstor.org/stable/4102510>
- Baker, M. A. [& al. 2009], Rebman, J., Parfitt, B., Pinkava, D., Christy, C., Salywon, A., Puente-Martinez, R., Zimmerman, A. & Cota, J. H. (2009) Chromosome numbers of miscellaneous Angiosperm taxa. *J. Bot. Res. Inst. Texas* 3(1): 279–283. <http://www.jstor.org/stable/41972167>
- Baksh-Comeau, Y. S. [& al. 2016], Maharaj, S. S., Adams, C. D., Harris, S. A., Filer, D. L. & Hawthorne, W. D. (2016) An annotated checklist of the vascular plants of Trinidad and Tobago with analysis of vegetation types and botanical ‘hotspots’. *Phytotaxa* 250(1): 1–431. <https://doi.org/10.11646/phytotaxa.250.1.1>.
- Banerjee, S. & Sharma, A. K. (1989) Structure and behavior of chromosomes in four different species of *Agave*. *Cytologia* 54(4): 667–672. <https://doi.org/10.1508/cytologia.54.667>.
- Barba-Gonzalez, R. [& al. 2012], Rodríguez-Domínguez, J. M., Castañeda-Saucedo, C. A., Rodríguez, A., Tuyl, J. M. van & Tapia-Campos, E. (2012) Mexican geophytes. I. The genus *Polianthes*. *Floricult. Ornament. Biotechnol.* 6: Special Issue 1, pp. 122–128, map, ills.
- Barraza Morales, A. [& al. 2006], Sánchez Teyer, F. L., Robert, M., Esqueda, M. & Gardea, A. (2006) Variabilidad genética en *Agave angustifolia* Haw. de la Sierra Sonorense, México, determinada con marcadores AFLP. *Revista Fitotec. Mex.* 29(1): 1–8. <http://www.redalyc.org/pdf/610/61029101.pdf>
- Barriada-Bernal, G. [& al. 2013], Almaraz-Abarca, N., Gallardo-Velázquez, T., Torres-Morán, I., Herrera-Arrieta, Y., González-Elizondo, S. & Delgado-Alvarado, E. A. (2013) Seed vigor variation of *Agave durangensis* Gentry (*Agavaceae*). *Amer. J. Pl. Sci.* 4(11): 2227–2239. <https://doi.org/10.4236/ajps.2013.411276>.

- Barriada-Bernal, L. G. [ & al. 2014], Almaraz-Abarca, N., Delgado-Alvarado, E. A., Gallardo-Velázquez, T., Ávila-Reyes, J. A., Torres-Morán, M. I., González-Elizondo, M. del S. & Herrera-Arrieta, Y. (2014) Flavonoid composition and antioxidant capacity of the edible flowers of *Agave durangensis* (Agavaceae). *CYTA J. Food* 12(2): 105–114. <https://doi.org/10.1080/19476337.2013.801037>.
- Bennett, M. D. & Leitch, I. J. (1995) Nuclear DNA amounts in angiosperms. *Ann. Bot. (Oxford)*, n.s. 76(2): 113–176. <https://doi.org/10.1006/anbo.1995.1085>.
- Benson, L. (1943) Revisions of status of southwestern desert trees and shrubs. *Amer. J. Bot.* 30(3): 230–240. <http://www.jstor.org/stable/2437244>
- Bentham, J. & Hooker, J. D. (1883) *Genera Plantarum*. Vol. 3, part 2. London (GB): Lovell Reeve & Co; Williams & Norgate. <http://biodiversitylibrary.org/page/655981>
- Berazaín, R. [ & al. 2005], Areces, F., Lazcano, J. C. & González, L. R. (2005) Lista Roja de la flora vascular cubana. Gijón (ES): Jardín Botánico Atlántico.
- Berger, A. (1898) *Agaven*. *Gartenwelt* 2: 577–579, 591–594, 603–605, ill.
- Berger, A. (1901) Eine Reise nach dem botanischen Garten von Palermo. *Monatsschr. Kakt.-kunde* 11(3): 35–38. <http://biodiversitylibrary.org/page/14067721>
- Berger, A. (1904) Neue Sukkulenten aus dem Botanical Magazine 1903. *Monatsschr. Kakt.-kunde* 14(8): 125–127. <http://biodiversitylibrary.org/page/14257580>
- Berger, A. (1912) *Hortus mortolensis: Enumeratio plantarum in Horto Mortolensi cultarum*. Alphabetical catalogue of plants growing in the garden of the late Sir Thomas Hanbury at La Mortola, Italy. London (GB): West, Newman & Co. <https://doi.org/10.5962/bhl.title.10950>.
- Berger, A. (1915) *Die Agaven. Beiträge zu einer Monographie*. Jena (DE): Verlag Gustav Fischer. <https://doi.org/10.5962/bhl.title.15643>.
- Berger, A. (1918) *Agave fourcroydes*. *Curtis's Bot. Mag.* 144: t. 8746 + text. <http://biodiversitylibrary.org/page/471574>
- Bernal, R. [ & al. 2015], Gradstein, S. R. & Celis, M. (eds.) (2015) *Catálogo de plantas y líquenes de Colombia*. Bogotá (CO): Universidad Nacional de Colombia, Sede Bogotá, Facultad de Ciencias, Instituto de Ciencias Naturales. <http://catalogoplantadecolombia.unal.edu.co>
- Bernhard, S. (2012) Extraseite zur Blüte einer *Agave weberi* J. F. Cels ex J. Poiss. in den Tropengewächshäusern des Loki-Schmidt-Garten Botanischer Garten der Universität Hamburg. [http://www.sven-bernhard.de/anzeige\\_agave.htm](http://www.sven-bernhard.de/anzeige_agave.htm)
- Berthold, W. (2017) Auf biologischer Exkursion im Süden Mexikos—Selva el Ocote in Chiapas. *Berliner Kakt.-Blätt.* 17: 48–53, ills.
- Beutelspacher, C. R. & García-Martínez, R. (2017) Primer registro de *Agave lophantha* Schiede (*Asparagaceae*) para Chiapas, México. *Lacandonia* 11(1): 7–10.
- Bhattacharyya, G. N. (1968) Chromosomes in different species of *Agave*. *J. Cytol. Genet.* 3: 1–6.
- Biletzke, D. (2016) Zwischen Mangrove und Trockenbusch—ein Streifzug durch Fauna und Flora der kubanischen Cayos. *Berliner Kakt.-Blätt.* 16: 26–34, ills.
- Binh, L. T. [ & al. 1990], Muoi, L. T., Oanh, H. T. K., Thang, T. D. & Phong, D. T. (1990) Rapid propagation of *Agave* by in vitro tissue culture. *Pl. Cell Tissue Organ Cult.* 23(1): 67–70. <https://doi.org/10.1007/BF00116091>.
- Blancas, J. [ & al. 2010], Casas, A., Rangel-Landa, S., Moreno-Calles, A., Torres, I., Pérez-Negrón, E., Solís, L., Delgado-Lemus, A., Parra, F., Arellanes, Y., Caballero, J., Cortés, L., Lira, R. & Dávila, P. (2010) Plant management in the Tehuacán-Cuicatlán Valley, Mexico. *Econ. Bot.* 64(4): 287–302. <http://www.jstor.org/stable/41001197>
- Blunden, G. [ & al. 1973], Yi, Y. & Jewers, K. (1973) The comparative leaf anatomy of *Agave*, *Beschorneria*, *Doryanthes* and *Furcraea* species (*Agavaceae: Agaveae*). *Bot. J. Linn. Soc.* 66: 157–179. <https://doi.org/10.1111/j.1095-8339.1973.tb02167.x>.
- Boeuf, T. (2007) *Yucca* & Co. Winterharte Wüstengärten in Mitteleuropa anlegen und pflegen. Berlin (DE): Medemia.
- Boeuf, T. [ & al. 2017], Greulich, M. & Bechtold, M. (2017) *Die Welt der Agaven*. Adelsdorf (DE): Deutsche Kakteen-Gesellschaft e.V.
- Bogler, D. J. & Simpson, B. B. (1996) Phylogeny of *Agavaceae* based on ITS rDNA sequence variation. *Amer. J. Bot.* 83(9): 1225–1235. <http://www.jstor.org/stable/2446206>
- Bogler, D. J. [ & al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on *ndhF*, *rbcl*, and ITS sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>.
- Boldingh, I. (1913) *Flora voor de Nederlandsch West-Indische Eilanden*. Ed. 3. Amsterdam (NL): J. H. de Bussy. <https://doi.org/10.5962/bhl.title.3772>.
- Boldingh, I. (1914) *The flora of the Dutch West Indian Islands*. Second volume. Curaçao, Aruba and Bonaire. Leiden (NL): Brill.
- Bolliger, T. (2014) *Agave bracteosa*, eine attraktive Pflanze. *Kakt. and Sukk.* 65(5): 113–117, ills.
- Borbón-Palomares, D. B. [ & al. 2018], Laborin-Sivirian, F., Tinoco-Ojanguren, C., Peñalba, M. C., Reyes-Ortega, I. & Molina-Freaner, F. (2018) Reproductive ecology of *Agave colorata*: The importance of nectar-feeding bats and the germination consequences of self-pollination. *Pl. Ecol.* 219(8): 927–939. <https://doi.org/10.1007/s11258-018-0847-x>.
- Bradley, P. E. & Rey-Millet, Y.-J. (2013) *A photographic guide to the birds of the Cayman Islands*. London (GB): Christopher Helm.
- Brand, T. (2012) *Agave dasylirioides* in Blüte. *Kakt. and Sukk.* 63(3): 77–81, ills.

- Brandham, P. E. (1969) Inversion heterozygosity and sub-chromatid exchange in *Agave stricta*. *Chromosoma* 26(3): 270–286. <https://doi.org/10.1007/BF00326522>.
- Bray, W. L. (1903) The tissues of some plants of the Sotol region. *Bull. Torrey Bot. Club* 30(11): 621–633, ills. <http://biodiversitylibrary.org/page/713368>
- Breitung, A. J. (1959) Cultivated and native Agaves in the southwestern United States. Part 1/Part 2/Part 3/Part 4/Part 5. *Cact. Succ. J. (US)* 31(2): 44–48, (3): 90–93, (4): 114–117, (5): 142–146, (6): 175–179, ills.
- Breitung, A. J. (1960) Cultivated and native Agaves in the southwestern United States. Part 6/Part 7/Part 8/Part 9/Part 10/Part 11. *Cact. Succ. J. (US)* 32(1): 20–23, (2): 35–38, (3): 79–81, (4): 118–121, (5): 163–165, (6): 181–183, ills.
- Breitung, A. J. (1961) Cultivated and native Agaves in the southwestern United States. Part 12/Part 13/Part 14/Part 15/Part 16/Part 17. *Cact. Succ. J. (US)* 23(1): 22–24, (2): 35–38, (3): 88–90, (4): 119–121, (5): 148–150, (6): 179–181, ills.
- Breitung, A. J. (1962) Cultivated and native Agaves in the southwestern United States. Part 18/Part 19/Part 20/Part 21/Part 22. *Cact. Succ. J. (US)* 24(1): 25–26, (2): 42–45, (3): 75–77, (4): 112–114, (5): 141–144, ills.
- Breitung, A. J. (1963) Cultivated and native Agaves in the southwestern United States. Part 23/Part 24/Part 25/Part 26/Part 27/Part 28. *Cact. Succ. J. (US)* 35(1): 14–17, (2): 49–52, (3): 74–77, (4): 120–122, (5): 149–151, (6): 173–174, ills.
- Breitung, A. J. (1964) Cultivated and native Agaves in the southwestern United States. Part 29/Part 30/Part 31/Part 32/Part 33. *Cact. Succ. J. (US)* 36(1): 11–14, (2): 34–37, (3): 71–73, (4): 101–104, (5): 138–139, ills.
- Breitung, A. J. (1968) The Agaves. *Cact. Succ. J. (US) Yearbook 1968*: 107 pp., ills.
- Brena-Bustamante, P. [et al. 2013], Lira-Saade, R., García-Moya, E., Romero-Manzanares, A., Cervantes-Maya, H., López-Carrer, M. & Chávez-Herrera, S. (2013) Aprovechamiento del escapo y los botones florales de *Agave kerchovei* en el Valle de Tehuacán-Cuicatlán, México. *Bot. Sci.* 91(2): 181–186, ills.
- Breslin, P. (2015) Eccentric hermits: Island isolates of Isla Cedros and their peninsular relatives. *Cact. Succ. J. (US)* 87(5): 196–200, ills. <https://doi.org/10.2985/015.087.0501>.
- Brian, N. J. (2000) A field guide to the special status plants of Grand Canyon National Park. Grand Canyon (US): Science Center, Grand Canyon National Park.
- Britton, N. L. & Millspaugh, C. F. (1920) The Bahama Flora. New York (US): New York Botanical Garden. <https://doi.org/10.5962/bhl.title.54084>.
- Britton, N. L. & Wilson, P. (1923) Botany of Porto Rico and the Virgin Islands. Scientific Survey of Porto Rico and the Virgin Islands, vol. 5, part 1. New York (US): New York Academy of Sciences.
- Brown, J. R. (1945) Two well known Agaves. *Cact. Succ. J. (US)* 17(8): 107–110, ills.
- Brummitt, R. K. (2005) Report of the Committee for Spermatophyta: 56. *Taxon* 54(2): 527–536. <https://doi.org/10.2307/25065389>.
- Brunel, O. & Rull, J. (2010) Natural history and mating behavior of *Pseudodyscrasis scutellaris*, a fly species (Ulidiidae) associated with *Agave* in Mexico. *Ann. Entomol. Soc. Amer.* 103(3): 430–438. <https://doi.org/10.1603/AN08164>.
- Bulot, L. G. (2010) Le genre *Agave* aux Etats-Unis. *Cact. Succ.* 2: 36–41, ills.
- Burgess, T. L. (1986) *Agave* adaptation to aridity. *Desert Pl.* 7(2): 39–50, ills. <http://repository.arizona.edu/handle/10150/554187>
- Burton, F. J. (2005) Restoring a new wild population of Blue Iguanas (*Cyclura lewisi*) in the Salina Reserve, Grand Cayman. *Iguana* 12(3): 167–174.
- Bye, R. A. [et al. 1975], Burgess, D. & Trias, A. M. (1975) Ethnobotany of the Western Tarahumara of Chihuahua, Mexico: I. Notes on the genus *Agave*. *Bot. Mus. Leaflet*. [Harvard Univ.] 24(3): 85–112.
- Carlquist, S. (2012) Monocot xylem revisited: New information, new paradigms. *Bot. Rev. (Lancaster)* 78: 87–153, ills. <https://doi.org/10.1007/s12229-012-9096-1>.
- Carnevali, G. (2013) *Agave, Manfreda* o ambos: *Manfreda paniculata*. Desde el Herbario CICY 5: 66–68, ills.
- Castañeda Rojas, A. [et al. 2005], Franco Martínez, I. S. & García-Mendoza, A. (2005) *Manfreda galvaniae* (Agavaceae), especie nueva de México, con nota sobre la ubicación taxonómica de *M. malinaltenangensis* Matuda y su lectotipificación. *Acta Bot. Mex.* 72: 65–76, ills., key. <http://www.redalyc.org/articulo.oa?id=57407206>
- Castetter, E. F. [et al. 1938], Bell, W. H. & Grove, A. R. (1938) The early utilization and the distribution of *Agave* in the American Southwest. Albuquerque (US): University of New Mexico. [http://digitalrepository.unm.edu/unm\\_bulletin/31](http://digitalrepository.unm.edu/unm_bulletin/31)
- Castillejos-Cruz, C. (2009) Sistemática del género *Manfreda* Salisb. (Agavaceae). Texcoco (MX): Colegio de Postgraduados, Campus Montecillo, unpublished Ph. D. thesis.
- Castillejos-Cruz, C. & Solano, E. (2008) *Manfreda bulbulifera* (Agavaceae), especie nueva de México. *Acta Bot. Mex.* 82: 67–73, ill. <http://www.redalyc.org/pdf/574/57408206.pdf>
- Castillo Quiroz, D. [et al. 2011], Mares Arreola, O. & Villavicencio Gutiérrez, E. E. (2011) Lechuguilla (*Agave lechuguilla* Torr.), planta suculenta de importancia económica y social de las zonas áridas y semiáridas de México. *Bol. Soc. Latinoamer. Caribe Cact. otras Suc.* 8(2): 6–9, ills., map.
- Castillo-Hernández, H. & Treviño-Carreón, J. (2014) Biología floral de *Agave gentryi* Ullrich (Agavaceae) en la localidad de La Marcela, Miquihuana, Tamaulipas. *Ciencia UAT* 4(2): 62–66.
- Castillo-Hernández, L. A. & Flores-Olvera, H. (2017) Floristic composition of the cloud forest of the Bicentenario Reserve, Zongolica, Veracruz, México.

- Bot. Sci. 95(3): 539–563. <https://doi.org/10.17129/botsci.1223>.
- Castorena Sanchez, I. [& al. 1991], Escobedo, R. M. & Quiroz, A. (1991) New cytotoxicological determinants recognized in six taxa of *Agave* in the sections *Rigidae* and *Sisalanae*. *Canad. J. Bot.* 69(6): 1257–1265, ills. <https://doi.org/10.1139/b91-163>.
- Castro-Castro, A. (2017) Los amoles, izotes, magueyes, nardos y yucas (familia *Agavaceae*). In: Cruz Angón, A. & al. (eds.): La biodiversidad de Jalisco: Estudio del Estado Vol. II; pp. 135–141. México (MX): CONABIO.
- Castro-Castro, A. [& al. 2010], Rodríguez, A., Vargas-Amado, G. & Ramírez-Delgadillo, R. (2010) Variación morfológica del género *Prochnyanthes* (*Agavaceae*). *Acta Bot. Mex.* 92: 29–49, ills. <https://doi.org/10.21829/abm92.2010.282>.
- Castro-Castro, A. [& al. 2015], González-Gallegos, J. G. & Rodríguez, A. (2015) A new species of *Polianthes* subgenus *Bravoia* (*Asparagaceae*, *Agavoideae*) from Jalisco, Mexico. *Phytotaxa* 201(2): 140–148, map, key, ills. <https://doi.org/10.11646/phytotaxa.201.2.4>.
- Castro-Castro, A. [& al. 2016], Flores-Argüelles, A., Hernández-López, L. & Rodríguez, A. (2016) *Polianthes quilae* (*Poliantheae*, *Agavaceae*), a new and endemic species to western Mexico. *Syst. Bot.* 41(3): 720–726, ills., maps, key. <https://doi.org/10.1600/036364416X692316>.
- Castro-Castro, A. [& al. 2017], Munguia-Lino, G., Carrillo-Reyes, P. & Rodríguez, A. (2017) *Manfreda occidentalis* (*Agavoideae*, *Asparagaceae*), a new species from western Mexico. *Phytotaxa* 321(1): 60–70, ills., map, key. <https://doi.org/10.11646/phytotaxa.321.1.2>.
- Castro-Castro, A. [& al. 2018], Zamora-Tavares, P., Carrillo-Reyes, P. & Rodríguez, A. (2018) *Manfreda santanamicheelii* (*Asparagaceae* subfamily *Agavoideae*), a striking new species from Sierra Madre del Sur in western Mexico. *Syst. Bot.* 43(2): 497–501. <https://doi.org/10.1600/036364418X697229>.
- Cave, M. S. (1964) Cytological observations on some genera of the *Agavaceae*. *Madroño* 17: 163–170. <http://biodiversitylibrary.org/page/47826625>
- Cedano, M. [& al. 1995], Ramírez, R. & Enciso, I. (1995) Una nueva especie de *Polianthes* (*Agavaceae*) del Estado de Michoacán y nota complementaria sobre *Polianthes longiflora* Rose. *Bol. Inst. Bot. Univ. Guadalajara* 1(7): 521–530, ills., map.
- Chagoya-Méndez, V. M. (2004) Diagnóstico de la cadena productiva del sistema producto maguey-mezcal. Oaxaca (MX): Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación SAGARPA, Delegación Oaxaca.
- Chalmers, W. S. (1965) The vegetation of Grand Font, Monos. J. Trinidad Field Natural. Club 1965: 10–14.
- Chamorro, M. L. [& al. 2016], Persson, J., Torres-Santana, C. W., Keularts, J., Scheffer, S. J. & Lewis, M. L. (2016) Molecular and morphological tools to distinguish *Scyphophorus acupunctatus* Gyllenhal, 1838 (*Curculionidae*: *Dryophthorinae*): A new weevil pest of the endangered Century Plant, *Agave eggersiana* from St. Croix, US Virgin Islands. *Proc. Entomol. Soc. Washington* 118(2): 218–243. <https://doi.org/10.4289/0013-8797.118.2.218>.
- Cházaro Basáñez, M. J. (1981) Nota sobre la tipificación de *Agave obscura* Schiede y su confusión con *Agave xalapensis* Roez. *Biotica* 6(4): 435–446, ills.
- Cházaro Basáñez, M. J. (1995) Una nueva especie de *Agave* (*Agavaceae*) del Sureste de Veracruz, México. *Cact. Suc. Mex.* 40(4): 92–96, ills., map.
- Cházaro Basáñez, M. J. (1997) A new species from Mexico: *Agave wendtii* Cházaro. *Cact.-Avent.* 35: 12–14, ills.
- Cházaro Basáñez, M. J. (2001) In situ: *Agave pendula* Schnitts. *Cact.-Avent.* 49: 12–15, ills., map.
- Cházaro Basáñez, M. J. & Machuca Núñez, J. A. (1995) Nota sobre *Polianthes longiflora* Rose (*Agavaceae*). *Cact. Suc. Mex.* 30(1): 20–22.
- Cházaro Basáñez, M. J. & Mostul, B. (1999) In habitat: *Agave guadalajarana* Trel. *Cact.-Avent.* 44: 10–12, ills.
- Cházaro Basáñez, M. J. & Narave-Flores, H. V. (2015) *Agave jimenoii* (*Agavaceae*): Another brand new species of “Century Plant” from Veracruz, Mexico. *Int. Cact.-Advent.* 106–107(7): 41–47, ills., map.
- Cházaro Basáñez, M. J. & Vázquez-García, A. (2006) In situ: *Agave durangensis*. *Cact.-Avent. Int.* 72: 24–30, ills.
- Cházaro Basáñez, M. J. & Vázquez-García, J. A. (2013) *Agave jimenoii* (*Polycephalae* group, *Asparagaceae*), a new species from the Totonacapan region, Veracruz, Mexico. *Phytotaxa* 134(1): 55–60, ills, map, key. <https://doi.org/10.11646/phytotaxa.134.1.5>.
- Cházaro Basáñez, M. J. & Valencia, O. M. (2003) Introducing the succulent flora of Mexico: *Agave impressa*. *Cact.-Avent.* 57: 31–34, ills.
- Cházaro Basáñez, M. J. [& al. 1998], Acevedo-Rosas, R. & Mostul, B. (1998) *Agave pedunculifera* Trelease & *Agave attenuata* Salm-Dyck. *Cact.-Avent.* 37: 9–13, ills.
- Cházaro Basáñez, M. J. [& al. 2004a], Valencia, O. M. & Vázquez, J. A. (2004) Introducing the succulent flora of Mexico: *Agave rzedowskiana*, a brand new species. *Cact.-Avent.* 62: 27–31, ills.
- Cházaro Basáñez, M. J. [& al. 2004b], Vázquez-García, J. A. & Valencia-Pelayo, O. (2004) *Agave geminiflora* in habitat. *Cact.-Avent.* 63: 30–33, ills.
- Cházaro Basáñez, M. J. [& al. 2005a], Vázquez-García, J. A., Valencia-Pelayo, O. M. & Machuca-Nuñez, J. A. (2005) In situ: *Agave nayaritensis*. *Cact.-Avent.* 66: 33–37, ills.
- Cházaro Basáñez, M. J. [& al. 2005b], Vázquez-García, J. A. & Varga-Rodríguez, Y. L. (2005) *Agave valenciana*: A brand new gigantic species from Mexico. *Cact.-Avent.* 68: 24–30, ills.
- Cházaro Basáñez, M. J. [& al. 2006a], Valencia-Pelayo, O. M., Machuca-Nuñez, J. A. & Vázquez-García, J. A. (2006) In situ: *Agave gypsophila* H. S. Gentry. *Cact.-Avent. Int.* 70: 15–19, ills.



- Cházaro Basáñez, M. J. [ & al. 2006b], Vázquez-García, J. A. & Vargas, Y. L. (2006) *Agave valenciana*: Una nueva especie de Jalisco, México. Bol. Soc. Latinoamer. Caribe Cact. otras Suc. 3(1): 3–6, ills.
- Cházaro Basáñez, M. J. [ & al. 2008a], Lomelí-Sencián, J. A., Valencia-Pelayo, O. M. & Vargas-Rodríguez, Y. L. (2008) Otra nueva especie de *Agave* (*Agavaceae*) del Estado de Jalisco, Mexico. *Bouteloua* 3: 23–28, ills.
- Cházaro Basáñez, M. J. [ & al. 2008b], Jimeno-Sevilla, D., Meer, P. van & Roosbroek, J. van (2008) *Agave warelliana* (*Agavaceae*), a new record from Veracruz, Mexico. *Cact.-Avent. Int.* 78: 24–30, ills.
- Cházaro Basáñez, M. J. [ & al. 2010a], Jimeno-Sevilla, H. D. & Oliva-Rivera, H. (2010) *Agave gomezpompa* Cházaro & Jimeno-Sevilla. A new species of *Agave* (*Agavaceae*) from central Veracruz, Mexico. *Cact.-Avent. Int.* 88: 2–11, ills., map.
- Cházaro Basáñez, M. J. [ & al. 2010b], Machuca-Núñez, J. A. & López-Velázquez, R. (2010) *Polianthes longiflora* Rose (*Agavaceae*). *Cact.-Avent. Int.* 86: 2–9, ills.
- Cházaro Basáñez, M. J. [ & al. 2012], Gheno Heredia, Y. A., Oliva Rivera, H. & Ramón Farías, F. (2012) *Agave ellemeetiana* (*Agavaceae*). A new record for the State of Veracruz, Mexico. *Int. Cact.-Advent.* 96: 29–35, ills.
- Cházaro Basáñez, M. J. [ & al. 2013], Vázquez-García, J. A. & López-Velázquez, R. (2013) *Agave temacapulinensis* (*Agavaceae*), another brand new species from Jalisco, Mexico. *Int. Cact.-Advent.* 100: 8–16, ills., map.
- Cházaro Basáñez, M. J. [ & al. 2014], Ramos-Villarreal, R. & López-Velázquez, R. (2014) *Polianthes pringlei* Rose (*Agavaceae*). *Cact. Succ. J. (US)* 86(3): 106–109, ills. <https://doi.org/10.2985/015.086.0303>.
- Cházaro Basáñez, M. J. [ & al. 2015], Ramos-Villarreal, R. & López-Velázquez, R. (2015) Notas generales sobre *Polianthes pringlei* Rose (*Agavaceae*). *Bouteloua* 22: 15–20, ills.
- Colli, C. (1983) Our British Virgin Islands: A cultural and historical tour of the British Virgin Islands. Road Town? (GB): British Virgin Islands Tourist Board.
- Colunga-García Marín, P. (2003) The domestication of Henequen (*Agave fourcroydes* Lem.). In: Gómez-Pompa, A. & al. (eds.): The lowland Maya area. Three millennia at the human-wildland interface; pp. 439–446 New York (US) etc.: Food Products Press/Haworth Press. <https://doi.org/10.13140/RG.2.1.1370.5768>.
- Colunga-García Marín, P. & May-Pat, F. (1997) Morphological variation of henequén (*Agave fourcroydes*, *Agavaceae*) germplasm. *Amer. J. Bot.* 84(11): 1449–1465, ills., maps. <https://doi.org/10.2307/2446608>.
- Colunga-García Marín, P. [ & al. 1996], Estrada-Loera, E. & May-Pat, F. (1996) Patterns of morphological variation, diversity, and domestication of wild and cultivated populations of *Agave* in Yucatán, Mexico. *Amer. J. Bot.* 83(8): 1069–1082. <http://www.jstor.org/stable/2445997>
- Colunga-García Marín, P. [ & al. 1999], Coello-Coello, J., Eguiarte, L. E. & Piñero, D. (1999) Isozymatic variation and phylogenetic relationships between Henequen (*Agave fourcroydes*) and its wild ancestor *A. angustifolia* (*Agavaceae*). *Amer. J. Bot.* 86(1): 115–123. <http://www.amjbot.org/content/86/1/115.full.pdf+html>
- Colunga-García Marín, P. [ & al. 2007], Zizumbo-Villarreal, D. & Martínez-Torres, J. (2007) Nombres comunes de 102 taxa de *Agave* reportados por su uso en México como alimento humano, bebida fermentada, bebida destilada, fibra o forraje. In: Colunga-García Marín, P. & al. (eds.): En lo ancestral hay futuro: Del tequila, los mezcales y otros Agaves; Anexo 3, pp. xxi–xxxviii. Mérida (MX): Centro de Investigación Científica de Yucatán A.C.
- Contreras-Hernández, M. G. [ & al. 2016], González-Herrera, S. M., Ochoa-Martínez, L. A., López, M. G. & Rutiaga-Quñones, O. M. (2016) Potencial del uso industrial del *Agave durangensis*. *TecnoAgave* 6(42): 16–19.
- Correll, D. S. & Correll, H. B. (1982) Flora of the Bahama Archipelago (including the Turks and Caicos islands). Vaduz (FL): J. Cramer.
- Coulson, J. (1897) *Agave taylori*, century plant. *Meehan's Monthly* 7(6): 110–111, ill. <http://biodiversitylibrary.org/page/33026864>
- Cruz-Ramos, C. A. [ & al. 1985], Orellana, R. & Robert, M. L. (1985) *Agave* research progress in Yucatan. *Desert Pl.* 7(2): 71–73, 80, 89–92, ills. <http://hdl.handle.net/10150/554189>
- Cseh, T. A. (1993) In search of *Agave panamana* Trel. *Haseltonia* 1: 34–44, ills., map.
- Cseh, T. A. (2008) *Agave pygmaea* (Gentry & McClure) in Honduras—its habitat in imminent danger of destruction by human encroachment. *To The Point* 80(5): 119–124, ills., map.
- Cuautle, M. [ & al. 1998], García-Franco, J. G. & Rico-Garay, V. (1998) Estructura poblacional y características foliares de *Agave kerchovei*. Relación con la presencia de homópteros y hongos en el Valle de Zapotitlán, Puebla. *Cact. Suc. Mex.* 43(4): 75–80.
- Cuautle, M. [ & al. 1999], Gray, V. R., García-Franco, J. G., Portillo, J. L. & Thien, L. B. (1999) Description and seasonality of a Homoptera-ant-plant interaction in the semiarid Zapotitlan Valley, Puebla, México. *Acta Zool. Mex.*, n.s. (2) 78: 73–82. <http://www.redalyc.org/articulo.oa?id=57507802>
- Cuevas Figueroa, X. M. & Flores Berrios, E. P. (2006) Distancias genéticas entre *Agave tequilana* Weber var. Azul y especies y variedades afines. *Scientia CUCBA* 8(2): 231–249, ills., map.
- Cuevas Guzmán, R. [ & al. 2012], Santana-Michel, F. J. & Balcazar-Medina, O. (2012) *Agave manantlanicola* (*Agavaceae*), a new species from western Mexico. *Brittonia* 64(3): 330–335, ills., key. <https://doi.org/10.1007/s12228-012-9240-6>.
- Cutak, L. (1943) Spine chats. *Cact. Succ. J. (US)* 15(10): 151, ill.



- Datta, S. K. (2017) Breeding of ornamentals: Tuberose (*Pollianthes tuberosa* L.). *Curr. Sci.* 113(7): 1255–1263. <https://doi.org/10.18520/cs/v113/i07/1255-1263>.
- David, J. C. (2009) A review of trunk-forming species of *Furcraea* (*Agavaceae*) in cultivation in the UK. *Hanburyana* 4: 23–32, ills., key.
- Davis, S. C. [& al. 2011], Dohleman, F. G. & Long, S. P. (2011) The global potential for *Agave* as a biofuel feedstock. *Global Change Biol.* 3(1): 68–78, ills. <https://doi.org/10.1111/j.1757-1707.2010.01077.x>.
- De-Nova, J. A. [& al. 2018], Castillo-Lara, P., Gudiño-Cano, A. K. & García-Pérez, J. (2018) Flora endémica del estado de San Luis Potosí y regiones adyacentes en México. *Árido-Ciencia* 3(1): 21–41. <http://aridociencia.mx/numeros/2018/VIIINI/v3n12018.pdf>
- Delanoy, G. (2002) Een reis door Cuba. *Succulenta* 81(1): 28–35, ills.
- Delgado-Lemus, A. [& al. 2014], Casas, A. & Téllez, O. (2014) Distribution, abundance and traditional management of *Agave potatorum* in the Tehuacán Valley, Mexico: Bases for sustainable use of non-timber forest products. *J. Ethnobiol. Ethnomed.* 10(1): 63, 12 pp. <https://doi.org/10.1186/1746-4269-10-63>.
- Diggs, G. M. [& al. 1999], Lipscomb, B. L. & O’Kennon, R. J. (1999) *Shinners & Mahler’s Illustrated Flora of North Central Texas*. Fort Worth (US): Botanical Research Institute of Texas.
- Diggs, G. M. [& al. 2006], Lipscomb, B. L., Reed, M. D. & O’Kennon, R. J. (2006) *Illustrated flora of East Texas*. Volume 1: Introduction, Pteridophytes, gymnosperms and monocotyledons. Fort Worth (US): Botanical Research Institute of Texas & Austin College.
- Doughty, L. R. (1936) Chromosome behaviour in relation to genetics in *Agave*. I. Seven species of fibre *Agave*. *J. Genet.* 33(2): 197–205. <https://doi.org/10.1007/BF02982532>.
- Drummond, J. R. (1910) *Agave lurida*. *Bull. Misc. Inform. Kew* 1910: 344–349. <http://biodiversitylibrary.org/page/11623389>
- Drummond, J. R. (1912) *Agave disceptata*. *Curtis’s Bot. Mag.* 138: t. 8451 + text. <http://biodiversitylibrary.org/page/465781>
- Eguiarte, L. E. & Búrquez, A. (1987) Reproductive ecology of *Manfreda brachystachya*, an iteroparous species of *Agavaceae*. *Southw. Naturalist* 32(2): 169–178.
- Eguiarte, L. E. & Scheinvar, E. (eds.) (2008) *Agaves y cactáceas de Metztlán: Ecología, evolución y conservación*. sine loco (MX): Unpublished preliminar version.
- Eguiarte, L. E. [& al. 2013], Aguirre-Planter, E., Aguirre, X., Colín, R., González, A., Rocha, M., Scheinvar, E., Trejo, L. & Souza, V. (2013) From isozymes to genomics: Population genetics and conservation of *Agave* in Mexico. *Bot. Rev. (Lancaster)* 79(4): 483–506. <https://doi.org/10.1007/s12229-013-9123-x>.
- Emlen, J. T. (1973) Territorial aggression in wintering warblers at Bahama *Agave* blossoms. *Wilson Bull.* 85(1): 71–74.
- Engelmann, G. (1875) Notes on *Agave*. *Trans. Acad. Sci. St. Louis* 3: 291–322. <http://www.biodiversitylibrary.org/item/28719#page/309/>
- Engelmann, G. (1878) The flowering of *Agave shawii*. *Trans. Acad. Sci. St. Louis* 3: 579–582, t. IV. <http://biodiversitylibrary.org/page/26378283>
- Espejo Serna, A. & López Ferrari, A. R. (1993) Las monocotiledóneas Mexicanas, una sinopsis florística: 1. Lista de referencias: parte 1. *Agavaceae*, etc. México D.F. (MX): Consejo Nacional de la Flora de México.
- Espinosa-Jiménez, J. A. [& al. 2011], Pérez-Farrera, M. A. & Martínez-Camilo, R. (2011) Inventario florístico del Parque Nacional Cañón del Sumidero, Chiapas, México. *Bol. Soc. Bot. México* 89: 37–92. <http://www.scielo.org.mx/pdf/bsbm/n89/n89a4.pdf>
- Espinosa-Jiménez, J. A. [& al. 2014], López-Cruz, A., Pérez-Farrera, M. Á. & López, S. (2014) Inventario florístico de la cañada La Chacona-Juan Crispín y zonas adyacentes, depresión Central de Chiapas, México. *Bot. Sci.* 92(2): 205–241. <https://doi.org/10.17129/botsci.30>.
- Ettelt, J. (2014) Agaven in Kultur. *Avonia* 32(3): 110–127, ills.
- Ettelt, J. & Riedel, W. (1998) Ein Jahrhundertereignis: *Agave potatorum* var. *verschaffeltii* (Lemaire) Berger blüht in Kultur. *Kakt. and Sukk.* 49(12): 276–279, ills.
- Etter, J. & Kristen, M. (1997) Agaven und *Melocactus intortus* auf den Kleinen Antillen. *Kakt. and Sukk.* 48(5): 97–101, ills.
- Etter, J. & Kristen, M. (1997+) The *Agavaceae* database. [www.agavaceae.com](http://www.agavaceae.com). <http://www.agavaceae.com>
- Etter, J. & Kristen, M. (2001) Alla ricerca dell’agavi “da parete” di Sonora. In search of the “cliff-hanger” Agaves of Sonora. *Cactus & Co.* 5(3): 166–185, ills.
- Etter, J. & Kristen, M. (2002) *Agave nayaritensis*. *Cact. Succ. J. (US)* 74(5): 241–244, ills.
- Etter, J. & Kristen, M. (2003a) At the Rio Mayo, in the land of the Guarjio: On the track of Howard Scott Gentry. *Cact.-Avent.* 59: 2–10, ills.
- Etter, J. & Kristen, M. (2003b) Bayusa. *Cact. Succ. J. (US)* 75(3): 108.
- Etter, J. & Kristen, M. (2006) Mexican cliff-dwellers. In search of *Graptopetalum*, *Pachyphytum* and *Cremnophila*. *Cact. Succ. J. (US)* 78(6): 251–260, ills. [https://doi.org/10.2985/0007-9367\(2006\)78\[251:MC\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[251:MC]2.0.CO;2).
- Etter, J. & Kristen, M. (2007a) Neuigkeiten von den Fundorten. *Avonia* 25(2): 58–59, ills.
- Etter, J. & Kristen, M. (2007b) Tequila. Lo spirito del Messico. The spirit of Mexico. *Cactus & Co.* 11(3): 173–185, ills.
- Etter, J. & Kristen, M. (2007c) Distribución y hábitat de *Agave nayaritensis* Gentry. In: Vázquez-García, J. A. & al. (eds.): *Agaves del occidente de México*; pp. 19–22. Guadalajara (MX): Universidad de Guadalajara.
- Etter, J. & Kristen, M. (2008) Neuigkeiten von den Fundorten. *Agave ovatifolia* Starr & Villarreal 2002. *Avonia* 26(3): 80–81, ills.

- Etter, J. & Kristen, M. (2009a) La sfuggente/The elusive *Agave albopilosa*. *Cactus & Co.* 13(1): 44–57, ills.
- Etter, J. & Kristen, M. (2009b) *Agave ovatifolia* in Sierra de Lampazos. *Cactus & Co.* 13(3): 5–19, ills.
- Etter, J. & Kristen, M. (2011) Note su/Notes on *Agave impressa*. *Cactus & Co.* 15(2): 42–59, ills., map.
- Etter, J. & Kristen, M. (2012) Agaven im mexikanischen Bundesstaat Jalisco. *Agave species in the Mexican State of Jalisco*. *Avonia* 30(2): 79–96, XXVIII–XXXII, ills.
- Euro+Med (2006+) Euro+Med PlantBase—the information resource for Euro-Mediterranean plant diversity. Berlin (DE): <http://ww2.bgbm.org/EuroPlusMed/>
- Felger, R. S. [& al. 2011], Wilder, B. T. & Gallo-Reynoso, J. P. (2011) Floristic diversity and long-term vegetation dynamics of San Pedro Nolasco Island, Gulf of California, Mexico. *Proc. San Diego Soc. Nat. Hist.* 43: 1–42, ills.
- Félix-Valdez, L. I. [& al. 2016], Vargas-Ponce, O., Cabrera-Toldeo, D., Casas, A., Cibrian-Jaramillo, A. & Cruz-Larios, L. de la (2016) Effects of traditional management for mescal production on the diversity and genetic structure of *Agave potatorum* (*Asparagaceae*) in central Mexico. *Genet. Resources Crop Evol.* 63: 1255–1271, ills., map. <https://doi.org/10.1007/s10722-015-0315-6>.
- Feria-Arroyo, T. P. [& al. 2010], Solano, E. & García-Mendoza, A. (2010) Reevaluación del riesgo de extinción de cinco especies del género *Polianthes* L. (*Agavaceae*). *Acta Bot. Mex.* 91: 11–28, ills, map. <http://www.redalyc.org/pdf/574/57415475002.pdf>
- Fernández Nava, R. [& al. 1998], Rodríguez Jiménez, C., Arreguín Sánchez, M. de la L. & Rodríguez Jiménez, A. (1998) Listado florístico de la cuenca del Río Balsas, México. *Polibotánica* 9: 1–151.
- Fernández Velázquez, A. [& al. 2018], Franke, S. & Sigarreta Vilches, S. (2018) Valoración del estado de conservación de *Caracolus cimarron* (*Gastropoda: Solaropsidae*) en el Parque Nacional Mensura Piloto. *Poeyana* 506: 36–41, ills. <http://revistas.geotech.cu/index.php/poey/article/view/231>
- Figueiredo, E. & Smith, G. F. (2013a) Proposal to conserve the name *Agave ×leopoldii* W. Watson against *A. leopoldii* Rafarin (*Agavaceae/Asparagaceae*). *Taxon* 62(5): 1061. <https://doi.org/10.12705/625.28>.
- Figueiredo, E. & Smith, G. F. (2013b) Proposal to conserve the name *Littaea geminiflora* (*Agave geminiflora*) against *Yucca boscii* (*Agavaceae/Asparagaceae*). *Taxon* 62(5): 1062. <https://doi.org/10.12705/625.29>.
- Figueiredo, E. & Smith, G. F. (2014) Proposal to conserve the name *Agave hookeri* Jacobi against *A. hookeri* K. Koch (*Agavaceae/Asparagaceae*). *Taxon* 63(1): 187. <https://doi.org/10.12705/631.18>.
- Figueiredo, C. J. (2010) Historia, producción y conservación del cocuy de penca: Orgullo y tradición de las zonas áridas de Venezuela. *Bol. Soc. Latinoamer. Caribe Cact. otras Suc.* 7(2): 19–23, ills.
- Figueiredo, C. J. & Nassar, J. M. (2011) Population genetics of *Agave cocui*: Evidence for low genetic diversity at the southern geographic limit of genus *Agave*. *J. Heredity* 102: 306–314. <https://doi.org/10.1093/jhered/esr018>.
- Figueiredo, C. J. [& al. 2014], Casas, A., Colunga-García Marín, P., Nassar, J. M. & González-Rodríguez, A. (2014) Morphological variation, management and domestication of ‘maguey alto’ (*Agave inaequidens*) and ‘maguey manso’ (*A. hookeri*) in Michoacán, México. *J. Ethnobiol. Ethnomed.* 10(1): 66, 12 pp., ills. <https://doi.org/10.1186/1746-4269-10-66>.
- Figueiredo, C. J. [& al. 2015], Casas, A., González-Rodríguez, A., Nassar, J. M., Colunga-García Marín, P. & Rocha-Ramírez, V. (2015) Genetic structure of coexisting wild and managed *Agave* populations: Implications for the evolution of plants under domestication. *AoB Pl.* 2015(7): plv114, 14 pp. <https://doi.org/10.1093/aobpla/plv114>.
- Figueiredo-Urbina, C. J. & Casas, A. (2012) Domesticación y divergencias morfológicas y genéticas entre poblaciones silvestres y cultivadas de *Agave inaequidens* y *A. hookeri*. *Bol. Soc. Latinoamer. Caribe Cact. otras Suc.* 9(2): 6–9, ills.
- Figueiredo-Urbina, C. J. [& al. 2017], Casas, A. & Torres-García, I. (2017) Morphological and genetic divergence between *Agave inaequidens*, *A. cupreata* and the domesticated *A. hookeri*. Analysis of their evolutionary relationships. *PLoS One* 12(11): e187260, 24 pp., ills. <https://doi.org/10.1371/journal.pone.0187260>.
- Flores-Abreu, I. N. [& al. 2019], Trejo-Salazar, R. E., Sánchez-Reyes, L. L., Good, S. V., Magallón, S., García-Mendoza, A. & Eguiarte, L. E. (2019) Tempo and mode of coevolution of *Agave* sensu lato (*Agavoideae, Asparagaceae*) and its bat pollinators, *Glossophaginae* (*Phyllostomidae*). *Molec. Phylog. Evol.* 133: 176–188. <https://doi.org/10.1016/j.ympev.2019.01.004>.
- Flores-Maya, S. [& al. 2010], Moreno-Ramírez, J. C., Romero-Rangel, S. & Rojas-Zenteno, C. (2010) Análisis morfológico y cariológico de *Agave karwinskii* Zucc. y *Agave macroacantha* Zucc. en el municipio de Zapotitlán Salinas, Puebla. *Biocyt: Biol. Ci. & Tecnol.* 3(1): 181–196. <http://dialnet.unirioja.es/servlet/articulo?codigo=3414946>
- Flores-Maya, S. [& al. 2015], Vargas-Jurado, M. Á., Suárez-Mota, M. E. & Barrera-Escorcía, H. (2015) Análisis cariotípico de *Agave marmorata* y *Agave peacockii* (*Agavaceae*) ubicados en las terrazas aluviales del Río Zapotitlán, Puebla, México. *Polibotánica* 40: 109–125. <https://doi.org/10.18387/polibotanica.40.7>.
- Flores-Torres, A. & Galindo-Escamilla, A. (2017) Pollination biology of *Agave horrida* (*Agavaceae*) in the Chichinautzin mountain range, Central Mexico. *Bot. Sci.* 95(3): 423–431. <https://doi.org/10.17129/botsci.1022>.

- Forster, P. I. (2006) Variazioni su/Variations on *Agave potatorum* (Agavaceae). *Cactus & Co.* 10(3): 167–182, ills.
- Francis, J. K. (ed.) (2004) Wildland shrubs of the United States and its territories: Thamnisc descriptions, volume 1. San Juan (PR)/Fort Collins (US): USDA Forest Service & International Institute of Tropical Forestry. <http://www.fs.usda.gov/treesearch/pubs/27005>
- Franck, A. R. (2012) Guide to *Agave*, *Cinnamomum*, *Corymbia*, *Eucalyptus*, *Pandanus*, and *Sansevieria* in the flora of Florida. *Phytoneuron* 2012(102): 1–23, keys, ills. <https://doi.org/10.13140/2.1.3641.4081>.
- Freeman, C. E. & Reid, W. H. (1985) Aspects of the reproductive biology of *Agave lechuguilla* Torr. *Desert Pl.* 7(2): 75–80, ills, map. <http://repository.arizona.edu/handle/10150/554210>
- Freid, E. [ & al. 2014], Francisco-Ortega, J. & Jestro, B. (2014) Endemic seed plants in the Bahamian Archipelago. *Bot. Rev. (Lancaster)* 80: 204–230, ills. <https://doi.org/10.1007/s12229-014-9137-z>.
- Galván, R. & Zamudio, S. (2013) Una nueva especie de *Agave* del subgénero *Liitaea* (Agavaceae) de la Sierra Madre Oriental, México. *Acta Bot. Mex.* 105: 1–10, ills. <https://doi.org/10.21829/abm105.2013.228>.
- García-Mendoza, A. J. (1995) Riqueza y endemismos de la familia Agavaceae en México. In: Linares, E. & al. (eds.): Conservación de plantas en peligro de extinción: Diferentes enfoques; pp. 51–75, maps. México (MX): Universidad Nacional Autónoma de México.
- García-Mendoza, A. J. (2002) Distribution of *Agave* (Agavaceae) in Mexico. *Cact. Succ. J. (US)* 74(4): 177–187, ills., maps.
- García-Mendoza, A. J. (2003) Revisión de las Agavaceae (sensu stricto), *Crassulaceae* y *Liliaceae* incluidas en el PROY-NOM-059-ECOL-2000. Mexico (MX): Jardín Botánico, Instituto de Biología, UNAM, Proyecto W020, bases de datos SNIB-CONABIO.
- García-Mendoza, A. J. (2010) Revisión taxonómica del complejo *Agave potatorum* Zucc. (Agavaceae): Nuevas taxa y neotipificación. *Acta Bot. Mex.* 91: 71–93, ills., key, map. <http://www.redalyc.org/pdf/574/57412477008.pdf>
- García-Mendoza, A. J. (2011a) Flora del Valle de Tehuacán-Cuicatlán. 88. Agavaceae. Mexico (MX): Instituto de Biología, Universidad Nacional Autónoma de México.
- García-Mendoza, A. J. (2011b) Tres especies nuevas de *Manfreda* (Agavaceae) del sur de México. *Revista Mex. Biodivers.* 82: 747–757, ills., key. <http://www.redalyc.org/pdf/425/42520988002.pdf>
- García-Mendoza, A. J. & Chiang, F. (2003) The confusion of *Agave vivipara* L. and *A. angustifolia* Haw., two distinct taxa. *Brittonia* 55(1): 82–87, ill. [https://doi.org/10.1663/0007-196X\(2003\)055\[0082:TCOAVL\]2.0.CO;2](https://doi.org/10.1663/0007-196X(2003)055[0082:TCOAVL]2.0.CO;2).
- García-Mendoza, A. J. & Esparza Alvarado, E. (2010) Flora y fauna mexicanas de los centenarios. México D.F. (MX): Instituto de Biología, Universidad Nacional Autónoma de México.
- García-Mendoza, A. J. & Galván, R. (1995) Riqueza de las familias Agavaceae y Nolinaceae en México. *Bol. Soc. Bot. México* 56: 7–24, maps.
- García-Mendoza, A. J. & Martínez, E. (1998) Una nueva especie de *Agave*, subgénero *Liitaea* (Agavaceae) de Guerrero y Oaxaca, México. *Sida* 18(1): 227–230, ills. <http://www.jstor.org/stable/41967297>
- García-Mendoza, A. J. & Solano, E. (2007) *Polianthes oaxacana* y *P. geminiflora* var. *pueblensis* (Agavaceae), taxa nuevos de México. *Acta Bot. Mex.* 78: 111–123, ills., key. <https://doi.org/10.21829/abm78.2007.1034>.
- García-Mendoza, A. J. [ & al. 2000], Castañeda Rojas, A. & Franco Martínez, I. S. (2000) *Manfreda littoralis* (Agavaceae), nueva especie de Guerrero y Oaxaca, México. *Acta Bot. Mex.* 50: 39–45, ills., key. <http://www.redalyc.org/pdf/574/57405007.pdf>
- García-Mendoza, A. J. [ & al. 2019], Franco Martínez, I. S. & Sandoval Gutiérrez, D. (2019) Cuatro especies nuevas de *Agave* (Asparagaceae, Agavoideae) del sur de México. *Acta Bot. Mex.* 126: e1461, 18 pp., ills., map. <https://doi.org/10.21829/abm126.2019.1461>.
- García-Moya, E. & Ayala-Sosa, J. C. (2007) La lechuguilla: El rescate de un recurso? In: Colunga-García Marín, P. & al. (eds.): En lo ancestral hay futuro: Del tequila, los mezcales y otros Agaves; pp. 355–365. Mérida (MX): Centro de Investigación Científica de Yucatán A.C.
- García-Moya, E. & Nobel, P. S. (1990) Leaf unfolding rates and responses to cuticle damaging for Pulque Agaves in Mexico. *Desert Pl.* 10(2): 55–57. <http://repository.arizona.edu/handle/10150/609137>
- García-Moya, E. [ & al. 2011], Romero-Manzanares, A. & Nobel, P. S. (2011) Highlights for *Agave* productivity. *Global Change Biol.* 3(1): 4–14, map. <https://doi.org/10.1111/j.1757-1707.2010.01078.x>.
- Gentry, H. S. (1942) Rio Mayo plants. A study of the flora and vegetation of the valley of the Rio Mayo, Sonora. Washington D.C. (US): Carnegie Institution of Washington. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=5224>
- Gentry, H. S. (1967) Putative hybrids in *Agave*. *J. Heredity* 58(1): 32–36. <https://doi.org/10.1093/oxfordjournals.jhered.a107536>.
- Gentry, H. S. (1968) *Agave geminiflora* and *Agave colimana* spec. nov. *Cact. Succ. J. (US)* 40: 208–213, ills.
- Gentry, H. S. (1972) The *Agave* family in Sonora. Agricultural handbook No. 399. Washington D.C. (US): US Department of Agriculture. <http://naldc.nal.usda.gov/download/CAT87209091/PDF>
- Gentry, H. S. (1975) The case of *Agave scabra* and *Agave wislizenii*. *Cact. Succ. J. (US)* 47: 102–104, 259.
- Gentry, H. S. (1977a) *Agave arizonica*, a rare species. *Saguaroland Bull.* 31(4): 40–42. <http://biodiversitylibrary.org/page/54635335>
- Gentry, H. S. (1977b) *Agave potrerana*, the Pastureland *Agave*. *Saguaroland Bull.* 31(7): 76–79, ills. (incl. p. 73), map. <http://biodiversitylibrary.org/page/54635371>

- Gentry, H. S. (1978) The Agaves of Baja California. Occas. Pap. Calif. Acad. Sci. 130: 119 pp., ills., maps, keys. <http://biodiversitylibrary.org/page/8860294>
- Gentry, H. S. (1982) Agaves of Continental North America. Tucson (US): University of Arizona Press.
- Gil-Vega, K. C. [& al. 2001], González Chavira, M., Martínez de la Vega, O., Simpson, J. & Vandemark, G. (2001) Analysis of genetic diversity in *Agave tequilana* var. Azul using RAPD markers. Euphytica 119(3): 335–341. <https://doi.org/10.1023/A:1017553107303>.
- Gil-Vega, K. C. [& al. 2006], Diaz, C. & Nava-Cedillo, A. (2006) AFLP analysis of *Agave tequilana* varieties. Pl. Sci. (Elsevier) 170(4): 904–909. <https://doi.org/10.1016/j.plantsci.2005.12.014>.
- Gil-Vega, K. C. [& al. 2007], Díaz-Quezada, C. E., Nava-Cedillo, A., García-Mendoza, A. & Simpson, J. (2007) Análisis AFLP del género *Agave* refleja la clasificación taxonómica basada en caracteres morfológicos y otros métodos moleculares. In: Colunga-García Marín, P. & al. (eds.): En lo ancestral hay futuro: Del tequila, los mezcales y otros Agaves; pp. 23–39. Mérida (MX): Centro de Investigación Científica de Yucatán A.C.
- Gillis, W. T. (1976) *Agave* in the Bahama Islands. Phytologia 33(1): 78–81.
- Giraldo-Cañas, D. (2017) Una nueva especie de *Agave* (*Asparagaceae*) de Colombia y una clave taxonómica para las especies sudamericanas. Caldasia 39(1): 33–49, ills., key. <https://doi.org/10.15446/caldasia.v39n1.63318>.
- Glass, C. (1983) Mexican logbook. 1978 expedition to Central Mexico (part II). Cact. Succ. J. (US) 55(3): 108–112, ills.
- Godínez-Alvarez, H. [& al. 2012], Morín, C. & Rivera-Aguilar, V. (2012) Germination, survival and growth of three vascular plants on biological soil crusts from a Mexican tropical desert. Pl. Biol. (Stuttgart) 14: 157–162, ills. <https://doi.org/10.1111/j.1438-8677.2011.00495.x>.
- Goldman, E. A. (1916) Plant records of an expedition to Lower California. Contr. US Nation. Herb. 16: 309–371. <http://www.jstor.org/stable/23492290>
- Gomez Rhine, T. (2009) Propagating rare plants in the Huntington's tissue culture lab. Huntington Frontiers 2009: fall/winter, pp. 23–27.
- Gómez-Aíza, L. & Zuria, I. (2010) Bird visitation to maguey flowers (*Agave salmiana*) in an urban area of central Mexico. Ornitol. Neotrop. 21: 17–30.
- Gómez-Bellver, C. [& al. 2019], Nualart, N., Ibáñez, N., Burguera, C., Álvarez, H. & López-Pujol, J. (2019) Noves dades per a la flora allòctona de Catalunya i del País Valencià. Butl. Inst. Catalana Hist. Nat. 83: 23–40. <https://doi.org/10.2436/20.1502.01.2>.
- Gómez-Pompa, A. [& al. 1971], Villalobos-Pietrini, R. & Chimal, A. (1971) Studies in the *Agavaceae* I. Chromosome morphology and number of seven species. Madroño 21(4): 208–221, ills. <http://www.jstor.org/stable/41423783>
- Gomez-Rodriguez, V. M. [& al. 2013], Rodríguez-Garay, B., Palomino, G., Martínez, J. & Barba-Gonzalez, R. (2013) Physical mapping of 5S and 18S ribosomal DNA in three species of *Agave* (*Asparagales*, *Asparagaceae*). Comp. Cytogen. 7(3): 191–203, ills. <https://doi.org/10.3897/CompCytogen.v7i3.5337>.
- Gonzales, K. & Mera, J. (2015) Der ethnobotanische Garten von Oaxaca, Mexico. Avonia 33(1): 10–16, ills.
- González Medrano, F. (1991) Nota sobre la tipificación de *Manfreda guerrensis* Matuda (*Agavaceae*). Cact. Succ. Mex. 36(1): 16.
- González, A. (2004) Biología reproductiva y genética de poblaciones del *Agave garciae-mendozae*. México D.F. (MX): Facultad de Ciencias, Universidad Nacional Autónoma de México; unpublished M.Sc. thesis.
- González, A. (2008) *Agave victoriae-reginae*. Cactus & Co. 12(3): 133–150, ills.
- González-Castillo, M. P. [& al. 2011], Escalante, M. Q. & Castaño-Meneses, G. (2011) Arthropods in natural communities in mescal Agave (*Agave durangensis* Gentry) in an arid zone. Amer. J. Appl. Sci. 8(10): 933–944. <https://doi.org/10.3844/ajassp.2011.933.944>.
- González-Elizondo, M. S. [& al. 2011], González-Elizondo, M., López-Enríquez, I. L., Reséndiz-Rojas, L., Tena-Flores, J. A. & Retana-Rentería, F. L. (2011) El complejo *Agave victoriae-reginae* (*Agavaceae*). Acta Bot. Mex. 95: 65–94, ills., maps, key. <http://www.redalyc.org/pdf/574/57418937007.pdf>
- González-Elizondo, M. [& al. 2009], Galván Villanueva, R., López Enriquez, I., Reséndiz Rojas, L. & González Elizondo, M. S. (2009) Agaves. Magueyes, lechuguillas y noas del Estado de Durango y sus alrededores. Durango (MX): CIIDIR Unidad Durango/CONABIO.
- González-Gutiérrez, A. G. [& al. 2014], Gutiérrez-Mora, A. & Rodríguez-Garay, B. (2014) Embryo sac formation and early embryo development in *Agave tequilana* (*Asparagaceae*). SpringerPlus 3: 575, 11 pp., ills. <https://doi.org/10.1186/2193-1801-3-575>.
- González-Oliva, L. [& al. 2014], González-Torres, L. R., Palmarola, A., Barrios, D. & Testé, E. (2014) Categorización de taxones de la flora de Cuba—2014. Bissea 8: 1–322. <https://doi.org/10.13140/RG.2.1.2898.0965>.
- González-Torres, L. R. [& al. 2016], Palmarola, A., González-Oliva, L., Bécquer, E. R., Testé, E., Castañeira-Colomé, M. A., Barrios, D., Gómez-Hechavarría, J. L., García-Beltrán, J. A., Granado, L., Rodríguez-Cala, D., Berazaín, R. & Regalado, L. (eds.) (2016) Lista Roja de la flora de Cuba. Bissea 10(esp. 1): 33–283. <https://doi.org/10.13140/RG.2.2.24056.65288>.
- Good-Avila, S. V. [& al. 2006], Souza, V., Gaut, B. S. & Eguiarte, L. E. (2006) Timing and rate of speciation in *Agave* (*Agavaceae*). Proc. Nation. Acad. Sci. USA 103(24): 9124–9129. <https://doi.org/10.1073/pnas.0603312103>.
- Govaerts, R. H. A. (comp.) (2014+) World checklist of selected plant families [continuously updated]. Richmond (GB): Trustees of the Royal Botanic Gardens, Kew. <http://apps.kew.org/wcsp>
- Govaerts, R. H. A. & Thiede, J. (2013) Transfer of *Polianthes geminiflora* into *Agave* (*Asparagaceae*): New combinations (Nomenclature of *Agave* II). Willdenowia 43(2): 331–333. <https://doi.org/10.3372/wi.43.43215>.



- Granick, E. B. (1944) A karyosystematic study of the genus *Agave*. Amer. J. Bot. 31(5): 283–298. <https://doi.org/10.2307/2437546>.
- Grayum, M. H. (2003) *Agavaceae*. In: Hammel, B. E. & al. (eds.): Manual de plantas de Costa Rica. Vol. 2. Gimnospermas y Monocotiledóneas (*Agavaceae—Musaceae*); pp. 29–34, ills., keys. St. Louis (US): Missouri Botanical Garden. <http://www.biodiversitylibrary.org/item/15458#page/49/>
- Greulich, M. (2005a) Eine blühende Hybride von *Agave sebastianiana* Greene. Berliner Kakt.-Blätt. 5: 23–25.
- Greulich, M. (2005b) *Agave titanota*—eine interessante Pflanze mit vielfältigem Habitus. Kakt. and. Sukk. 57(1): 19–22, ills.
- Greulich, M. (2010) *Agave albescens* Trelease—eine interessante und seltene Art aus dem östlichen Kuba. Berliner Kakt.-Blätt. 10: 45–47, ills.
- Greulich, M. (2012a) Am Standort von *Agave angustiarum* Trelease (*Agavaceae*) in Chalcatzingo (Morelos, Mexiko) und Anmerkungen zur Variabilität und Taxonomie. Avonia 30(1): 25–36, ills.
- Greulich, M. (2012b) *Agave cundinamarcensis* A. Berger—eine interessante Agavenart aus Kolumbien. Avonia 30(2): 113–117, ills.
- Greulich, M. (2012c) *Agave montana* Villareal und *Agave gentryi* Ullrich. Am Standort im mexikanischen Bergland der Sierra Madre Oriental. Wüstengarten 3: 35–55, ills.
- Greulich, M. (2013) Cerro Guiengola—eine Fels-Insel im Isthmus de Tehuantepec. Berliner Kakt.-Blätt. 13: 33–38, ills.
- Greulich, M. (2014a) Am Neotyp-Standort von *Agave inaequidens* ssp. *inaequidens* Koch. Avonia 32(2): 51–62, ills, map.
- Greulich, M. (2014b) Unterwegs im Huasteca-Canyon. Auf der Suche nach *Agave albopilosa* Cabral, C. et al. Wüstengarten 4: 48–69, ills.
- Greulich, M. (2015) Ein Habitat von *Agave inaequidens* ssp. *inaequidens* Koch auf dem Vulkan Tequila (Mexiko). Berliner Kakt.-Blätt. 15: 36–49, ills.
- Greulich, M. (2016a) Vergleichende Untersuchungen zu *Agave lechuguilla* Torrey und deren Hybriden *Agave* × *glomeruliflora* (Engelmann) Berger sowie *Agave* × *gracilipes* Trelease. Wüstengarten 6: 19–39, ills.
- Greulich, M. (2016b) Wintereinbruch in Mexiko—*Agave montana* Villareal [sic!] im Schnee. Berliner Kakt.-Blätt. 16: 38–45, ills.
- Greulich, M. (2016c) A glimpse into the rich cactus and succulent flora of the Barranca de Metztitlán, Mexico (part 1). CactusWorld 34(3): 141–152, ills.
- Greulich, M. (2017a) *Agave pelona*—ein seltenes Juwel aus der *Agavaceae* in der Sierra del Viejo. Kaktusblüte 2017: 41–53, ills.
- Greulich, M. (2017b) Der Nacapule Canyon, eine Oase in der Sonorawüste Nordmexikos—Habitat von *Agave chrysoglossa* und *Agave* aff. *fortiflora*. Berliner Kakt.-Blätt. 17: 39–47, ills.
- Greulich, M. (2017c) Zu Besuch in einer der umfangreichsten Agaven- und Yuccasammlungen Europas. Kakt. and. Sukk. 68(6): 157–162, ills.
- Greulich, M. (2018a) Unterwegs in der Sierra Madre Oriental auf der Suche nach *Agave parviflora* Torr. ssp. *densiflora* G. D. Starr & T. Van Devender. Berliner Kakt.-Blätt. 18: 30–36, ills.
- Greulich, M. (2018b) Ein Blick in die Blütenmorphologie der Gattung *Agave*. Avonia 36(2): 74–97, ills.
- Greuter, W. & Rankin Rodríguez, R. (2017) Plantas vasculares de Cuba: Inventario preliminar. Segunda edición, actualizada, de Espermatófitos de Cuba con inclusión de los Pteridófitos. Vascular plants of Cuba: A preliminary checklist. Second updated edition of The Spermatophyta of Cuba with Pteridophyta added. Berlin (DE): Botanischer Garten und Botanisches Museum Berlin/La Habana (CU): Jardín Botánico Nacional, Universidad de La Habana. <https://doi.org/10.3372/cubalist.2017.1>.
- Grieco, D. (2013) *Agave montana*, one of the best agaves for the garden. Acta Succ. 1(2): 147–158, ills.
- Groman, J. D. & Pellmyr, O. (1999) The pollination of *Manfreda virginica* (*Agavaceae*): Relative contribution of diurnal and nocturnal visitors. Oikos 87(2): 373–381. <https://doi.org/10.2307/3546753>.
- Guadalupe, P. [& al. 2008], Martínez, J. & Méndez, I. (2008) Karyotype studies in cultivars of *Agave tequilana* Weber. Caryologia 61(2): 144–153. <https://doi.org/10.1080/00087114.2008.10589622>.
- Guillot Ortiz, D. (2015) Claves para las especies y taxones infraespecíficos alóctonos del género *Agave* L. en la Península Ibérica e Islas Baleares. Bouteloua 21: 57–61, key.
- Guillot Ortiz, D. & Meer, P. van der (2002a) Sobre el icono designado como *Agave angustifolia* por Sessé & Mociño. Blancoana 19: 97–105. <http://digitblancoana.googlepages.com/AE002091.pdf>
- Guillot Ortiz, D. & Meer, P. van der (2002b) Sobre dos especies de *Agave* y una de *Yucca* (*Agavaceae*) descritas por Cavanilles en 1802. Flora Montiber. 21: 38–49. <http://dialnet.unirioja.es/descarga/articulo/1394846.pdf>
- Guillot Ortiz, D. & Meer, P. van der (2003a) Las familias *Agavaceae* y *Aloaceae* en la Comunidad Valenciana. Flora Montiber. 23: 29–43, keys. <http://dialnet.unirioja.es/servlet/articulo?codigo=1394791>
- Guillot Ortiz, D. & Meer, P. van der (2003b) Acerca de *Agave americana* L. var. *marginata* Trel. en la costa occidental de la Península Ibérica. Toll Negre 2: 16–17, key.
- Guillot Ortiz, D. & Meer, P. van der (2004) *Agave americana* var. *oaxacensis* y el icono de Valentini (1719). Bot. Complut. 28: 101–103, ill.
- Guillot Ortiz, D. & Meer, P. van der (2006a) Claves para los distintos taxones cultivados como ornamentales en la Península Ibérica e Islas Baleares de la especie *Agave americana* L. Bouteloua 1: 13–20, key, ills.
- Guillot Ortiz, D. & Meer, P. van der (2006b) *Prochnyanthes bulliana* (Baker) Baker, un nuevo taxón para la flora ornamental Europea. Bouteloua 1: 70–71.
- Guillot Ortiz, D. & Meer, P. van der (2006c) Un nuevo taxón alóctono potencialmente invasor para la flora ibérica, *Agave sisalana* var. *armata* Trel. Stud. Bot. (Salamanca) 25: 139–141, ills. <http://hdl.handle.net/10366/56400>



- Guillot Ortiz, D. & Meer, P. van der (2008a) Una nueva cita de la especie *Agave salmiana* Otto ex Salm-Dyck en la Comunidad Valenciana. *Bouteloua* 2: 19–23, ills.
- Guillot Ortiz, D. & Meer, P. van der (2008b) Algunas citas nuevas del género *Agave* L., para la flora alóctona española. *Bouteloua* 4: 23–31, ills.
- Guillot Ortiz, D. & Meer, P. van der (2008c) Primera noticia acerca del cultivo de *Agave geminiflora* (Tagl.) Ker-Gawler en España. *Bouteloua* 4: 47–48, ills.
- Guillot Ortiz, D. & Meer, P. van der (2009a) *Agave sisalana* Perr. ex Engelm. y sus cultivares en España. *Bouteloua* 6: 72–75, ills., key.
- Guillot Ortiz, D. & Meer, P. van der (2009b) Claves para los taxones infraespecíficos de *Agave attenuata* Salm-Dyck cultivados en España. *Bouteloua* 6: 134–140, ills., key.
- Guillot Ortiz, D. & Meer, P. van der (2011) Tres especies del género *Agave* L. recientemente introducidas en cultivo en España. *Bouteloua* 8: 8–12, ills.
- Guillot Ortiz, D. & Meer, P. van der (2012) *Agave lophantha* and its cultivars in Spain. *Cact.-Avent. Int.* 97: 28–35, ills.
- Guillot Ortiz, D. & Meer, P. van der (2014) Cultivares de *Agave titanota* Gentry en la Península Ibérica e Islas Baleares. *Bouteloua* 17: 3–6, ills., key.
- Guillot Ortiz, D. & Meer, P. van der (2016a) Especies y variedades del género *Polianthes* L. cultivadas en España en la segunda mitad del siglo XIX y la primera mitad del XX. *Bouteloua* 23: 72–82, ills.
- Guillot Ortiz, D. & Meer, P. van der (2016b) Variedades de *Agave angustifolia* Haw. cultivadas en la Península Ibérica e Islas Baleares. *Bouteloua* 24: 59–66, ills.
- Guillot Ortiz, D. & Meer, P. van der (2016c) *Agave kristenii* A. Vázquez & M. Cházaro en España. *Bouteloua* 26: 27–30, ills.
- Guillot Ortiz, D. & Meer, P. van der (2016d) Cultivares de *Agave desmetiana* Jacobi en la Península Ibérica e Islas Baleares. *Blancoana* 21: 102–106.
- Guillot Ortiz, D. [ & al. 2006], Meer, P. van der & Escudero Ruiz, L. (2006) El género *Polianthes* L. en la Península Ibérica e Islas Baleares. *Bouteloua* 1: 63–69, key, ills.
- Guillot Ortiz, D. [ & al. 2008], Meer, P. van der, Laguna Lumbreras, E. & Rosselló Picornell, J. A. (2008) El género *Agave* L. en la flora alóctona Valenciana. *Monogr. Revista Bouteloua* 3: 94 pp., ills., key.
- Guillot Ortiz, D. [ & al. 2012], Meer, P. van der & Puche, C. (2012) *Agave ingens* A. Berger y sus cultivares en España. *Bol. Soc. Latinoamer. Caribe Cact. otras Suc.* 9(1): 11–18, ills.
- Hannon, D. P. (2002) *Manfreda* and its allies. *Cact. Succ. J. (US)* 74(5): 245–251, ills.
- Hawker, J. L. (2016) Agaves, Yuccas and their kin. Seven genera of the Southwest, including the genera *Agave*, *Dasyliirion*, *Hechtia*, *Hesperaloe*, *Hesperoyucca*, *Nolina* and *Yucca*. Lubbock (US): Texas Tech University Press.
- Haworth, A. H. (1812) Synopsis plantarum succulentarum cum descriptionibus, synonymis, locis, observationibus anglicanis, culturaque. London (GB): Richard Taylor & Socii. <http://www.biodiversitylibrary.org/item/38208>
- Heim, A. (2014) Vier kulturwürdige Arten der Untergattung *Agave* im Vergleich: *Agave avellanidens* mit *Agave shawii* var. *goldmaniana* und *Agave shawii* mit *Agave sebastiana*. *Wüstengarten* 4: 4–24, ills., map.
- Heller, T. (2006) Agaven. Münster (DE): Natur und Tier-Verlag. Ed. 2.
- Hemsley, W. B. (1879–1888) *Biologia Centrali-Americana*. Botany. Vol. V. London (GB): Porter & Dulau & Co. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=3118>
- Hernández López, J. de J. [ & al. 2017], Medina-Rodríguez, J. & Aguirre Zúñiga, E. J. (2017) *Agave durangensis*. *TecnoAgave* 7(49): 14–19.
- Hernández-Sandoval, L. G. (1995) Análisis cladístico de la familia *Agavaceae*. *Bol. Soc. Bot. México* 56: 57–68.
- Hernández-Sandoval, L. G. [ & al. 2008], Orellana, R. & Carnevali, G. (2008) Two new species of *Manfreda* Salisb. (*Agavaceae*) from the Yucatan Peninsula, Mexico. *J. Torrey Bot. Soc.* 135(2): 168–177, ills., map. <https://doi.org/10.3159/08-RA-023.1>.
- Hernández-Sandoval, L. [ & al. 2016], Martínez, M. & Gómez-Sánchez, M. (2016) Plantas: Análisis florístico del orden Asparagales en Querétaro. In: Jones, R. W. & Serrano, V. (eds.): *Historia natural de Querétaro*; pp. 197–221. Querétaro (MX): Editorial Universitaria, Universidad Autónoma de Querétaro.
- Hernández-Vera, G. [ & al. 2007a], Cházaro Basáñez, M. J. & Flores-Berrios, E. (2007) Inventory and distribution of *Agave* (*Agavaceae*) species in Jalisco, Mexico. *J. Bot. Res. Inst. Texas* 1(1): 499–509, maps, ills. <http://www.jstor.org/stable/41971446>
- Hernández-Vera, G. [ & al. 2007b], Cházaro Basáñez, M. J. & Flores-Berrios, E. P. (2007) Inventario, distribución y hábitat del género *Agave* en Jalisco. In: Vázquez-García, J. A. & al. (eds.): *Agaves del occidente de México*; pp. 6–12. Guadalajara (MX): Universidad de Guadalajara.
- Hernández-Vera, G. [ & al. 2019], Vázquez-García, J. A., Padilla-Lepe, J. & Nieves-Hernández, G. (2019) *Agave garciaruzii* (*Asparagaceae*, *Agavoideae*, Subgenus *Littaea*), a new species from the Chorrros del Varal State Reserve in western Mexico. *Phytotaxa* [in press].
- Hester, J. P. (1943) Two Agaves from southwestern Nevada and eastern California. *Cact. Succ. J. (US)* 15(9): 131–135, ills.
- Heyduk, K. [ & al. 2016], McKain, M. R., Lalani, F. & Leebens-Mack, J. (2016) Evolution of a CAM anatomy predates the origins of Crassulacean Acid Metabolism in the *Agavoideae* (*Asparagaceae*). *Molec. Phylog. Evol.* 105: 102–113, ills. <https://doi.org/10.1016/j.ympev.2016.08.018>.
- Hils, M. (2001) Selten kultiviert: *Agave chiapensis* Jacobi. *Kakt. and. Sukk.* 52(11): 294, ill.
- Hochstätter, F. (2015) *Agave* Linné (*Agavaceae*). Mannheim (DE): Digitally published by the author.
- Hochstätter, F. (2016) *Manfreda* Salisbury, *Polianthes* Linné, *Prochnyanthes* Watson (*Agavaceae*). Mannheim (DE): Digitally published by the author.
- Hodgson, W. C. (1999a) A new Flora for Arizona in preparation. *Agavaceae*. *Agave* Family. Part one.

- Agave* L. Century Plant, Maguey. J. Arizona-Nevada Acad. Sci. 32(1): 1–21, keys, maps, ills. <http://www.jstor.org/stable/40024909>
- Hodgson, W. C. (1999b) Agaves and humans: The continuing story of a continuing connection. *Sonoran Quart.* 53(4): 6–8, ills.
- Hodgson, W. C. (2001a) Taxonomic novelties in American *Agave* (Agavaceae). *Novon* 11(4): 410–416, ills. <https://doi.org/10.2307/3393152>.
- Hodgson, W. C. (2001b) Food plants of the Sonoran Desert. Tucson (US): University of Arizona Press.
- Hooker, J. D. (1903) *Agave bakeri*. *Curtis's Bot. Mag.* 129: t. 7890 + text. <http://biodiversitylibrary.org/page/451112>
- Hooker, W. J. (1860) *Agave yuccaeifolia*. *Curtis's Bot. Mag.* 86: t. 5213 + 2 pp. text. <https://biodiversitylibrary.org/page/432267>
- Horich, C. K. (1973) *Agave wercklei* Weber ex Trelease. *Kakt. and. Sukk.* 24(7): 158–160, ills.
- Howard, R. A. (1961) The botanical results of the U.S. Commission of Inquiry to Santo Domingo in 1871. *J. Arnold Arbor.* 42(2): 115–143. <http://biodiversitylibrary.org/page/8441938>
- Howard, R. A. & Dunbar, H. F. (1964) Additions to the flora of Inagua, the Bahamas. *Rhodora* 66(765): 6–15. <http://biodiversitylibrary.org/page/628792>
- Howard, R. A. & Thompson-Mills, B. (ed.) (1979) Flora of the Lesser Antilles. Leeward and Windward Islands. Volume 3. *Monocotyledoneae*. Jamaica Plain (US): Arnold Arboretum.
- Howard, T. M. (1977) *Polianthes × blissii* Worsley. *Pl. Life (Stanford)* 33: 82–84, ill.
- Howard, T. M. (1978) *Polianthes* hybrids. *Pl. Life (Stanford)* 34(2–4): 126–129, ills.
- Howard, T. M. (2001) *Bulbs for warm climates*. Austin (US): University of Texas Press.
- Hoyos F., J. (1985) Flora de la Isla Margarita, Venezuela. Caracas (VE): Sociedad y Fundación La Salle de Ciencias Naturales.
- Huang, K.-L. [ & al. 2001 ], Miyajima, I., Okubo, H., Shen, T. M. & Huang, T. S. (2001) Flower colours and pigments in hybrid Tuberose (*Polianthes*). *Sci. Hort.* 88(3): 235–241. [https://doi.org/10.1016/S0304-4238\(00\)00213-2](https://doi.org/10.1016/S0304-4238(00)00213-2)
- Hummelincq, P. W. (1927) De Agaven van Jamaica. *Succulenta* 9(3): 29–36.
- Hummelincq, P. W. (1936) Notes on *Agave* in Aruba, Curaçao, Bonaire and some parts of the South American continent. *Recueil Trav. Bot. Néerl.* 33: 223–249, tt. 1–8.
- Hummelincq, P. W. (1938) Notes on *Agave* in the Netherlands West Indies and North Venezuela. *Recueil Trav. Bot. Néerl.* 35: 14–28, tt. 1–4, key.
- Hummelincq, P. W. (1984) Agavenproblemen op de Cayman-Eilanden. *Agave sobolifera—A. sisalana—A. angustifolia*. *Succulenta* 63(9): 206–212, (10): 226–228, (11): 259–263, (12): 277–282, maps, ills.
- Hummelincq, P. W. (1986) Agavenproblemen op de Bovenwindse Eilanden der Kleine Antillen. *Succulenta* 65(6–7): 138–142, (8): 161–164, (10): 215–219, ills., map.
- Hummelincq, P. W. (1987) Agavenproblemen op de Bovenwindse Eilanden der Kleine Antillen. *Succulenta* 66(1): 10–13, (3): 65–69, (6): 127–132, (9): 187–189, (10): 205–211, (12): 265–270, key, ills., tab.
- Hummelincq, P. W. (1993) Agaven op Curaçao, Aruba en Bonaire. 1–3. *Succulenta* 72(1): 5–11, (3): 104–109, (5): 214–223, ills., key.
- Hurrell, J. A. & Delucchi, G. (2009) *Agavaceae*. In: Hurrell, J. A. (ed.): *Flora Rioplatense. Sistemática, ecología y ethnobotánica de las plantas vasculares rioplatenses. Parte 3 (Monocotiledóneas)*. Vol. 4; pp. 19–34. Buenos Aires (RA): Lola.
- Illsley, C. [ & al. 2007 ], Vega, E., Pisanty, I., Tlacotempa, A., García, P., Morales, P., Rivera, G., García, J., Jiménez, V., Castro, F. & Calzada, M. (2007) Maguey papalote: Hacia el manejo campesino sustentable de un recurso colectivo en el trópico seco de Guerrero, México. In: Colunga-García Marín, P. & al. (eds.): *En lo ancestral hay futuro: Del tequila, los mezcales y otros Agaves*; pp. 319–338, maps. Mérida (MX): Centro de Investigación Científica de Yucatán A.C.
- Infante, D. (2006) Asexual genetic variability in *Agavaceae* determined with inverse sequence-tagged repeats and amplification fragment length polymorphism analysis. *Pl. Molec. Biol.* 24: 205–217. <https://doi.org/10.1007/BF02914059>.
- Infante, D. [ & al. 2003 ], González, G., Peraza-Echeverría, L. & Keb-Llanes, M. (2003) Asexual genetic variability in *Agave fourcroydes*. *Pl. Sci. (Elsevier)* 164(2): 223–230. [https://doi.org/10.1016/S0168-9452\(02\)00404-1](https://doi.org/10.1016/S0168-9452(02)00404-1).
- Irish, M. & Irish, G. (2000) *Agaves, Yuccas and related plants. A gardener's guide*. Portland (US): Timber Press.
- Jacobi, G. A. von (1864) Versuch zu einer systematischen Ordnung der Agaveen. Hamburg. *Gart.- & Blumenzeit.* 20: 455–466, 498–515, 539–562. <http://biodiversitylibrary.org/page/47219322>
- Jacobi, G. A. von (1865) Versuch zu einer systematischen Ordnung der Agaveen (Fortsetzung). Hamburg. *Gart.- & Blumenzeit.* 21: 53, 114, 154, 213, 249, 341, 383, 445, 555–567. <http://biodiversitylibrary.org/page/48298319>
- Jacobi, G. A. von (1869) Nachtraege zu dem Versuch einer systematischen Ordnung der Agaveen (I). *Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss.* 1868–1869: 138–176. [http://archive.org/details/bub\\_gb\\_xlY3AQAA/MAAJ/page/n148](http://archive.org/details/bub_gb_xlY3AQAA/MAAJ/page/n148)
- Jacobi, G. A. von (1871) Zweiter Nachtrag zu dem Versuch einer systematischen Ordnung der Agaveen. *Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss.* 1869–1872: 89–90, 147–175.
- Jacobsen, H. (1954) *Handbuch der sukkulenten Pflanzen. Band 1. Abromeitiella bis Euphorbia*. Jena (DDR): VEB Gustav Fischer Verlag.
- Janeba, Z. (2008) *Agave utahensis*. Jewel of the genus. *Cact. Succ. J. (US)* 80(6): 299–303, ills. <https://doi.org/10.2985/0007-9367-80.6.299>.
- Janeba, Z. (2010) [Czech]: Komplex *Agave utahensis* Engelm. *Kaktusy* 46(Speciál 2): 2–36, ills., key.

- Janeba, Z. (2013) *Agave albopilosa*. The recently described gem of the genus. *Cact. Succ. J. (US)* 85(3): 108–111, ills. <https://doi.org/10.2985/0007-9367-85.3.108>.
- Jennings, O. E. (1917) A contribution to the botany of the Isle of Pines, Cuba: Based upon the specimens of plants from that island contained in the herbarium of the Carnegie Museum under date of October, 1916. *Ann. Carnegie Mus.* 11: 19–290, tt. V–XXVIII. <http://biodiversitylibrary.org/page/9479344>
- Jestrow, B. [ & al. 2014], Freid, E., Arango-Garces, S. & Francisco-Ortega, J. (2014) The Bahamian flora: Plant exploration, living collections, and DNA—a journey started in 1963. *Bot. Rev. (Lancaster)* 80: 231–244, map, ills. <https://doi.org/10.1007/s12229-014-9136-0>.
- Jiménez-Valdés, M. [ & al. 2010], Godínez-Alvarez, H., Caballero, J. & Lira, R. (2010) Population dynamics of *Agave marmorata* Roehl. under two contrasting management systems in Central Mexico. *Econ. Bot.* 64(2): 149–160. <https://doi.org/10.1007/s12231-010-9117-0>.
- Jimeno-Sevilla, H. D. (2010) Especies endémicas. *Agave gomezpompae* Cházaro & Jimeno-Sevilla *sp. nov.*, inédito/*Agave wendtii* Cházaro. Especies notables. *Agave horrida* subsp. *perotensis* B. Ullrich/*Agave obscura* Schiede. In: Gómez-Pompa, A. & al. (eds.): Atlas de la flora de Veracruz: Un patrimonio natural en peligro; pp. 97–102, 377–380. Veracruz (MX): Gobierno del Estado de Veracruz, Comisión del Estado de Veracruz para la Conmemoración de la Independencia Nacional y la Revolución Mexicana, Universidad Veracruzana.
- Jordan, P. W. & Nobel, P. S. (1979) Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the northwestern Sonoran Desert. *Amer. J. Bot.* 66: 1079–1084. <http://www.jstor.org/stable/2442574>
- José Jacinto, R. & García Moya, E. (2001) Remoción cuticular (“mixiote”) y desarrollo foliar en los Agaves Pulqueros (*Agave salmiana* y *A. mapisaga*). *Bol. Soc. Bot. México* 66: 73–79, map. <https://doi.org/10.17129/botsci.1613>.
- Kattermann, F. (2012) IOS Congress 2012. *Cact. Succ. J. (US)* 84(6): 271–282, ills. <https://doi.org/10.2985/0007-9367-84.6.271>.
- Kemble, B. (2002) *Agave dasylirioides*. *Cact. Succ. J. (US)* 74(5): 235–236, ills.
- Kemble, B. (2004) *Agave parrasana*. *Cact. Succ. J. (US)* 76(4): 207–209, ills.
- Kemble, B. (2006) *Agave guadalajara*. *Cact. Succ. J. (US)* 78(3): 126–130, ills. [https://doi.org/10.2985/0007-9367\(2006\)78\[126:AGJ2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[126:AGJ2.0.CO;2).
- Kimmach, M. (1995) A new *Agave* from Sinaloa, Mexico: *A. filifera* ssp. *microceps*. *Cact. Succ. J. (US)* 67(5): 306–310, ills.
- Klaassen, P. (2011) Succulents of Isla de Cedros. *Cact. Explorer* 2: 27–32, ills.
- Klein, D. (2010)  $\times$ Mangave ‘Bloodspot’ und  $\times$ Mangave ‘Macho Mocha’. *Kakt. and. Sukk.* 61(8): 211–215, ills.
- Klopper, R. R. [ & al. 2010], Smith, G. F., Figueiredo, E. & Crouch, N. R. (2010) Notes on *Agave palmeri* Engelm. (Agavaceae) and its allies in the *Ditepalae*. *Bradleya* 28: 53–66, ills., maps, key. <https://doi.org/10.25223/brad.n28.2010.a8>.
- Koch, K. (1862) Die Pflanzen mit bunten Blättern. Eine vorläufige Skizze (Fortsetzung). 85. Familie: Agavaceae (Agavaceen). *Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten* 5: 59.
- Koch, K. (1865) Agaveen-Studien (II–IV). *Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten* 8: 92–95, 100–104, 108–112. <http://biodiversitylibrary.org/page/36445374>
- Köhres, G. (2008) *Agave ellemeetiana* in Oaxaca wiederentdeckt. *Kakt. and. Sukk.* 59(8): 201–206, ills.
- Koptur, S. & Truong, N. (1998) Facultative ant-plant interactions: Nectar sugar preferences of introduced pest ant species in South Florida. *Biotropica* 30(2): 179–189. <https://doi.org/10.1111/j.1744-7429.1998.tb00053.x>.
- Kristen, M. & Etter, J. (2014) *Agave manantlanicola*, una nuova specie di alta montagna nella Sierra de Manantlán nello stato di Jalisco. Visiting *Agave manantlanicola*, a new species from the highest peaks of the Sierra de Manantlán in Jalisco. *Cactus & Co.* 18(1): 24–55, ills.
- Kuban, J. F. & Neill, R. L. (1980) Feeding ecology of hummingbirds in the highlands of the Chisos Mountains, Texas. *Condor* 80(2): 180–185. <https://doi.org/10.2307/1367475>.
- Kuban, J. F. [ & al. 1983], Lawley, J. & Neill, R. L. (1983) The partitioning of flowering century plants by black-chinned and lucifer hummingbirds. *Southw. Naturalist* 28(2): 143–148. <https://doi.org/10.2307/3671382>.
- Kümmel, F. & Klügling, K. (2006) Winterharte *Agave lechuguilla* in Kultur. *Kakt. and. Sukk.* 57(8): 206–209.
- Kunte, L. (2013) [Czech:] *Agave albescens* Trel. A beautiful endemite from southeastern Cuba. *Adenium* 26: 28–32, ills.
- Kuppen, P. J. K. (2000) Agaven. What’s in a name? *Deel* 6: besluit. *Succulenta* 79(4): 182–187, ills.
- Ladenburg, B. von (1893) Die Kakteen und Sukkulente auf der internationalen Ausstellung Gent. *Monatsschr. Kakt.-kunde* 3: 70–74. <http://biodiversitylibrary.org/page/14249443>
- Laferrière, J. E. (1995a) I come not to praise *Agave hartmanii* (Agavaceae). *Haseltonia* 3: 24.
- Laferrière, J. E. (1995b) Neotypification of *Agave rhodacantha* (Agavaceae). *Haseltonia* 3: 33.
- Larqué Saavedra, A. (2007) Valor agregado al henequén. El establecimiento de una agroindustria productora de bebida alcohólica. In: Colunga-García Marín, P. & al. (eds.): En lo ancestral hay futuro: Del tequila, los mezcales y otros Agaves; pp. 341–346. Mérida (MX): Centro de Investigación Científica de Yucatán A.C.
- León Vázquez, N. I. [ & al. 2013], Campos Ángeles, G. V., Enríquez-del Valle, J. R., Velasco Velasco, V. A., Marini Zúñiga, F. & Rodríguez Ortis, G. (2013) Diversidad de especies de *Agave* en San Miguel Tilquiapam, Ocotlán, Oaxaca. *Revista Mex. Ci. Agríc.*

- Publ. Espec. 6: 1185–1195. <http://www.redalyc.org/articulo.oa?id=263128353010>
- León, H. (1946) Flora de Cuba. Vol. 1: Gimnospermas, Monocotiledóneas. Contr. Ocas. Mus. Hist. Nat. Colegio “De La Salle” 8.
- Lev-Yadun, S. (2017) How monocarpic is *Agave*? Flora (Jena) 230: 12–13. <https://doi.org/10.1016/j.flora.2017.03.002>.
- Lindsay, D. L. [& al. 2012], Edwards, C. E., Jung, M. G., Bailey, P. & Lance, R. F. (2012) Novel microsatellite loci for *Agave parryi* and cross-amplification in *Agave palmeri* (Agavaceae). Amer. J. Bot. 99(7): e295–e297, ills., map. <https://doi.org/10.3732/ajb.1200033>.
- Lindstrom, J. T. (2006) Intergeneric hybrids between *Polianthes* and *Manfreda*. In: Ranney, T. G. (ed.): Plant breeding and evaluation section, SNA Research Conference 51: 599–601. <http://sna.org/Resources/Documents/06resprocsec12.pdf>
- Little, E. L. (1981) *Agave*. In: Benson, L. & Darrow, R. A.: Trees and shrubs of the Southwestern Deserts; pp. 63–76. Tucson (US): University of Arizona Press.
- Lochner, A. (2010) Ein Traum wurde wahr: *Agave aff. chiapensis* blühte. Avonia-News 2010(5): 8–10, ills.
- Lodé, J. (2011) La véritable histoire de *Agave albopilosa*. Cact.-Avent. Int. 78: 28–34, ills.
- Lodé, J. (2015) *Agavaceae: Agave albescens* Trelease 1913. Int. Cact.-Advent. 106–107: 54, ill.
- López Almira, A. (2013) Contribución al catálogo de flora cubana: Endemismos de suelos derivados de ofiolitas. Bot. Complut. 37: 135–152. [https://doi.org/10.5209/rev\\_BOCM.2013.v37.42276](https://doi.org/10.5209/rev_BOCM.2013.v37.42276).
- López-Pujol, J. [& al. 2015a], Guillot Ortiz, D. & Meer, P. van der (2015) Tres nuevos ágaves para la flora alóctona catalana. *Bouteloua* 22: 55–63, ills.
- López-Pujol, J. [& al. 2015b], Guillot Ortiz, D. & Meer, P. van der (2015) New data from alien *Agavaceae* on the Mediterranean coast of the Iberian Peninsula. *Xerophilia* 4(3): 103–118, ills.
- López-Pujol, J. [& al. 2016], Guillot Ortiz, D., Nájera Quezada, P. Nualart, N. & Meer, P. van der (2016) Primera cita del endemismo mexicano *Agave difformis* A. Berger (*Agavaceae*) fuera de su área de distribución nativa. *Acta Bot. Mex.* 115: 9–25, maps, ills. <http://hdl.handle.net/10261/131789>
- Lorea Hernández, F. & Munn-Estrada, D. X. (2005) Estudio florístico de los bosques mesófilos de la Sierra Mazateca de Oaxaca, México. Informe final SNIB-CONABIO proyecto No. U028. México D. F. (MX): Instituto de Ecología, División de Vegetación y Flora.
- Lott, E. J. & García-Mendoza, A. (1994) *Agavaceae*. In: Davidse, G. & al. (eds.): Flora Mesoamericana, Volumen 6, *Alismataceae a Cyperaceae*; pp. 35–47, keys. México (MX): UNAM, Instituto de Biología/St. Louis (US): Missouri Botanical Garden/London (GB): Natural History Museum. <http://www.tropicos.org/Project/FM>
- Lott, E. J. & Verhoek-Williams, S. E. (1991) *Manfreda chamelensis* (Agavaceae: Poliantheae), a new species from western Mexico. *Phytologia* 70(5): 366–370.
- Ludlow-Wiechers, B. & Ojeda, L. (1983) El polen del género *Agave* para la Península de Yucatán. *Bol. Soc. Bot. México* 44: 29–42, ills.
- Lv, L. [& al. 2009], Sun, G., Xie, J., Zhang, X., Hu, Y. & Duan, J. (2009) Determination of chromosomal ploidy in *Agave* spp. *Afr. J. Biotechnol.* 8(20): 5248–5252. <https://doi.org/10.5897/AJB09.1126>.
- Lyons, G. (2002) Among the agaves of the Huntington Desert Garden. *Cact. Succ. J. (US)* 74: 160–164, ills.
- MacDougall, T. (1956) Cacti and succulents in a prehistoric city. *Cact. Succ. J. (US)* 28(6): 171–173, ills.
- MacDougall, T. (1960) *Agave nizandensis*—a re-introduction. *Cact. Succ. J. (US)* 32(6): 184, ills.
- MacDougall, T. (1966) Cacti and succulents on Cerro Guiengola, Mexico. *Cact. Succ. J. (US)* 38(1): 24–25, ills.
- MacDougall, T. (1970) Seed collecting in Oaxaca, Mexico. *Cact. Succ. J. (US)* 43(6): 243, ills.
- MacDougall, T. (1971) Plant exploration in the states of Oaxaca and Chiapas. The cactus and succulent field notes of Tom MacDougall, 1936 to 1971. Santa Barbara (US): The Cactus and Succulent Journal.
- Machuca Núñez, J. A. & Cházaro Basáñez, M. J. (2015) La distribución geográfica, el hábitat y los usos de *Polianthes longiflora* Rose (*Agavaceae*), en el estado de Jalisco, México. *Bouteloua* 20: 144–152, ills.
- Madrigal-Sanchez, X. & Diaz-Barriga, H. (1991) Un caso teratológico de fasciación en *Agave inaequidens* C. Koch (*Amaryllidaceae*) en la Cuenca de Pátzcuaro, Michoacán (México). *Acta Bot. Mex.* 15: 65–70, ill. <https://doi.org/10.21829/abm15.1991.621>.
- Magallán Hernández, F. & Hernández Sandoval, L. (2001) La familia *Agavaceae* en el Estado de Querétaro, México. *Bol. Soc. Bot. México* 66: 103–112, maps. <http://www.redalyc.org/pdf/577/57706610.pdf>
- Magallán Hernández, F. [& al. 2012], Maruri Aguilar, B. & Sánchez Martínez, E. (2012) La colección de Agaváceas del Jardín Botánico Regional de Cadereyta, Querétaro, México. *Bol. Soc. Latinoamer. Caribe Cact. otras Suc.* 9(1): 26–31, ills.
- Magaña-González, K. C. [& al. 2007], Vázquez-García, J. A. & Reyna Bustos, Ó. F. (2007) Visitantes florales de *Agave valenciana* (*Agavaceae*) en Mascota, Jalisco: Observaciones preliminares. In: Vázquez-García, J. A. & al. (eds.): *Agaves del occidente de México*; pp. 32–36, ills. (tt. NN-OO). Guadalajara (MX): Universidad de Guadalajara.
- Mahr, D. (2015) Production of artisanal mezcal, tequila’s sassy little sister. *Cact. Succ. J. (US)* 87(1): 4–14, ills. <https://doi.org/10.2985/015.087.0102>.
- Mancina, C. A. (2010) *Phylloncyrtis poeyi* (Chiroptera: Phyllostomidae). *Mammalian Species* 42(852): 41–48. <https://doi.org/10.1644/852.1>.
- Martin, M. P. [& al. 2011], Peters, C. M., Palmer, M. I. & Illsley, C. (2011) Effect of habitat and grazing on the regeneration of wild *Agave cupreata* in Guerrero, Mexico. *Forest. Ecol. Managem.* 262: 1443–1451. <https://doi.org/10.1016/j.foreco.2011.06.045>.
- Martin, P. S. [& al. 1998], Yetman, D., Fishbein, M. E., Jenkins, P. D., Devender, T. R. Van & Wilson, R. K.



- (eds.) (1998) Gentry's Rio Mayo plants: The tropical deciduous forest and environs of northwest Mexico. Tucson (US): University of Arizona Press.
- Martínez Castro, L. E. [& al. 2015], Martínez-Palacios, A., Sánchez Vargas, N. M., Lobitte, P., Nápoles Alvarez, C. R., Martínez Palacios, O., Villegas, J., Martínez Avalos, J. G. & Golubov, J. (2015) Poblaciones silvestres de Maguey Chino (*Agave cupreata*) en el Estado de Michoacán. In: Martínez-Palacios, A. & al. (eds.): Aspectos sobre el manejo y la conservación de agaves mezcaleros en Michoacán; pp. 165–175, maps. Morelia (MX): Consejo Estatal de Ciencia, Tecnología e Innovación de Michoacán.
- Martínez Gordillo, M. [& al. 1997], Valencia Ávalos, S. & Calónico Soto, J. (1997) Flora de Papalutla, Guerrero y de sus alrededores. Anales Inst. Biol. UNAM, Ser. Bot. 68(2): 107–133. <http://www.redalyc.org/pdf/400/40068203.pdf>
- Martínez Salvador, M. [& al. 2012], Mata-González, R., Morales Nieto, C. & Valdez-Cepeda, R. (2012) *Agave salmiana* plant communities in Central Mexico as affected by commercial use. Environm. Managem. 49: 55–63, map, ills. <https://doi.org/10.1007/s00267-011-9759-4>.
- Martínez, M. [& al. 2017], Salas, D. & Hernández Sandoval, L. (eds.) (2017) Guía ilustrada de la flora del valle de Querétaro. Querétaro (MX): Universidad Autónoma de Querétaro.
- Martínez-Gutiérrez, G. A. [& al. 2013], Íñiguez-Covarrubias, G., Ortiz-Hernández, Y. D., López-Cruz, J. Y. & Bautista Cruz, M. A. (2013) Tiempos de apilado del bagazo del maguey mezcalero y su efecto en las propiedades del compost para sustrato de tomate. Revista Int. Contam. Amb. 29(3): 209–216. <http://projecteuid.redalyc.org/articulo.oa?id=37028276007>
- Martínez-Meléndez, J. [& al. 2008], Pérez-Farrera, M. Á. & Farrera-Sarmiento, O. (2008) Inventario florístico del cerro el Cebú y zonas adyacentes en la Reserva de la Biosfera El Triunfo (Polígono V), Chiapas, México. Bol. Soc. Bot. México 82(1): 21–40. <http://www.redalyc.org/articulo.oa?id=57708204>
- Martínez-Morales, R. & Meyer, S. E. (1985) A demographic study of maguey verde (*Agave salmiana* ssp. *crassispina*) under conditions of intense utilization. Desert Pl. 7(2): 61–64, ills. <http://repository.arizona.edu/handle/10150/554209>
- Martínez-Palacios, A. & Eguiarte, L. E. (2011) *Agave victoriae-reginae* T. Moore (*Agavaceae*): Die Wildpopulationen und deren genetische Differenzierung/Las poblaciones silvestres y su diferenciación. Avonia 29(4): 139–145, xxv–xxvii, ills., map.
- Martínez-Palacios, A. [& al. 1999], Eguiarte, L. E. & Furnier, G. R. (1999) Genetic diversity of the endangered endemic *Agave victoriae-reginae* (*Agavaceae*) in the Chihuahuan Desert. Amer. J. Bot. 86(8): 1093–1098. <http://www.amjbot.org/content/86/8/1093.full>
- Martínez-Palacios, A. [& al. 2011], Gómez-Sierra, J. M., Sáenz-Romero, C., Pérez-Nasser, N. & Sánchez-Vargas, N. (2011) Genetic diversity of *Agave cupreata* Trel. & Berger. Considerations for its conservation. Revista Fitotec. Mex. 34(3): 159–165. <http://www.redalyc.org/pdf/610/61019746002.pdf>
- Martínez-Salvador, M. [& al. 2007], Beltrán-Morales, L., Valdes-Cepeda, R., Rubio Arias, H., Troyo-Dieguez, E., Murillo-Amador, B., Jiménez Gaindo, J. & Ortega-Rubio, A. (2007) Assessment of sustainability performance on the utilization of Agave (*Agave salmiana* ssp. *crassispina*) in Zacatecas, Mexico. Int. J. Sustain. Developm. World Ecol. 14(4): 362–371. <https://doi.org/10.1080/13504500709469736>.
- Mata-Sucre, J. [& al. 2017], Imery-Buiza, J. & Cequea-Ruiz, H. (2017) Estudio cariotípico en plantas de *Agave cocui* Trelease (*Asparagaceae*) nativas del estado Sucre, Venezuela. Saber (Univ. Oriente, Venezuela) 29: 174–182. <http://ojs.udo.edu.ve/index.php/saber/articulo/view/2608>
- Matuda, E. (1974) *Manfreda nanchititlensis* Matuda sp. nov. Anales Inst. Biol. UNAM, Ser. Bot. 43(1): 54–55.
- Matuda, E. (1975) Una nueva *Manfreda* de Guerrero. Cact. Suc. Mex. 20(2): 46–48, ill.
- Mays, H. (2005) Sukkulente aus den Huntington Botanical Gardens. Avonia 23: 44–47, ills. (incl. front cover).
- McKelvey, S. D. & Sax, K. (1933) Taxonomic and cytological relationships of *Yucca* and *Agave*. J. Arnold Arbor. 14: 76–81. <https://www.jstor.org/stable/43780651>
- McKinney, K. K. (1993) *Agave*. In: Hickman, J. C. (ed.): The Jepson Manual. Higher plants of California; p. 1172. Berkeley etc. (US): University of California Press.
- McVaugh, R. (1989) Flora Novo-Galiciana. A descriptive account of the vascular plants of Western Mexico. Vol. 15: *Bromeliaceae* to *Dioscoreaceae*. Ann Arbor (US): University of Michigan Herbarium.
- Meer, P. van der (2011) Las primeras floraciones de la especie *Agave americana* L. en Europa. Bouteloua 8: 51–59.
- Meer, P. van der (2012) *Agave gomezpompae* Cházaro & Jimeno-Sevilla en España. Bouteloua 11: 66–68, ills.
- Meer, P. van der (2014) *Agave cernua* Berger en el Jardín Botánico de Valencia. Bouteloua 17: 72–75, ills.
- Meer, P. van der (2016a) *Agave wendtii* Cházaro, primera noticia acerca de su cultivo en la provincia de Valencia. Bouteloua 24: 141–142, ill.
- Meer, P. van der (2016b) Primera referencia acerca del cultivo de *Agave nussavium* subsp. *nussavium* [sic!] en España. Bouteloua 24: 153–154, ill.
- Meer, P. van der (2016c) *Agave gilbertii* A. Berger en España. Bouteloua 25: 144, ill.
- Meer, P. van der (2016d) Primera referencia acerca del cultivo de *Agave abisaii* A. Vázquez & Nieves en España. Bouteloua 26: 108–109, ill.
- Meer, P. van der & Guillot Ortiz, D. (2015) *Agave macroacantha* Zucc. cultivars in Spain. Int. Cact.-Advent. 106–107(7): 55–61, ills.
- Meer, P. van der & Guillot Ortiz, D. (2016) *Agave thomasae* Trelease cultivada en España. Bouteloua 23: 188–189, ill.
- Meer, P. van der & Puche, C. (2014) *Agave univittata* var. *ensifera* (Jacobi) P. van der Meer & C. Puche. Bouteloua 19: 58–64, ills.
- Meer, P. van der [& al. 2014], Guillot Ortiz, D., Puche, C. & Nájera Quezada, P. (2014) Iconography of *Agave*



- univittata* Haw. and *Agave lechuguilla* Torr. (*Agavaceae*). *Xerophila* 10: 31–41, ills.
- Mesquida, V. [ & al. 2016], López-Pujol, J. & Guillot-Ortiz, D. (2016) A new species and new populations of the genus *Agave* L. for the alien flora of Catalonia (north-eastern Iberian Peninsula). *Xerophila* 5(4): 45–58, ills.
- Metzler, W. (1924) Beiträge zur vergleichenden Anatomie blattsukkulenter Pflanzen. *Bot. Arch.* 6(1–3): 50–83, ills.
- Mitich, L. W. (1975) *Agave telegraphica*, an extinct species? *Cact. Succ. J. (US)* 47(3): 106–107, ill.
- Molina-Freaner, F. & Eguiarte, L. E. (2003) The pollination biology of two paniculate *Agaves* (*Agavaceae*) from northwestern Mexico: Contrasting roles of bats as pollinators. *Amer. J. Bot.* 90(7): 1016–1024. <http://www.jstor.org/stable/4124121>
- Moore, J. (2016) *Aloes & Agaves in cultivation*. Solana Beach (US): Solana Succulents.
- Mora-López, J. L. [ & al. 2011], Reyes-Agüero, J., Flores-Flores, J. L., Pena-Valdivia, C. & Aguirre-Rivera, J. R. (2011) Variación morfológica y humanización de la sección *Salmianae* del género *Agave*. *Agrociencia* (Chapingo) [ser. 3] 45(4): 465–477. <http://www.scielo.org.mx/pdf/agro/v45n4/v45n4a6.pdf>
- Moreno Salazar, S. F. [ & al. 2007], Esqueda, M., Martínez, J. & Palomino, G. (2007) Tamaño del genoma y cariotipo en *Agave angustifolia* y *A. rhodacantha* de Sonora, México. *Revista Fitotec. Mex.* 30(1): 13–23.
- Morris, D. (1889) *Agave candelabrum*. *Gard. Chron.*, ser. 3, 5: 76–77, ill. <http://biodiversitylibrary.org/page/16449349>
- Mostul, B. L. (2005) The succulents of Venezuela's Rio Chama canyon. *Cact. Succ. J. (US)* 77(2): 68–74, ills., map. [https://doi.org/10.2985/0007-9367\(2005\)77\[68:TSOVR\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[68:TSOVR]2.0.CO;2).
- Mottram, R. (2015) An annotated checklist of the infragenera of *Agave* L. *Cactician* 8: 1–38.
- Mulford, A. I. (1896) A study of the *Agaves* of the United States. *Annual Rep. Missouri Bot. Gard.* 7: 47–100, tt. 26–63. <http://biodiversitylibrary.org/page/47765142>
- Muller, C. H. (1939) A new species of *Agave* from Trans-Pecos Texas. *Amer. Midl. Naturalist* 21(3): 763–765. <https://doi.org/10.2307/2420529>.
- Munter, M. de (1981) The geographical distribution of succulents in Colombia. *Nation. Cact. Succ. J.* 36(3): 73–76. <http://www.jstor.org/stable/42790166>
- Nabhan, G. P. (1995) Finding the hidden garden. *J. Southwest* 37(2): 401–415. <http://www.jstor.org/stable/40169984>
- Nájera Quezada, P. [ & al. 2015], Hernandez, J. J., Lopez Martinez, C. & Neri Cardona, S. K. (2015) Sierra de San Miguelito. A preliminary regional ecological analysis. *Xerophila* 4(1): 4–24, map, ills.
- Navarro-Quezada, A. [ & al. 2003], González-Chauvet, R., Molina-Freaner, F. & Eguiarte, L. E. (2003) Genetic differentiation in the *Agave deserti* (*Agavaceae*) complex of the Sonoran desert. *Heredity* 90(3): 220–227, map. <https://doi.org/10.1038/sj.hdy.6800216>.
- Nelson, E. C. (2001) Towards a taxonomic revision of the *Telecomiaceae*. *BSBI [Bot. Soc. Brit. Isles] News* 87: 9–10, ills.
- Newton, L. E. (1999) *Agave gypsophila*—an underrated species. *Brit. Cact. Succ. J.* 17(2): 99. <https://www.jstor.org/stable/42794464>.
- Newton, L. E. (2004) Flowering of *Agave gypsophila*. *Brit. Cact. Succ. J.* 22(2): 66–67, ills. <http://www.jstor.org/stable/42793938>
- Nobel, P. S. (1988) *Environmental biology of agaves and cacti*. Cambridge (GB) etc.: Cambridge University Press.
- Nobel, P. S. (1992) Annual variations in flowering percentage, seedling establishment, and ramet production for a desert perennial. *Int. J. Pl. Sci.* 153(1): 102–107. <https://doi.org/10.1086/297011>.
- Nobel, P. S. & Quero, E. (1986) Environmental productivity indices for a Chihuahuan desert CAM plant, *Agave lechuguilla*. *Ecology* 67: 1–11. <https://doi.org/10.2307/1938497>.
- North, G. B. & Baker, E. A. (2007) Water uptake by older roots: Evidence from desert succulents. *HortScience* 42(5): 1103–1106.
- North, G. B. [ & al. 2004], Martre, P. & Nobel, P. S. (2004) Aquaporins account for variations in hydraulic conductance for metabolically active root regions of *Agave deserti* in wet, dry, and rewetted soil. *Pl. Cell Environm.* 27(2): 219–228. <https://doi.org/10.1111/j.1365-3040.2003.01137.x>.
- North, G. B. [ & al. 2008], Brinton, E. K. & Garrett, T. Y. (2008) Contractile roots in succulent monocots: Convergence, divergence and adaptation to limited rainfall. *Pl. Cell Environm.* 31: 1179–1189, ills. <https://doi.org/10.1111/j.1365-3040.2008.01832.x>.
- Núñez, H. M. [ & al. 2011], Rodríguez, L. F. & Khanna, M. (2011) *Agave* for tequila and biofuels: An economic assessment and potential opportunities. *GCB Bioenergy* 3: 43–57, maps. <https://doi.org/10.1111/j.1757-1707.2010.01084.x>.
- Orellana, R. (2012) La que mancha con el sol. *Desde el Herbario CICY* 4: 20–21, ills.
- Ornelas, J. F. [ & al. 2002], Ordano, M., Hernández, A., Carlos López, J., Mendoza, L. & Perroni, Y. (2002) Nectar oasis produced by *Agave marmorata* Roezl (*Agavaceae*) lead to spatial and temporal segregation among nectarivores in the Tehuacan Valley, Mexico. *J. Arid Environm.* 52(1): 37–51. <https://doi.org/10.1006/jare.2002.0971>.
- Ortiz-Hernández, Y. D. [ & al. 2018], Gutiérrez-Hernández, G. F., Corzo-Ríos, L. J., García-Ramírez, E. & Martínez-Tomás, S. H. (2018) Varietal and germinative characterization of *Agave potatorum* (*Asparagaceae*) seeds with different origins. *Bot. Sci.* 96(4): 628–639. <https://doi.org/10.17129/botsci.1914>.
- Ortiz-Maciel, S. G. [ & al. 2010], Hori-Ochoa, C. & Enkerlin-Hoefflich, E. (2010) Maroon-fronted parrot (*Rhynchopsitta terrisi*) breeding home range and habitat selection in the northern Sierra Madre Oriental, Mexico. *Wilson J. Ornithol.* 122(3): 513–517. <https://doi.org/10.1676/08-002.1>.
- Ostenfeld, C. H. (1924) Botanisk have gennem 50 aar, 1874–1924. København (DK): Schultz.
- Padilla Velarde, E. [ & al. 2008], Cuevas Guzmán, R. & Koch, S. D. (2008) Plantas vasculares y vegetación de la parte alta del Arroyo Agua Fría, municipio de

- Minatitlán, Colima, México. Acta Bot. Mex. 84: 25–72. <https://doi.org/10.21829/abm84.2008.1066>.
- Palma Cruz, F. de J. (1991) El género *Agave* L. y su distribución en el estado de Oaxaca. México D.F. (MX): UNAM, Escuela Nacional de Estudios Profesionales “Iztacala”; thesis.
- Palomino, G. [& al. 2003], Dolezal, J., Méndez, I. & Rubluo, A. (2003) Nuclear genome size analysis of *Agave tequilana* Weber. Caryologia 56(1): 37–46. <https://doi.org/10.1080/00087114.2003.10589305>.
- Palomino, G. [& al. 2005], Martínez, J. & Méndez, I. (2005) Citotipos en *Agave angustifolia* Haw. determinados por citometría de flujo y análisis de sus cariotipos. Revista Int. Contam. Amb. 21(Supl. 1): 49–54.
- Palomino, G. [& al. 2007], Martínez, J. & Méndez, I. (2007) Variación inter e intraespecífica en especies de *Agave* por citometría de flujo y análisis de sus cromosomas. In: Colunga-García Marín, P. & al. (eds.): En lo ancestral hay futuro: Del tequila, los mezcales y otros Agaves; pp. 41–65. Mérida (MX): Centro de Investigación Científica de Yucatán A.C.
- Palomino, G. [& al. 2010], Martínez, J. & Méndez, I. (2010) Análisis del tamaño del genoma y cariotipo de *Agave akites* Gentry (*Agavaceae*) de Sonora, México. Revista Mex. Biodivers. 81(3): 655–662. <http://www.biodiversitylibrary.org/part/112009#/summary>
- Palomino, G. [& al. 2012], Martínez, J., Cepeda-Cornejo, V. & Pimental-Barrios, E. (2012) Nuclear genome size and cytotype analysis in *Agave cupreata* Trel. & Berger (*Agavaceae*). Caryologia 65(4): 281–294, ills. <https://doi.org/10.1080/00087114.2012.752915>.
- Palomino, G. [& al. 2015], Martínez, J., Méndez, I., Cepeda-Cornejo, V., Barba-González, R. & Rodríguez-Garay, B. (2015) Nuclear genome size and cytotype analysis in *Agave parviflora* Torr. subsp. *flexiflora* Gentry (*Asparagales*, *Asparagaceae*). Caryologia 68(3): 159–168. <https://doi.org/10.1080/00087114.2015.1032575>.
- Pando-Moreno, M. [& al. 2008], Pulido, R., Castillo, D., Jurado, E. & Jiménez, J. (2008) Estimating fiber for lechuguilla (*Agave lechuguilla* Torr., *Agavaceae*), a traditional non-timber forest product in Mexico. Forest. Ecol. Managem. 255: 3686–3690. <https://doi.org/10.1016/j.foreco.2008.02.053>.
- Pardo, O. (2007) El agave (*Agave americana* L., *Agavaceae*) en las culturas prehispánicas: Una revisión bibliográfica. Chloris Chilensis 10(1): [unpaged].
- Parker, K. C. [& al. 2007], Hamrick, J. L., Hodgson, W. C., Trapnell, D. W., Parker, A. J. & Kuzoff, R. K. (2007) Genetic consequences of pre-columbian cultivation for *Agave murpheyi* and *A. delamateri* (*Agavaceae*). Amer. J. Bot. 94(9): 1479–1490, maps. <https://doi.org/10.3732/ajb.94.9.1479>.
- Parker, K. C. [& al. 2010], Trapnell, D. W., Hamrick, J. L., Hodgson, W. C. & Parker, A. J. (2010) Inferring ancient *Agave* cultivation practices from contemporary genetic patterns. Molec. Ecol. 19: 1622–1637. <https://doi.org/10.1111/j.1365-294X.2010.04593.x>.
- Parker, K. C. [& al. 2014], Trapnell, D. W., Hamrick, J. L. & Hodgson, W. C. (2014) Genetic and morphological contrasts between wild and anthropogenic populations of *Agave parryi* var. *huachucensis* in south-eastern Arizona. Ann. Bot. (Oxford), n.s. 113(6): 939–952, ills., map. <https://doi.org/10.1093/aob/mcu016>.
- Parker, R. (2017) *Agaves* of Arizona. Cact. Succ. J. (US) 89(6): 256–265, ills., map. <https://doi.org/10.2985/015.089.0603>.
- Parker, R. (2018a) *Agaves* of Arizona. Part II. Cact. Succ. J. (US) 90(1): 20–28, ills. <https://doi.org/10.2985/015.090.0103>.
- Parker, R. (2018b) *Agave* Mite, a quick and dirty primer. Cact. Succ. J. (US) 90(2): 104–106, ills. <https://doi.org/10.2985/015.090.0205>.
- Pavlisca, L. L. [& al. 2015], Fehmi, J. S. & Smith, S. E. (2015) Assessing emergence of a long-lived monocarpic succulent in disturbed, arid environments: Evaluating abiotic factors in effective *Agave* restoration by seed. Arid Lands Res. Manag. 29: 98–109. <https://doi.org/10.1080/15324982.2014.909905>.
- Pax, F. (1893) Eine neue Agavenart des Berliner botanischen Gartens. Gartenflora 42: 66–68, ill. <https://biodiversitylibrary.org/page/40103275>
- Peña Ramos, J. F. & Sánchez Gullón, E. (2016) *Agave salmiana* (*Asparagaceae*, *Agavoideae*) novedad corológica para Huelva (SW España). Bouteloua 26: 74–77, ills., key.
- Perez Badillo, C. (2016) Taking pictures in the ... desert. Xerophilia 5(4): 111–126, ills.
- Pérez, A. J. [& al. 2013], Calle, J. M., Simonet, A. M., Guerra, J. O., Stochmal, A. & Macías, F. A. (2013) Bioactive steroidal saponins from *Agave offoyana* flowers. Phytochemistry 95: 298–307. <https://doi.org/10.1016/j.phytochem.2013.06.020>.
- Pérez, A. J. [& al. 2014], Simonet, A. M., Calle, J. M., Pecio, L., Guerra, J. O., Stochmal, A. & Macías, F. A. (2014) Phytotoxic steroidal saponins from *Agave offoyana* leaves. Phytochemistry 105: 92–100. <https://doi.org/10.1016/j.phytochem.2014.05.014>.
- Pérez, A. L. F. [& al. 2010], Castro-Castro, A. & Rodríguez, A. (2010) Redescubrimiento de *Polygonum palustris* (*Agavaceae*), un nardo poco conocido en Nueva Galicia. In: Memoria del XVIII Congreso Mexicano de Botánica, Guadalajara, Jalisco, Mexico; pp. 390–391. Guadalajara (MX): Prometeo Editores.
- Pérez-Farrera, M. Á. [& al. 2012], Martínez-Camilo, R., Martínez-Meléndez, N., Farrera-Sarmiento, O. & Maza-Villalobos, S. (2012) Listado florístico del Cerro Quetzal (Polígono III) de la Reserva de la Biosfera El Triunfo, Chiapas. Bot. Sci. 90(2): 113–142. <https://doi.org/10.17129/botsci.479>.
- Pérez-Farrera, M. Á. [& al. 2016], Espinosa Jiménez, J. A., López, A., Gómez-Domínguez, H. & Gordillo Ruiz, M. C. (2016) Flora y vegetación de la selva zoque de Chiapas. In: SEMAHN (ed.): Ecoregión Zoque: Retos y oportunidades ante el cambio climático; pp. 52–76. Tuxtla Gutierrez (MX): Secretaría de Medio Ambiente

- e Historia Natural. [http://issuu.com/difusionsemahn/docs/ecorregion\\_zoque](http://issuu.com/difusionsemahn/docs/ecorregion_zoque)
- Pérez-García, E. [ & al. 2001 ], Meave, J. & Gallardo, C. (2001) Vegetación y flora de la región de Nizanda, Istmo de Tehuantepec, Oaxaca, México. *Acta Bot. Mex.* 56: 19–88, maps. <https://doi.org/10.21829/abm56.2001.879>.
- Pérez-Sarabia, J. E. [ & al. 2017 ], Duno de Stefano, R., Carnevali Fernández-Concha, G., Ramírez-Morillo, I., Méndez-Jiménez, N., Zamor-Crescencio, P. & Cetzal-Ix, W. (2017) Al conocimiento florístico de la Península de Yucatán, México. *Polibotánica* 44: 39–49, ills. <https://doi.org/10.18387/polibotanica.44.3>.
- Petersen, O. G. (1893) Lidt om *Agave antillarum* Desc. *Bot. Tidsskr.* 18: 266–270, t. XIX. <http://biodiversitylibrary.org/page/44709908>
- Pfendbach, E. (2005) Trekking for Cuban cacti. *Cact. Succ. J. (US)* 77(2): 75–81, ills., map. [https://doi.org/10.2985/0007-9367\(2005\)77\[75:TFCC\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[75:TFCC]2.0.CO;2).
- Phillips, C. (2013) “Rare and novel species”. Singular words and curious plants sent by Karwinski from Oaxaca & Puebla, 1826–1832. *Cact. Succ. J. (US)* 85(4): 132–142, ills., map. <https://doi.org/10.2985/0007-9367-85.4.132>.
- Pilbeam, J. (2011) *Echeveria laui* is in care. *Cact. Explorer* 2: 36–39, ills.
- Pilbeam, J. (2013) A gallery of Agaves (including variegates). Hornchurch (GB): British Cactus & Succulent Society.
- Piña Luján, I. (1985) Consideraciones sobre el género *Manfreda*. I–III. *Cact. Suc. Mex.* 30(2): 27–32, (3): 56–64, (4): 84–90, ills., maps, key.
- Piña Luján, I. (1986) Consideraciones sobre el género *Manfreda*. IV/V. *Cact. Suc. Mex.* 31(1): 12–18, (2): 34–35, ills., maps.
- Piña Luján, I. (1994) Consideraciones sobre la localidad de *Agave atrovirens*. *Cact. Suc. Mex.* 39(1): 8–12, ill.
- Pinkava, D. J. & Baker, M. A. (1985) Chromosome and hybridization studies of Agaves. *Desert Pl.* 7(2): 93–100, ills. <http://repository.arizona.edu/handle/10150/554212>
- Polka, W. (2006) *Agave dasylirioides* Jacobi & Bouché. *Berliner Kakt.-Blätt.* 6: 25–26, ills.
- Portal Datos Abiertos UNAM (2018+) Portal de Datos Abiertos UNAM Colecciones Universitarias, Colecciones Biológicas. México (MX): Universidad Nacional Autónoma de México. <http://datosabiertos.unam.mx/biodiversidad>
- Powers, D. E. & Backhaus, R. A. (1989) In vitro propagation of *Agave arizonica* Gentry & Weber. *Pl. Cell Tissue Organ Cult.* 16(1): 57–60. <https://doi.org/10.1007/BF00044072>.
- Proctor, G. R. (1984) Flora of the Cayman Islands. London (GB): Her Majesty's Stationary Office.
- Proctor, G. R. & Acevedo-Rodríguez, P. (2005) *Agavaceae*. In: Acevedo-Rodríguez, P. & Strong, M. T. (eds.): *Monocotyledons and Gymnosperms of Puerto Rico and the Virgin Islands*; pp. 116–125. Washington D.C. (US): Department of Botany, National Museum of Natural History. <http://www.fs.usda.gov/treeearch/pubs/30275>
- Puche, C. (2014) Iconografía Botánica. *Agave lophantha* ‘Quadricolor’. *Bouteloua* 17: 145–146, ills.
- Puche, C. & Meer, P. van der (2014) *Agave albomarginata* Gentry. *Bouteloua* 19: 229–230, ills.
- Quílez, A. M. [ & al. 2004 ], Saenz, M. T., García, M. D. & Puerta, R. de la (2004) Phytochemical analysis and anti-allergic study of *Agave intermixta* Trel. and *Cissus sicyoides* L. *J. Pharm. Pharmacol.* 56(9): 1185–1189. <https://doi.org/10.1211/0022357044102>.
- Quinn, M. (2014) *Manfreda* Giant-Skipper. *Stallingsia maculosa* (H. A. Freeman, 1955). <http://www.texasento.net/Stallingsia.htm>, accessed Dec. 2018.
- Radding, C. (2012) The children of Mayahuel: Agaves, human cultures, and desert landscapes in northern Mexico. *Environm. Hist.* 17(1): 84–115, ills. <https://doi.org/10.1093/envhiv/emr118>.
- Ramírez Prieto, J. (2014) Flora de la cima de la Sierra de las Candelas, Municipio de Jerez de García Salinas, Zacatecas, México. Montecillo (MX): Colegio de Postgraduados; unpublished M.Sc. thesis.
- Ramírez-Tobías, H. M. [ & al. 2012 ], Peña-Valdivia, C. B., Aguirre, J. R., Reyes-Aguero, J. A., Sánchez-Urdaneta, A. B. & Valle G., S. (2012) Seed germination temperatures of eight Mexican *Agave* species with economic importance. *Pl. Spec. Biol.* 27(2): 124–137, ills. <https://doi.org/10.1111/j.1442-1984.2011.00341.x>.
- Ramírez-Tobías, H. M. [ & al. 2016 ], Niño Vásquez, R., Aguirre Rivera, J. R., Flores, J., De-Nova Vázquez, J. A. & Jarquin Gálvez, R. (2016) Seed viability and effect of temperature on germination of *Agave angustifolia* subsp. *tequilana* and *A. mapisaga*; two useful *Agave* species. *Genet. Resources Crop Evol.* 63: 881–888. <https://doi.org/10.1007/s10722-015-0291-x>.
- Ravenna, P. (1987) Notes on *Agavaceae*. I. A new species of *Manfreda*. *Herbertia* [ser. 3], 43(1): 17–19, ill.
- Redouté, P. J. (1802–1816) *Les Liliacées*. Paris (FR): Imprimerie Didot Jeune. <https://doi.org/10.5962/bhl.title.537>.
- Reichenbacher, F. W. (1985) Conservation of southwestern Agaves. *Desert Pl.* 7(2): 103–106, 88 [continuation], maps. <http://repository.arizona.edu/handle/10150/554213>
- Reid, W. H. [ & al. 1985 ], Freeman, C. E. & Becvar, J. E. (1985) Nectar sugar variability in two species of *Agave* (*Agavaceae*). *Southw. Naturalist* 30(3): 443–445. <https://doi.org/10.2307/3671278>.
- Reveal, J. L. (1977) *Agavaceae*. In: Cronquist, A. & al. (eds.): *Intermountain Flora*, 6: 526–538, ills., keys. New York (US): The New York Botanical Gardens/Columbia University Press.
- Reveal, J. L. (2012) A divulgation of ignored or forgotten binomials. *Phytoneuron* 2012(28): 1–64. <http://www.phytoneuron.net/PhytoN-Divulgation.pdf>
- Reveal, J. L. & Hodgson, W. C. (2002) *Agave*. In: *Flora of North America north of Mexico*; 26: 442–461. New York (US)/Oxford (GB): Oxford University Press.
- Reveal, J. L. & Jarvis, C. E. (2009) Typification of names of temperate North American plants proposed by Linnaeus. *Taxon* 58(3): 977–984. <http://www.jstor.org/stable/27756964>

- Richardson, A. & King, K. (2011) *Plants of Deep South Texas: A field guide to the woody and flowering species*. College Station (US): Texas A & M University Press.
- Richter, I. (2007) Von *Manfreda* Salisbury (*Agavaceae*) aus Berlin bis zum Weihnachtsstern. *Berliner Kakt.-Blätt.* 7: 41–46.
- Richter, I. (2010) Karibische Agaven. *Berliner Kakt.-Blätt.* 10: 39–44, ills.
- Richter, I. (2011) Die Gattung *Agave*. *Geschichte, Systematik, Vorkommen, Kultur*. Roma (IT): Associazione Italiana Amatori delle Piante Succulente.
- Riffell, J. A. [& al. 2008], Alarcón, R., Abrell, L., Davidowitz, G., Bronstein, J. L. & Hildebrand, J. G. (2008) Behavioral consequences of innate preferences and olfactory learning in hawkmoth–flower interactions. *Proc. Nation. Acad. Sci. USA* 105(9): 3404–3409, ills. <https://doi.org/10.1073/pnas.0709811105>.
- Rigerszki, Z. [& al. 2013], Békefi, J. & Kajdacs, J. (2013) [Hungarian:] Roamings in Cuba, 2010. Part 5: Searching the southern valleys. *Kakt. Vilag* 37(6): 252–263, ills., map.
- Ritchie, W. & Lindstrom, J. T. (2014) ×*Polifreda* ‘Lindstrom’, a cross between False Aloe and Mexican Tuberose. *J. Environm. Hort.* 32(1): 51–53, ill. <https://hrijournal.org/doi/full/10.24266/0738-2898.32.1.51>.
- Rivera-Hernández, J. E. [& al. 2015], Cházaro Basáñez, M. J., Vargas-Rueda, A. F., Ramón-Farías, F., Oliva-Rivera, H. & Alcántara-Salinas, G. (2015) Nuevas adiciones para la flora de Veracruz. *Acta Bot. Mex.* 112: 45–65, ills., maps. <https://doi.org/10.21829/abm112.2015.1088>.
- Rivera-Hernández, J. E. [& al. 2019], Flores-Hernández, N., Vargas-Rueda, A. F., Alcántara-Salinas, G., Cházaro Basáñez, M. J. & García-Albarado, J. C. (2019) Flora y vegetación de la región semiárida de Acultzingo-Maltrata, Veracruz, México. *Acta Bot. Mex.* in press: <https://doi.org/10.21829/abm126.2019.1433>.
- Robbins, R. L. (2001) *Agavaceae*. In: Steven, W. D. & al. (eds.): *Flora de Nicaragua, Introducción, Gimnospermas y Angiospermas (Acanthaceae–Euphorbiaceae)*; pp. 41–47. St. Louis (US): Missouri Botanical Garden. <http://www.tropicos.org/Project/FN>
- Robert, M. L. [& al. 2008], Lim, K. Y., Hanson, L., Sanchez-Teyer, F., Bennett, M. D., Leitch, A. R. & Leitch, I. J. (2008) Wild and agronomically important *Agave* species (*Asparagaceae*) show proportional increases in chromosome number, genome size, and genetic markers with increasing ploidy. *Bot. J. Linn. Soc.* 158(2): 215–222, ill. <https://doi.org/10.1111/j.1095-8339.2008.00831.x>.
- Rocha, M. [& al. 2005], Valera, A. & Eguiarte, L. E. (2005) Reproductive ecology of five sympatric *Agave* (*Littaea*) (*Agavaceae*) species in Central Mexico. *Amer. J. Bot.* 92(8): 1330–1341. <https://doi.org/10.3732/ajb.92.8.1330>.
- Rocha, M. [& al. 2006], Good-Ávila, S. V., Molina-Freaner, F., Arita, H. T., Castillo, A., García-Mendoza, A., Silva-Montellano, A., Gaut, B. S., Souza, V. & Eguiarte, L. E. (2006) Pollination biology and adaptive radiation of *Agavaceae*, with special emphasis on the genus *Agave*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 329–344, maps. <https://doi.org/10.5642/aliso.20062201.27>.
- Rodríguez, A. (2009) *Manfreda parva* (*Agavaceae*), especie nueva del Estado de Guerrero, México. *Acta Bot. Mex.* 88: 1–8, ills. <http://www.redalyc.org/pdf/574/57411548001.pdf>
- Rodríguez, A. & Castro-Castro, A. (2006) Potencial ornamental de los “amoles” (*Manfreda*, *Agavaceae*) en México. *Avances Invest. Ci. CUCBA* 2006: 620–630, ills.
- Rodríguez, A. & Castro-Castro, A. (2007) Potencial ornamental de los “amoles” (*Manfreda*, *Agavaceae*) en México. *Ibugana* 15(1–2): 3–11, ills.
- Rodríguez, A. [& al. 2008], Carrillo-Reyes, P. & Castro-Castro, A. (2008) Nota sobre la distribución geográfica y morfología de *Manfreda involuta* (*Agavaceae*). *Acta Bot. Mex.* 84: 17–23, ills., map. <http://www.redalyc.org/pdf/574/57408403.pdf>
- Rogers, G. K. (1999) Notes on the biology and distribution of the Barbados Maypole (*Agave barbadensis* Trel.). *Caribbean J. Sci.* 35(3–4): 318–321, ills., map.
- Rogers, G. K. (2000) A taxonomic revision of the genus *Agave* (*Agavaceae*) in the Lesser Antilles, with an ethnobotanical hypothesis. *Brittonia* 52(3): 218–233, ills. <https://doi.org/10.2307/2666571>.
- Roosbroeck, J. van (2004) *Agave gilberti* [sic!] Berger terug in de verzamelingen. *Succulenta* 83(5): 223–228, ills.
- Roosbroeck, J. van (2012) Het complex *Agave victoriae-reginae*. *Succulenta* 91(4): 163–166, ills.
- Roosbroeck, J. van (2014) *Agave ensifera* terug in cultuur. *Succulenta* 93(2): 79–80, ills.
- Rose, J. N. (1899) A proposed rearrangement of the suborder *Agaveae*. *Contr. US Nation. Herb.* 5(4): 151–157, ills., t. 18. <http://biodiversitylibrary.org/page/364941>
- Rose, J. N. (1903a) Revision of *Polianthes* with new species. *Contr. US Nation. Herb.* 8: 8–13, ills., key. <http://www.biodiversitylibrary.org/item/13768#page/26>
- Rose, J. N. (1903b) *Prochnyanthes* and its species. *Contr. US Nation. Herb.* 8: 13–14, ills. <http://biodiversitylibrary.org/page/366834>
- Rose, J. N. (1903c) *Manfreda* and its species. *Contr. US Nation. Herb.* 8: 15–23, ills., key. <http://www.biodiversitylibrary.org/item/13768#page/40>
- Rose, J. N. (1905) Five new species of Mexican plants. *Proc. US Nation. Mus.* 29(1427): 437–439. <http://biodiversitylibrary.org/page/15666181>
- Rose, J. N. (1922) *Runyonia longiflora*. *Addisonia* 7: 39–40, t. 244. <https://biodiversitylibrary.org/page/4053387>



- Rubal Lobo, J. J. [ & al. 2013], Guillot Ortiz, D. & Meer, P. van der (2013) Dos nuevas especies del género *Agave* en la provincia de Cádiz (Andalucía, España). *Bouteloua* 16: 36–39, ills.
- Sáez, L. & Guillot Ortiz, D. (2015) Nuevos datos sobre xenófitos para el noreste de la Península Ibérica (Cataluña). *Bouteloua* 20: 55–61, ills.
- Sáez, L. [ & al. 2014], Guillot Ortiz, D. & Meer, P. van der (2014) Nuevas citas de Agaváceas (géneros *Agave* L. y *Yucca* L.) en la costa oriental de la Península Ibérica. *Bouteloua* 18: 131–140, ills.
- Sáez, L. [ & al. 2016], Serapio, J., Gómez-Bellver, C., Ardenghi, N. M., Guillot, D. & Rita, J. (2016) New records in vascular plants alien to the Balearic Islands. *Orsis* 30: 101–131. <https://doi.org/10.5565/rev/orisis.38>.
- Salazar, E. [ & al. 2009], Gonzalez, P. & Hernandez, C. (2009) Multiplicación in vitro de *Agave cocui* Trelease a través de yemas axilares. *Agron. Trop. (Maracay)* 59(2): 129–135. <http://dialnet.unirioja.es/servlet/articulo?codigo=5349091>
- Salm-Dyck, J. de (1834) Hortus Dyckensis oder: Verzeichniss der in dem botanischen Garten zu Dyck wachsenden Pflanzen. Düsseldorf (DE): Arnz & Comp. <http://www.biodiversitylibrary.org/bibliography/110144>
- Salm-Dyck, J. de (1859) Bemerkungen über die Gattungen *Agave* und *Fourcroya* nebst Beschreibung einiger neuen Arten. *Bonplandia* 7(7): 85–96. <http://biodiversitylibrary.org/page/5371825>
- Salm-Dyck, J. de (1861) Bemerkungen über die Familie der Agaveen. *Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten* 2(23): 177–182. <http://biodiversitylibrary.org/page/4029373>
- Sánchez Gullón, E. (2013) Flora alóctona ornamental naturalizada en la provincia de Huelva (Andalucía Occidental, España). II. *Bouteloua* 15: 45–61, ills.
- Sánchez-Teyer, F. [ & al. 2009], Moreno-Salazar, S., Esqueda, M., Barraza, A. & Robert, M. L. (2009) Genetic variability of wild *Agave angustifolia* populations based on AFLP: A basic study for conservation. *J. Arid Environm.* 73: 611–616. <https://doi.org/10.1016/j.jaridenv.2009.01.008>.
- Sanchez-Urbina, A. [ & al. 2008], Ventura-Canseco, L. M. C., Ayora-Talavera, T., Abud-Archila, M., Perez-Farrera, M. A., Dendooven, L. & Gutierrez Miceli, F. A. (2008) Seed germination and in vitro propagation of *Agave grijalvensis*, an endemic endangered Mexican species. *Asian J. Pl. Sci.* 7(8): 752–756.
- Santacruz-Ruvalcaba, F. [ & al. 1999], Gutiérrez-Pulido, H. & Rodríguez-Garay, B. (1999) Efficient in vitro propagation of *Agave parrasana* Berger. *Pl. Cell Tissue Organ Cult.* 56(3): 163–167. <https://doi.org/10.1023/A:1006232911778>.
- Santíz, J. A. [ & al. 2012], Rincón-Rosales, R. & Gutiérrez-Miceli, F. A. (2012) Propagación in vitro de *Agave grijalvensis* B. Ullrich, una especie endémica de Chiapas bajo protección especial. *Gayana, Bot.* 69(special): 23–30, ills.
- Santos Valencia, J. C. (2009) Micropropagación de *Agave warelliana* (Baker, 1877). Xalapa (MX): Universidad Veracruzana; M. Sc. thesis.
- Santos-Zea, L. [ & al. 2012], Leal-Díaz, A. M., Cortes-Ceballos, E. & Gutierrez-Urbe, J. A. (2012) *Agave* (*Agave* spp.) and its traditional products as a source of bioactive compounds. *Curr. Bioactive Compounds* 8(3): 218–231. <https://doi.org/10.2174/157340712802762410>.
- Sarmiento, O. F. & Ramos, R. E. G. (2013) Inventario florístico del Parque nacional Cañón del Sumidero, parte occidental y de la cañada La Chacona, Chiapas, México. *Lacandonia* 7(2): 25–42.
- Sató, D. (1935) Analysis of the karyotypes in *Yucca*, *Agave* and the related genera with special reference to the phylogenetic significance. *Jap. J. Genet.* 1: 272–278.
- Scheinvar, E. [ & al. 2016], Gámez, N., Castellanos-Morales, G., Aguirre-Planter, E. & Eguiarte, L. E. (2016) Neogene and Pleistocene history of *Agave lechuguilla* in the Chihuahuan Desert. *J. Biogeogr.* 44(2): 322–334. <https://doi.org/10.1111/jbi.12851>.
- Schiede, C. J. W. (1830) Botanische Berichte aus Mexico, mitgetheilt vom Dr. Schiede (Aus Briefen an den Herausgeber). Vierter Bericht. Excursionen in der Gegend von Jalapa und Reise von dort nach Mexico. *Linnaea* 5: 463–477. <http://biodiversitylibrary.org/page/96471>
- Schindhelm, W. (2006) *Agave hurteri* in der Sierra Cuchumatanes in Zentral-Guatemala. *Berliner Kakt.-Blätt.* 6: 21–24, ills.
- Scott, P. E. (2004) Timing of *Agave palmeri* flowering and nectar-feeding bat visitation in the Peloncillos and Chiricahua mountains. *Southw. Naturalist* 49(4): 425–434. <http://www.jstor.org/stable/3672398>
- Sheldon, S. (1980) Ethnobotany of *Agave lechuguilla* and *Yucca carnerosana* in Mexico's Zona Ixtlera. *Econ. Bot.* 34(4): 376–390. <https://doi.org/10.1007/BF02858314>.
- Shields, M. E. (1972) A garden under glass. *Bull. Afr. Succ. Pl. Soc.* 7(3): 93–100, ills.
- Shoeb, H. A. [ & al. 1990], El-Sayed, M. M., El-Askalany, M. A., El-Nahas, H. A. & Refai, L. A. (1990) Preliminary studies on the molluscicidal properties of some local plants. *Assiut Vet. Med. J.* 23(45): 39–47.
- Sidana, J. [ & al. 2016], Singh, B. & Sharma, O. P. (2016) Saponins of *Agave*: Chemistry and bioactivity. *Phytochemistry* 130: 22–46. <https://doi.org/10.1016/j.phytochem.2016.06.010>.
- Silva, V. [ & al. 2015], Figueiredo, E. & Smith, G. F. (2015) Alien succulents naturalized and cultivated on the central west coast of Portugal. *Bradleya* 33: 58–81, map, ills. <https://doi.org/10.25223/brad.n33.2015.a10>.
- Silva-Montellano, A. & Eguiarte, L. E. (2003a) Geographic patterns in the reproductive ecology of *Agave lechuguilla* (*Agavaceae*) in the Chihuahuan Desert.



- I. Floral characteristics, visitors, and fecundity. *Amer. J. Bot.* 90(3): 377–387, map, ill., diags. <https://doi.org/10.3732/ajb.90.3.377>.
- Silva-Montellano, A. & Eguiarte, L. E. (2003b) Geographic patterns in the reproductive ecology of *Agave lechuguilla* (*Agavaceae*) in the Chihuahuan Desert. II. Genetic variation, differentiation, and inbreeding estimates. *Amer. J. Bot.* 90(5): 700–706, diags. <https://doi.org/10.3732/ajb.90.5.700>.
- Simpson, J. [ & al. 2011 ], Martínez Hernández, M., Abraham Juárez, M. J., Delgado Sandoval, S., Sánchez Villareal, A. & Cortés Romero, C. (2011) Genomic resources and transcriptome mining in *Agave tequilana*. *GCB Bioenergy* 3(25): 25–36. <https://doi.org/10.1111/j.1757-1707.2010.01079.x>.
- Sims, J. (1816) *Polygonum tuberosum*. Common Tuberose. *Curtis's Bot. Mag.* 43: t. 1817 + 2 pp. text. <http://biodiversitylibrary.org/page/482946>
- Skinner, D. B. (1961) Seeking the elusive *Agave huachuensis*. *Cact. Succ. J. (US)* 33(4): 105–107, ill.
- Slauson, L. A. (2000) Pollination biology of two chiropterophilous *Agaves* in Arizona. *Amer. J. Bot.* 87(6): 825–836. <http://www.jstor.org/stable/2656890>
- Slauson, L. A. (2002a) Insights on the pollination biology of *Agave* (*Agavaceae*). *Haseltonia* 8: 10–23, ill.
- Slauson, L. A. (2002b) Effects of fire on the reproductive biology of *Agave palmeri* (*Agavaceae*). *Madroño* 49(1): 1–11, map, diags. <http://www.jstor.org/stable/41425433>
- Small, J. K. (1903) *Flora of the Southeastern United States*. New York (US): Published by the author. <https://doi.org/10.5962/bhl.title.133>.
- Small, J. K. & Runyon, R. (1934) *Manfreda maculosa*. *Addisonia* 18(4): 49–50, t. 601. <http://biodiversitylibrary.org/page/4511652>
- Smith, C. I. [ & al. 2008a ], Pellmyr, O., Althoff, D. M., Balcázar-Lara, M., Leebens-Mack, J. & Segraves, K. A. (2008) Pattern and timing of diversification in *Yucca* (*Agavaceae*): Specialized pollination does not escalate rates of diversification. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 275: 249–258. <https://doi.org/10.1098/rspb.2007.1405>.
- Smith, G. F. (2002) The Jardín Botánico in Mexico City and its National *Agave* Collection: A succulent paradise in the New World. *Cact. Succ. J. (US)* 74(5): 220–227, ill.
- Smith, G. F. (2004) *Agave attenuata* ‘Myron’s Magic’—a new cultivar of a horticulturally important species. *Brit. Cact. Succ. J.* 21(4): 199–201, ill. <http://www.jstor.org/stable/42793921>
- Smith, G. F. (2015) Request for a binding decision on the descriptive statement associated with *Agave gustaviana*. *Taxon* 64(4): 857. <https://doi.org/10.12705/644.28>.
- Smith, G. F. (2017a) Typification of the names *Agave gustaviana* J. N. Haage & E. Schmidt and *A. maximiliana* Baker (*Asparagaceae/Agavaceae*). *Haseltonia* 23: 92–96, ill. <https://doi.org/10.2985/026.023.0112>.
- Smith, G. F. (2017b) Proposal to conserve the name *Agave maximiliana* against *A. gustaviana* (*Asparagaceae: Agavoideae*). *Taxon* 66(4): 986. <https://doi.org/10.12705/664.18>.
- Smith, G. F. & Figueiredo, E. (2008) Naturalized species of *Agave* L. (*Agavaceae*) on the southeastern coast of Portugal. *Haseltonia* 13: 52–60, ill., key. [https://doi.org/10.2985/1070-0048\(2007\)13\[52:NSOALA\]2.0.CO;2](https://doi.org/10.2985/1070-0048(2007)13[52:NSOALA]2.0.CO;2).
- Smith, G. F. & Figueiredo, E. (2011) *Agave americana* L. (subsp. *americana*) var. *expansa* (Jacobi) Gentry (*Agavaceae*) naturalized in South Africa. *Bradleya* 29: 67–72, ill., map. <https://doi.org/10.25223/brad.n29.2011.a8>.
- Smith, G. F. & Figueiredo, E. (2012) A further species of *Agave* L., *A. salmiana* Otto ex Salm-Dyck (subsp. *salmiana*) var. *salmiana* (*Agavaceae*), naturalised in the Eastern Cape Province of South Africa. *Bradleya* 30: 179–186, ill. <https://doi.org/10.25223/brad.n30.2012.a22>.
- Smith, G. F. & Figueiredo, E. (2013) Notes on the nomenclature of species of *Agave* L. (*Agavaceae/Asparagaceae*) grown in and described from European gardens and nurseries. *Bradleya* 31: 53–57, ill. <https://doi.org/10.25223/brad.n31.2013.a8>.
- Smith, G. F. & Figueiredo, E. (2014a) The Hanbury Gardens at La Mortola in Italy: A perfect setting for succulents. *Cact. Succ. J. (US)* 86(1): 12–19, ill., map. <https://doi.org/10.2985/015.086.0104>.
- Smith, G. F. & Figueiredo, E. (2014b) Notes on the reproductive morphology and phenology of *Agave felgeri* Gentry (*Agavaceae*). *Bradleya* 32: 13–18, ill. <https://doi.org/10.25223/brad.n32.2014.a13>.
- Smith, G. F. & Figueiredo, E. (2014c) Typification of the names *Agave xpeacockii* Croucher and *A. warelliana* Hort. ex Baker (*Agavaceae/Asparagaceae*). *Bradleya* 32: 25–29, ill. <https://doi.org/10.25223/brad.n32.2014.a15>.
- Smith, G. F. & Figueiredo, E. (2014d) Out with the old, in with the new? Historical names recorded in *Agave* L. (*Agavaceae/Asparagaceae*). *Bradleya* 32: 64–69, ill. <https://doi.org/10.25223/brad.n32.2014.a15>.
- Smith, G. F. & Figueiredo, E. (2014e) State of our knowledge of online resources of the types of names of *Agave* L. (*Agavaceae/Asparagaceae*) with a list of names attributed to William Trelease, with notes on types, online resources and etymology. *Phytotaxa* 170(4): 221–249, ill. <https://doi.org/10.11646/phytotaxa.170.4.1>.
- Smith, G. F. & Figueiredo, E. (2015) Notes on *Agave weberi* J. F. Cels ex J. Poiss. (*Agavaceae*), a large-growing species with invasive tendencies in southern Africa. *Bradleya* 33: 161–170, ill. <https://doi.org/10.25223/brad.n33.2015.a22>.
- Smith, G. F. & Figueiredo, E. (2016) The correct author citation and date of publication of the name *Agave yuccifolia* F. Delaroché (*Agavaceae/Asparagaceae*).

- Bradleya 34: 10–14, ills. <https://doi.org/10.25223/brad.n34.2016.a15>.
- Smith, G. F. & Figueiredo, E. (2017) Notes on *Agave panamana* Trel. (*Asparagaceae: Agavoideae/Agavaceae*) from Panama, Central America, with reference to morphological variation in *Agave angustifolia*. *Bradleya* 35: 33–45, ills. <https://doi.org/10.25223/brad.n35.2017.a4>.
- Smith, G. F. & Klopper, R. R. (2007) Naturalised species of *Agave* L. (*Agavaceae*) in the Cape Floristic Region, South Africa. *Bradleya* 25: 193–195, ills, key. <https://doi.org/10.25223/brad.n25.2007.a14>.
- Smith, G. F. & Mössmer, M. (1996) FSA contributions 4: *Agavaceae*. *Bothalia* 26(1): 31–35, ills., maps. <https://doi.org/10.4102/abc.v41i1.48>.
- Smith, G. F. & Steyn, E. M. A. (1999) A first record of *Agave decipiens* naturalised in southern Africa. *South Afr. J. Bot.* 65(3): 249–252. [https://doi.org/10.1016/S0254-6299\(15\)30984-4](https://doi.org/10.1016/S0254-6299(15)30984-4).
- Smith, G. F. & Steyn, E. M. A. (2002a) *Agave wercklei*: A Mesoamerican species in South Africa. *Bradleya* 20: 45–50, maps, ills. <https://doi.org/10.25223/brad.n20.2002.a8>.
- Smith, G. F. & Steyn, E. M. A. (2002b) The first record of *Agave celsii* var. *albicans* (*Agavaceae*), a Mexican plant, in South Africa. *South Afr. J. Bot.* 68(3): 397–400. <http://www.ajol.info/index.php/sajb/article/view/20552>
- Smith, G. F. & Steyn, E. M. A. (2003) The correct author citation and date of publication of the name *Agave wercklei* (*Agavaceae*). *Taxon* 52(3): 619–620. <https://doi.org/10.2307/3647466>.
- Smith, G. F. & Steyn, E. M. A. (2004) *Agave hurteri* Trelease (*Agavaceae*): The perfect landscaping plant for large gardens. *Bradleya* 22: 15–20, ills., map. <https://doi.org/10.25223/brad.n22.2004.a3>.
- Smith, G. F. [et al. 2008], Walters, M., Figueiredo, E. & Klopper, R. R. (2008) Naturalised species of *Agave* L. (*Agavaceae*) in the Eastern Cape Province of South Africa. *Bradleya* 26: 33–40, ills., maps, key. <https://doi.org/10.25223/brad.n26.2008.a3>.
- Smith, G. F. [et al. 2012], Figueiredo, E., Klopper, R. R., Crouch, N. R., Janion, C. & Chown, S. L. (2012) A new specific plant host for the *Agave* snout weevil, *Scyphophorus acupunctatus* Gyllenhal, 1838 (*Coleoptera: Curculionidae*) in South Africa: A destructive pest of species of *Agave* L. (*Agavaceae*). *Bradleya* 30: 19–24, ills. <https://doi.org/10.25223/brad.n30.2012.a6>.
- Smith, G. F. [et al. 2018a], Starr, G. & Thiede, J. (2018) Request for a binding decision on the descriptive statement associated with *Agave lophantha* (*Asparagaceae/Agavaceae*). *Taxon* 67(3): 665. <https://doi.org/10.12705/673.34>.
- Smith, G. F. [et al. 2018b], Figueiredo, E. & Starr, G. (2018) Notes on the typification and nomenclature of *Agave dissimulans* Trelease, *Agave convallis* Trelease, and *Agave kerchovei* Lem. (*Asparagaceae: Agavoideae/Agavaceae*). *Haseltonia* 24: 36–39. <https://doi.org/10.2985/026.024.0106>.
- Smith, L. (2014) Nicaraguan field notes (1). Somoto Canyon. *Cact. Explorer* 11: 20–23, ills.
- Solano Camacho, E. (2002) Sistemática del género *Polianthes* L. (*Agavaceae*). México (MX): Facultad de Ciencias, Universidad Nacional Autónoma de México; unpublished Ph.D. thesis.
- Solano Camacho, E. & Dávila Aranda, P. D. (2003) *Polianthes multicolor* (*Agavaceae*), especie nueva de Guanajuato, México. *Novon* 13(1): 119–122, ills. <http://biostor.org/reference/64724>
- Solano Camacho, E. & García-Mendoza, A. (1998) Una nueva especie de *Polianthes* (*Agavaceae*) del Estado de Oaxaca, México. *Sida* 18(2): 473–477, ills. <http://www.jstor.org/stable/41967634>
- Solano, E. & Feria, T. P. (2007) Ecological niche modeling and geographic distribution of the genus *Polianthes* L. (*Agavaceae*) in Mexico: Using niche modeling to improve assessments of risk status. *Biodivers. & Conservation* 16: 1885–1900, maps. [https://doi.org/10.1007/978-1-4020-6444-9\\_20](https://doi.org/10.1007/978-1-4020-6444-9_20).
- Solano, E. & García-Mendoza, A. (2013) Neotipificación y reconocimiento de *Polianthes geminiflora* (Lex.) Rose (*Agavaceae*). *Acta Bot. Mex.* 104: 1–18, ills., map, key. <http://www.redalyc.org/pdf/574/57427415001.pdf>
- Solano, E. & Ríos-Gómez, R. (2011) *Polianthes zapopanensis* (*Agavaceae*), una especie nueva de Jalisco, México. *Brittonia* 63(1): 70–74, ills., key. <https://doi.org/10.1007/s12228-010-9132-6>.
- Solano, E. & Ríos-Gómez, R. (2014) *Polianthes alboaustralis* (*Asparagaceae, Agavoideae*), a new species from the State of Oaxaca, Mexico. *Phytotaxa* 174(2): 97–104, key. <https://doi.org/10.11646/phytotaxa.174.2.4>.
- Solano, E. [et al. 2014], Terrazas, T. & González-Becerril, A. (2014) Comparative anatomy of the stem, leaf and inflorescence basal axis of *Polianthes* L. (*Asparagaceae, Agavoideae*) species. *Feddes Repert.* 124: 105–115, ills. <https://doi.org/10.1002/fedr.201300017>.
- Solano, E. [et al. 2017], Terrazas, T., Reyes-Rivera, J. & Serrano-Casas, H. (2017) Anatomía comparativa de raíz, tallo, hoja y base del pedúnculo de *Manfreda* (*Asparagaceae: Agavoideae*). *Revista Mex. Biodivers.* 88: 899–911, ills. <https://doi.org/10.1016/j.rmb.2017.10.019>.
- Solano, E. [et al. 2019], García-Mendoza, A. & Ríos-Gómez, R. (2019) *Polianthes venustiflora* (*Asparagaceae, Agavoideae*), una especie nueva endémica de Michoacán, México. *Acta Bot. Mex.* 126: e1441. [126.2019.1441](https://doi.org/10.126.2019.1441).
- Spracklin, P. (2007) Searching for hardy *Agave*. *Plantsman*, n.s., 6(3): 146–151.
- Spracklin, P. (2014) Will the real *Agave atrovirens* var. *mirabilis* please step forward. Published on the web at <http://www.oasisdesigns.co.uk/atrovirens/atrovirens.htm>, accessed Dec. 2018.
- Standley, P. C. (1930) Flora of Yucatán. *Publ. Field Mus. Nat. Hist., Bot. Ser.* 3(3): 157–492. <https://doi.org/10.5962/bhl.title.2354>.

- Standley, P. C. & Steyermark, J. A. (1952) Flora of Guatemala. Part III. *Amaryllidaceae*. Fieldiana, Bot. 24(3): 103–145, ills., keys. <http://www.biodiversitylibrary.org/item/19685#page/117>
- Starr, G. (2004) *Agave ovatifolia*. The Whale's Tongue Agave. A recently described species from Nuevo León, Mexico. *Cact. Succ. J. (US)* 76(6): 303–307, ills., map, key.
- Starr, G. (2012) Agaves. Living sculptures for landscapes and containers. Portland (US)/London (GB): Timber Press.
- Starr, G. (2014) Some unusual, weird and special *Agave* cultivars. *Cact. Succ. J. (US)* 86(5): 218–225, ills. <https://doi.org/10.2985/015.086.0505>.
- Starr, G. & Devender, T. R. van (2011) *Agave parviflora* subspecies *densiflora*. A newly found treasure from the Sierra Madre in eastern Sonora, Mexico. *Cact. Succ. J. (US)* 83(5): 224–231, ills., map, key. <https://doi.org/10.2985/0007-9367-83.5.224>.
- Starr, G. & Webb, R. H. (2015) Validation of four sectional names in *Agave* L. (*Agavaceae*). *Cact. Succ. J. (US)* 87(2): 84–86, ills. <https://doi.org/10.2985/015.087.0206>.
- Starr, G. [ & al. 2008], Kemble, B. & Nixon, R. (2008) *Agave pelona* and *Agave zebra* in the Sierra El Viejo. *Cact. Succ. J. (US)* 80(4): 170–175, ills. [https://doi.org/10.2985/0007-9367\(2008\)80\[170:APAAZI\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2008)80[170:APAAZI]2.0.CO;2).
- Steinberg, M. & Taylor, M. (2008) Guatemala's Altos de Chiantla: Changes on the high frontier. *Mountain Res. & Developm.* 28(3): 255–262, ills., maps. <https://doi.org/10.1659/mrd.0891>.
- Stewart, J. R. (2015) *Agave* as a model CAM crop system for a warming and drying world. *Frontiers Pl. Sci.* 6: 684, 20 pp. <https://doi.org/10.3389/fpls.2015.00684>.
- Steyn, E. M. A. & Smith, G. F. (2000) *Agavaceae: Agave vivipara*: A naturalised alien in southern Africa. *Bothalia* 30(1): 43–46, ills., map. <https://doi.org/10.4102/abc.v30i1.537>.
- Stoner, K. E. [ & al. 2003], Karla, A. S., Roxana, C. F. & Quesada, M. (2003) Population dynamics, reproduction, and diet of the Lesser Long-Nosed Bat (*Leptonycteris curasoae*) in Jalisco, Mexico: Implications for conservation. *Biodivers. & Conservation* 12(2): 357–373. <https://doi.org/10.1023/A:1021963819751>.
- Tapia-Campos, E. [ & al. 2013], Rodríguez-Domínguez, J. M., Quiñones-Aguilar, E. E., Dupre, B. & Barba-González, R. (2013) Molecular cytogenetic characterization of wild Mexican geophytes. *Acta Hort.* 1000: 499–504. <https://doi.org/10.17660/ActaHortic.2013.1000.71>.
- Terracciano, A. (1885) *Primo contributo ad una monografia delle Agave*. Napoli (IT): Stabilimento Tipografico Barnaba Cons. di Antonio.
- Thiede, J. (2011) Die Geschichte und taxonomische Gliederung des *Agave victoriae-reginae* T. Moore-Komplexes (*Agavaceae*). *Avonia* 29(4): 146–156, ills.
- Thiede, J. (2012a) Geschichte, Einführung, Gartenkultur, Biologie und Taxonomie von *Agave bulliana* (Baker) Thiede & Egli (*Agavaceae/Asparagaceae*)—einzige Art der früheren Gattung *Prochnyanthes* S. Watson. *Avonia* 30(1): 37–45, xvi–xix, ills.
- Thiede, J. (2012b) *Prochnyanthes bulliana* (Baker) Baker, un nuevo taxón para la flora ornamental europea: Una corrección. *Bouteloua* 10: 121–122.
- Thiede, J. (2014a) *Agave dealbata* E. Morren ex K. Koch (*Asparagaceae*), the correct name for *Agave dasylirioides* Jacobi & C. D. Bouché (Nomenclature of *Agave* L. L.). *Phytotaxa* 163(5): 295–298. <https://doi.org/10.11646/phytotaxa.163.5.5>.
- Thiede, J. (2014b) A review of *Agave ellemeetiana* K. Koch (*Asparagaceae/Agavaceae*). *Bradleya* 32: 146–163, ills. <https://doi.org/10.25223/brad.n32.2014.a7>.
- Thiede, J. (2016) A review of *Agave mitis* (*Asparagaceae/Agavaceae*). *Bradleya* 34: 200–216, map, ills. <https://doi.org/10.25223/brad.n34.2016.a8>.
- Thiede, J. (2017a) Proposal to conserve the name *Agave dasylirioides* against *A. dealbata* (*Asparagaceae/Agavaceae*). *Taxon* 66(3): 751–752. <https://doi.org/10.12705/663.20>.
- Thiede, J. (2017b) Proposal to conserve the name *Agave franzosinii* against *A. beaulueriana* (*Asparagaceae/Agavaceae*). *Taxon* 66(4): 985–986. <https://doi.org/10.12705/664.18>.
- Thiede, J. & Egli, U. (1999) Einbeziehung von *Manfreda* Salisbury, *Polianthes* Linné und *Prochnyanthes* in *Agave* (*Agavaceae*). *Kakt. and. Sukk.* 50(5): 109–113, ill.
- Thiede, J. [ & al. 2019a], Smith, G. F. & Egli, U. (2019) Infrageneric classification of *Agave* L. (*Asparagaceae: Agavoideae/Agavaceae*): A nomenclatural assessment and updated classification at the rank of section, with new combinations. *Bradleya* 37: 240–264, ills. <https://doi.org/10.25223/brad.n37.2019.a22>
- Thiede, J. [ & al. 2019b], Starr, G. & Smith, G. F. (2019) Gustave-Philippe de Kerchove d'Ousselghem, his *Agave* collection, and the correct eponymy of *Agave kerchovei* Lem. (*Asparagaceae: Agavoideae/Agavaceae*). *Haseltonia* 26: in press.
- Thomson, G. (2014) The rediscovery of two endemic Agaves in Aruba. *CactusWorld* 32(3): 173–178, ills., map. <https://www.jstor.org/stable/44082609>
- Thorne, R. F. [ & al. 2010], Moran, R. V. & Minnich, R. A. (2010) Vascular plants of the high Sierra San Pedro Mártir, Baja California, Mexico: An annotated checklist. *Aliso* 28(1): 1–50, maps, ills. <https://doi.org/10.5642/aliso.20102801.02>.
- Todaro, A. (1876–92) *Hortus Botanicus Panormitanus*. Vols. 1–2. Palermo (IT): Hortus Botanicus. <https://doi.org/10.5962/bhl.title.49833>.
- Torres, I. [ & al. 2015], Casas, A., Vega, E., Martínez-Ramos, M. & Delgado-Lemus, A. (2015) Population

- dynamics and sustainable management of mescal Agaves in Central Mexico: *Agave potatorum* in the Tehuacán-Cuicatlán Valley. *Econ. Bot.* 69(1): 26–41. <https://doi.org/10.1007/s12231-014-9295-2>.
- Torres-Morán, M. I. [& al. 2013], Velasco-Ramirez, A. P., Hurtado-de la Pena, S. A., Rodriguez-Garcia, A. & Mena-Munguia, S. (2013) Variability and genetic structure in a commercial field of Tequila plants, *Agave tequilana* (*Agavaceae*). *Amer. J. Agricult. Biol. Sci.* 8(1): 44–53. <https://doi.org/10.3844/ajabssp.2013.44.53>.
- Toumey, J. W. (1901) An undescribed *Agave* from Arizona. *Annual Rep. Missouri Bot. Gard.* 12: 75–76, tt. 32–33. <http://biodiversitylibrary.org/page/672221>
- Trager, J. N. (2005) The Huntington Botanical Gardens presents the 2005 offering of International Succulent Introductions. *Cact. Succ. J. (US)* 77(2): 90–104, ills. [https://doi.org/10.2985/0007-9367\(2005\)77\[90:THBGPT\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[90:THBGPT]2.0.CO;2).
- Trager, J. N. (2011) The Huntington Botanical Gardens presents the 2011 offering of International Succulent Introductions. *Cact. Succ. J. (US)* 83(2): 67–77, ills. <https://doi.org/10.2985/0007-9367-83.2.67>.
- Trager, J. N. (2014) The Huntington Botanical Gardens presents the 2014 offering of International Succulent Introductions. *Cact. Succ. J. (US)* 86(2): 54–69, ills. <https://doi.org/10.2985/015.086.0203>.
- Trager, J. N. (2018) The Huntington Botanical Gardens presents the 2018 offering of the International Succulent Introductions. *Cact. Succ. J. (US)* 90(2): 84–102, ills. <https://doi.org/10.2985/015.090.0202>.
- Trame, A. M. [& al. 1995], Coddington, A. J. & Paige, K. N. (1995) Field and genetic studies testing optimal outcrossing in *Agave schottii*, a long-lived clonal plant. *Oecologia* 104(1): 93–100. <https://doi.org/10.1007/BF00365567>.
- Trejo, L. [& al. 2016], Alvarado-Cárdenas, L. O., Scheinvar, E. & Eguiarte, L. E. (2016) Population genetic analysis and bioclimatic modeling in *Agave striata* in the Chihuahuan Desert indicate higher genetic variation and lower differentiation in drier and more variable environments. *Amer. J. Bot.* 103(5): 1020–1029, map, ills. <https://doi.org/10.3732/ajb.1500446>.
- Trejo, L. [& al. 2018], Limones, V., Peña, G., Scheinvar, E., Vargas-Ponce, O., Zizumbo-Villarreal, D. & Colunga-García Marín, P. (2018) Genetic variation and relationships among Agaves related to the production of tequila and mezcal in Jalisco. *Industr. Crops Prod.* 125: 140–149. <https://doi.org/10.1016/j.indcrop.2018.08.072>.
- Trejo-Salazar, R. E. [& al. 2015], Scheinvar, E. & Eguiarte, L. E. (2015) ¿Quién poliniza realmente los agaves? Diversidad de visitantes florales en 3 especies de *Agave* (*Agavoideae: Asparagaceae*). *Revista Mex. Biodivers.* 86: 358–369. <https://doi.org/10.1016/j.rmb.2015.04.007>.
- Trejo-Salazar, R. E. [& al. 2016], Eguiarte, L. E., Suro-Piñera, D. & Medellín, R. A. (2016) Save our bats, save our tequila: Industry and science join forces to help bats and Agaves. *Nat. Areas J.* 36(4): 523–530. <https://doi.org/10.3375/043.036.0418>.
- Release, W. (1894) Notes and observations. 6. *Agave parviflora* Torrey. *Annual Rep. Missouri Bot. Gard.* 5: 164–165, t. 32. <http://biodiversitylibrary.org/page/675743>
- Release, W. (1907) *Agave macroacantha* and allied Euagaves. *Annual Rep. Missouri Bot. Gard.* 18: 231–256, 16 tt. <https://biodiversitylibrary.org/page/45470752>
- Release, W. (1908a) *Agave rigida*. *Furcraea rigida*. *Agave angustifolia*. *Annual Rep. Missouri Bot. Gard.* 19: 273–287, tt. 29–35. <https://doi.org/10.2307/2400067>.
- Release, W. (1908b) Variegation in the *Agaveae*. In: Linsbauer, K. (ed.): *Wiesner Festschrift*; pp. 332–356. Wien (AT): Verlagsbuchhandlung Carl Konegen (Ernst Stülpnagel). <http://biodiversitylibrary.org/page/11346464>
- Release, W. (1911) The smallest of the Century Plants. *Popular Sci. Monthly* 78(1): 5–15, ills. <http://biodiversitylibrary.org/page/40208464>
- Release, W. (1912a) The Agaves of Lower California. *Annual Rep. Missouri Bot. Gard.* 22: 37–65, tt. 18–71. <http://biodiversitylibrary.org/page/683257>
- Release, W. (1912b) Revision of the Agaves of the Group *Applanatae*. *Ann. Rep. Missouri Bot. Gard.* 22: 85–97, tt. 73–99. <http://biodiversitylibrary.org/page/683357>
- Release, W. (1913) *Agave* in the West Indies. *Mem. Nation. Acad. Sci.* 11: 55 pp., 116 tt., maps, key. <http://www.biodiversitylibrary.org/item/114003#page/7/>
- Release, W. (1914) *Agave*. In: Bailey, L. H. (ed.): *Standard Cyclopedia of Horticulture*; 1: 230–239. New York (US): Macmillan and Co.
- Release, W. (1915) The *Agaveae* of Guatemala. *Trans. Acad. Sci. St. Louis* 23(3): 129–152, tt. 6–35. <http://biodiversitylibrary.org/page/29092583>
- Release, W. (1920) *Amaryllidaceae*. In: Standley, P. C. (ed.): *Trees and shrubs of Mexico (Gleicheniaceae—Betulaceae)*. *Contr. US Nation. Herb.* 23(1): 105–142, key. <http://www.biodiversitylibrary.org/item/13783#page/115>
- Release, W. (1925) New species of *Agave* from the Republic of Salvador. *J. Washington Acad. Sci.* 15: 393–395, ills. <http://biodiversitylibrary.org/page/39897046>
- Trueblood, E. W. E. (1973) “Omixochitl!”—the Tuberose (*Polianthes tuberosa*). *Econ. Bot.* 27(2): 157–173. <http://www.jstor.org/stable/4253410>
- Tschapka, M. [& al. 2008], Sperr, E. B., Caballero-Martínez, L. A. & Medellín, R. A. (2008) Diet and cranial morphology of *Musonycteris harrisoni*, a highly specialized nectar-feeding bat in western Mexico. *J. Mammalogy* 89(4): 924–932. <https://doi.org/10.1644/07-MAMM-A-038.1>.
- Turner, R. M. [& al. 1995], Bowers, J. E. & Burgess, T. L. (1995) *Sonoran Desert plants. An ecological atlas.* Tucson (US): University of Arizona Press.
- Ullrich, B. (1989a) *Agave margaritae* Brandegees. *Kakt. and Sukk.* 40(6): centre-page pullout 1989/18, ills.



- Ullrich, B. (1989b) *Manfreda nanchititlensis* Matuda. Kakt. and. Sukk. 40(9): centre-page pullout 1989/28, ills.
- Ullrich, B. (1989c) *Agave polianthiflora* Gentry. Kakt. and. Sukk. 40(12): centre-page pullout 1989/36, ills.
- Ullrich, B. (1990a) Ein neuer Standort für *Agave atrovirens* Karwinski ex Salm-Dyck in Guerrero. Kakt. and. Sukk. 41(5): 98–99, ill., map.
- Ullrich, B. (1990b) *Agave bracteosa* S. Watson ex Engelm. Kakt. and. Sukk. 41(5): centre-page pullout 1990/13, ills.
- Ullrich, B. (1990c) *Agave striata* Zuccarini ssp. *stricta* (Salm-Dyck) Ullrich stat. nov. Kakt. and. Sukk. 41(5): centre-page pullout 1990/14, ills.
- Ullrich, B. (1990d) *Agave grijalvensis*—Eine neue Art aus Chiapas. Kakt. and. Sukk. 41(6): 102–108, ills.
- Ullrich, B. (1990e) Anmerkungen zu *Agave parviflora* Torrey und *Agave hartmanii* S. Watson. Kakt. and. Sukk. 41(7): 133–136, ills.
- Ullrich, B. (1990f) Ein neuer Standort für *Agave dasylirioides* Jacobi & Bouché in Oaxaca. Kakt. and. Sukk. 41(8): 164–166, ills., map.
- Ullrich, B. (1990g) *Agave shawii* Engelm. ssp. *shawii*. Kakt. and. Sukk. 41(9): centre-page pullout 1990/26, ills.
- Ullrich, B. (1990h) *Agave attenuata* Salm-Dyck op haar natuurlijke groeiplaatsen. Succulenta 69(6): 121–127, ills., map.
- Ullrich, B. (1990i) *Agave macroculmis* Todaro en *Agave gentryi* Ullrich spec. nov. Succulenta 69(9): 190–193, (10): 210–214, ills.
- Ullrich, B. (1990j) *Agave obscura* Schiede y *Agave horrida* Lemaire ex Jacobi ssp. *perotensis* Ullrich ssp. nov. Cact. Suc. Mex. 35(4): 75–82, ills.
- Ullrich, B. (1991a) *Agave colimana* Gentry oder *Agave ortgiesiana* Roetzl ? Kakt. and. Sukk. 42(1): 24–28, ills., map.
- Ullrich, B. (1991b) *Agave gypsophila*. Kakt. and. Sukk. 42(3): centre-page pullout 1991/8, ills.
- Ullrich, B. (1991c) *Agave pumila* De Smet ex Baker. Kakt. and. Sukk. 42(5): centre-page pullout 1991/14, ills.
- Ullrich, B. (1991d) Ein neuer Standort für *Agave striata* Zuccarini ssp. *stricta* (Salm-Dyck) Ullrich in Oaxaca. Kakt. and. Sukk. 42(6): 142–143, ills., map.
- Ullrich, B. (1991e) *Agave victoriae-reginae* T. Moore. Kakt. and. Sukk. 42(7): centre-page pullout 1991/22, ills.
- Ullrich, B. (1991f) Notiz zu *Agave breviscapa* Berger ex Roster und *Agave verna* Berger. Kakt. and. Sukk. 42(10): 242–243, ill.
- Ullrich, B. (1991g) Zum Verbreitungsgebiet von *Agave victoriae-reginae* T. Moore. Kakt. and. Sukk. 42(11): 262–263, ills., map.
- Ullrich, B. (1991h) *Agave parryi* Engelm. var. *parryi*. Kakt. and. Sukk. 42(11): centre-page pullout 1991/32, ills.
- Ullrich, B. (1991i) De taxonomische rangschikking van *Agave nizandensis* Cutak. Succulenta 70(4): 89–92, ills.
- Ullrich, B. (1991j) De systematische positie van *Agave felgeri* Gentry. Succulenta 70(7/8): 147–150, ills., map.
- Ullrich, B. (1991k) Aantekeningen bij *Agave guienkola* Gentry. Succulenta 70(12): 257–260, ills.
- Ullrich, B. (1992a) *Agave marmorata* Roetzl. Kakt. and. Sukk. 43(3): centre-page pullout 1992/10, ills.
- Ullrich, B. (1992b) Anmerkungen zu drei Taxa der Gattung *Agave* aus El Salvador. Kakt. and. Sukk. 43(3): 50–53, ills.
- Ullrich, B. (1992c) *Agave parrasana* Berger. Kakt. and. Sukk. 43(5): centre-page pullout 1992/15, ills.
- Ullrich, B. (1992d) Wer ist der Autor von *Agave wercklei*? Kakt. and. Sukk. 43(8): 181–183, (9): 212–216, ills.
- Ullrich, B. (1992e) *Agave schottii* Engelm. Kakt. and. Sukk. 43(12): centre-page pullout 1992/35, ills.
- Ullrich, B. (1992f) *Agave obscura* Schiede und *Agave horrida* Lemaire ex Jacobi ssp. *perotensis* Ullrich ssp. nov. Kaktusblüte 1992: 12–19, ills.
- Ullrich, B. (1992g) The discovery of *Agave seemanniana* Jacobi. Brit. Cact. Succ. J. 10(1): 24–28, ills., map. <http://www.jstor.org/stable/42792873>
- Ullrich, B. (1992h) On the discovery of *Agave schidigera* Lemaire and status of certain taxa of section *Xysmagave* Berger. Brit. Cact. Succ. J. 10(3): 61–70, ills., map. <http://www.jstor.org/stable/42794279>
- Ullrich, B. (1992i) Zum Status von *Agave chrysantha* Peebles. And. Sukk. 18: 3–5, map.
- Ullrich, B. (1992j) On the history of *Agave asperrima* and *A. scabra* (Agavaceae) as well as some taxa of the *Parryanae*. Sida 15(2): 241–261, ills. <http://www.jstor.org/stable/41966996>
- Ullrich, B. (1992k) Sobre *Agave langlassei* André y la tipificación de *Manfreda brachystachys* (Cav.) Rose. Cact. Suc. Mex. 37(3): 60–63, ills.
- Ullrich, B. (1992l) L'influsso italiano sulla tassonomia del genere *Agave*. Der italienische Einfluss auf die Taxonomie der Gattung *Agave*. Piante Grasse 12(2): 38–50, (3): 87–94, ills.
- Ullrich, B. (1993a) Observations sur *Agave mitis* Martius, *A. celsii* Hooker et *A. albicans* Jacobi. Succulentes 16(1): 26–32, ills.
- Ullrich, B. (1993b) L'influsso italiano sulla tassonomia del genere *Agave*. Der italienische Einfluss auf die Taxonomie der Gattung *Agave*. Piante Grasse 13(1): 22–32, (2): 51–56, (3): 81–90, ills.
- Ullrich, B. (1993c) Über eine im Palmengarten blühende Naturhybride aus der Gattung *Agave*. Palmengarten 57(2): 95–99, ills., map.
- Ullrich, B. (1993d) Agaven. Illustrationen blühender Exemplare bis 1800. Palmengarten Sonderheft 21: 83 pp., ills.
- Ullrich, B. (1993e) Early illustrations of *Polianthes tuberosa* L. (Agavaceae). Herbertia [ser. 3], 49(1–2): 50–57.
- Ullrich, B. (1993f) *Agave colorata*. Kakt. and. Sukk. 44(10): centre-page pullout 1993/28, ills.



- Ullrich, B. (1994a) *Agave chrysoglossa* I. M. Johnston. Kakt. and. Sukk. 45(4): centre-page pullout 1994/12, ills.
- Ullrich, B. (1994b) *Agave sobria* Brandegees ssp. *roseana* (Trelease) Gentry. Kakt. and. Sukk. 45(9): centre-page pullout 1994/26, ills.
- Ullrich, B. (1994c) *Agave parrasana* Berger am Typstandort. Kaktusblüte 1994: 12–15, ills.
- Ullrich, B. (1995a) *Agave geminiflora* (Tagl.) Ker Gawler am Typenstandort in Nayarit, Mexico. Kaktusblüte 1995: 41–44, ills.
- Ullrich, B. (1995b) La questione della priorità di *Agave spicata* Cavanilles su *Agave yuccaeifolia* F. Delaroché in Redouté (Parte I). Zur Priorität von *Agave spicata* Cavanilles über *Agave yuccaeifolia* F. Delaroché in Redouté. Pianta Grasse 15(4): 115–123, ills.
- Ullrich, B. (1996a) *Agave peacockii* Croucher. Kakt. and. Sukk. 47(3): centre-page pullout 1996/06, ills.
- Ullrich, B. (1996b) La questione della priorità di *Agave spicata* Cavanilles su *Agave yuccaeifolia* F. Delaroché in Redouté (Parte II). Zur Priorität von *Agave spicata* Cavanilles über *Agave yuccaeifolia* F. Delaroché in Redouté. Pianta Grasse 16(1): 23–32, ills.
- Ullrich, B. (2007) *Agave attenuata* ssp. *dentata* (Roetzl) Ullrich. Haseltonia 12: 22–30, ills. [https://doi.org/10.2985/1070-0048\(2006\)12\[22:AASDRU\]2.0.CO;2](https://doi.org/10.2985/1070-0048(2006)12[22:AASDRU]2.0.CO;2).
- Urquiola Cruz, A. J. [et al. 2010], González Oliva, L. & Novo Carbó, R. (2010) Libro rojo de la flora vascular de la provincia de Pinar del Río. Alicante (ES): Universidad de Alicante, Servicio de Publicaciones.
- Valenzuela, A. (2011) A new agenda for blue Agave landraces: Food, energy and tequila. Global Change Biol. 3: 15–24. <https://doi.org/10.1111/j.1757-1707.2010.01082.x>.
- Valenzuela-Zapata, A. G. (1985) The tequila industry in Jalisco, Mexico. Desert Pl. 7(2): 65–70, ills. <https://repository.arizona.edu/handle/10150/554188>
- Valenzuela-Zapata, A. G. & Nabhan, G. P. (2003) Tequila! A natural and cultural history. Tucson (US): University of Arizona Press.
- Valverde, P. L. [et al. 1996], Vite, F. & Zavala-Hurtado, J. A. (1996) A morphometric analysis of a putative hybrid between *Agave marmorata* Roetzl and *Agave kerchovei* Lem.: *Agave peacockii* Croucher. Bot. J. Linn. Soc. 122(2): 155–161, ills. <https://doi.org/10.1111/j.1095-8339.1996.tb02070.x>.
- Vanderplank, S. (2014) A conservation plan for *Agave shawii* subsp. *shawii* (Shaw's Agave, *Agavaceae*). Claremont (US): Rancho Santa Ana Botanic Garden.
- Vanderplank, S. [et al. 2017], Peralta García, A., Valdez Villavicencio, J. H. & Rosa, C. A. de la (2017) Unique plants and animals of the Baja California Pacific Islands/Plantas y animales únicos de las Islas del Pacífico de Baja California: Coronado, Todos Santos, San Martín, San Jerónimo, San Benito, Cedros, Natividad. Fort Worth (US): Botanical Research Institute of Texas.
- Vargas-Ponce, O. [et al. 2007], Zizumbo-Villarreal, D. & Colunga-García Marín, P. (2007) In situ diversity and maintenance of traditional *Agave* landraces used in spirits production in west-central Mexico. Econ. Bot. 61(4): 362–375. [https://doi.org/10.1663/0013-0001\(2007\)61\[362:ISDAMO\]2.0.CO;2](https://doi.org/10.1663/0013-0001(2007)61[362:ISDAMO]2.0.CO;2).
- Vargas-Ponce, O. [et al. 2009], Zizumbo-Villarreal, D., Martínez-Castillo, J., Coello-Coello, J. & Colunga-García Marín, P. (2009) Diversity and structure of landraces of *Agave* grown for spirits under traditional agriculture: A comparison with wild populations of *A. angustifolia* (*Agavaceae*) and commercial plantations of *A. tequilana*. Amer. J. Bot. 96(2): 448–457. <https://doi.org/10.3732/ajb.0800176>.
- Vázquez-García, J. A. [et al. 1995], Cuevas-Guzmán, R., Cochrane, T. S., Iltis, H. H., Santana-Michel, F. J. & Guzmán-Hernández, L. (1995) Flora de Manantlán. Sida Bot. Misc. 13: 1–312.
- Vázquez-García, J. A. [et al. 2007a], Cházaro Basañez, M. J., Hernández Vera, G., Flores Berrios, E. & Vargas-Rodríguez, Y. L. (eds.) (2007) Agaves del occidente de México. Guadalajara (MX): Universidad de Guadalajara.
- Vázquez-García, J. A. [et al. 2007b], Cházaro Basañez, M. J., Hernández Vera, G., Vargas-Rodríguez, Y. L. & Pilar Zamora T., M. del (2007) Taxonomía del género *Agave* en el occidente de México: Un panorámica preliminar. In: Vázquez-García, J. A. & al. (eds.): Agaves del occidente de México; pp. 38–82, ills. (tt. A-MM). Guadalajara (MX): Universidad de Guadalajara.
- Vázquez-García, J. A. [et al. 2013], Muñoz-Castro, M. A., Sahagún-Godínez, E., Cházaro Basañez, M. J., Castro-Arce, E. de, Nieves-Hernández, G. & Padilla-Lepe, J. (2013) Four new species of *Agave* (*Agavaceae*) of the *Marmoratae* group. Syst. Bot. 38(2): 320–331, ills., map, key. <https://doi.org/10.1600/036364413X666642>.
- Vázquez-García, J. A. [et al. 2016], Hernández Vera, G., Nieves-Hernández, G., Muñoz-Castro, M. A. & Cházaro Basañez, M. J. (2016) El maguey blanco exclusivo de Temacapulín, en los Altos de Jalisco: En peligro crítico por la presa El Zapotilla. TecnoAgave 6(42): 20–22, ills. <https://www.tecnoagave.com.mx/cl/revista/>
- Velazco Macías, C. G. & Alanís Flores, G. J. (2002) Listado preliminar de las Cactáceas y Agaváceas de la Sierra “El Viejo”, Sonora, región prioritaria para la conservación en Mexico. Sida 20(1): 349–354.
- Velázquez, E. [et al. 2003], Fonseca, R. M. & Domínguez-Licona, E. (2003) Estudios florísticos en Guerrero. No. 16. Bosque de *Quercus* en Tixtla de Guerrero. México (MX): Facultad de Ciencias, Universidad Nacional Autónoma de México, Prensas de Ciencias.
- Véliz Pérez, M. E. (2013) Determinación, caracterización y evaluación del estado actual y uso de las especies endémicas de Guatemala. Guatemala (GT): CONCYT etc.

- Verhoek-Williams, S. (1975) A study of the tribe *Poliantheae* (including *Manfreda*) and revision of *Manfreda* and *Prochnyanthes* (*Agavaceae*). Ithaca (US): Cornell University, unpublished Ph.D. thesis.
- Verhoek-Williams, S. (1976) *Polianthes howardii* (*Agavaceae*): A new species from Colima. *Phytologia* 34(4): 365–368, ill.
- Verhoek-Williams, S. (1978a) Two new species and a new combination in *Manfreda* (*Agavaceae*). *Brittonia* 30(2): 165–171, ill. <http://www.jstor.org/stable/2806644>
- Verhoek-Williams, S. (1978b) Huaco and amole: A survey of the uses of *Manfreda* and *Prochnyanthes*. *Econ. Bot.* 32(2): 124–130. <https://doi.org/10.1007/BF02866866>.
- Verhoek-Williams, S. (1998) *Agavaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 60–70, ill., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_8](https://doi.org/10.1007/978-3-662-03533-7_8).
- Verhoek-Williams, S. & Hess, W. J. (2002) *Agavaceae*. In: Flora of North America north of Mexico; 26: 413–465, ill., keys. New York (US)/Oxford (GB): Oxford University Press.
- Verloove, F. (2013) New xenophytes from Gran Canaria (Canary Islands, Spain), with emphasis on naturalized and (potentially) invasive species. *Collect. Bot. (Barcelona)* 32: 59–82. <https://doi.org/10.3989/collectbot.2013.v32.006>.
- Verloove, F. [et al. 2018], Guillot Ortiz, D. & Guiggi, A. (2018) New records of interesting non-native succulents from Alicante (Spain). *Xerophilia* 23(4): 33–42, ill.
- Vignoli, L. (1936) Cariologia del genere *Agave*. *Lav. Reale Ist. Bot. Palermo* 8: 176–217.
- Villarreal, J. A. (1996) Una nueva especie de *Agave* subgenero *Agave* (*Agavaceae*) de México. *Sida* 17(1): 191–195, ill. <http://biodiversitylibrary.org/page/9303188>
- Villarreal, J. A. [et al. 2003], Starr, G., Estrada, E. & Rosa, M. de la (2003) Proposal to reject the name *Agave noah* (*Agavaceae*). *Taxon* 52(4): 861–862. <https://doi.org/10.2307/3647364>.
- Villarreal, J. A. [et al. 2005], Estrada, E., Starr, G. & Rosa, M. de la (2005) The confusing identity of *Agave wislizeni* (*Agavaceae*). *Taxon* 54(3): 801–803. <http://www.jstor.org/stable/25065438>
- Villarreal-Espino, O. A. [et al. 2011], Plata-Pérez, F. X., Camacho-Ronquillo, J. C., Hernández-Hernández, J. E., Franco-Guerra, F. J., Aguilar-Ortega, B. & Mendoza-Martínez, G. D. (2011) El Venado Cola Blanca en la mixteca poblana. *Therya* 2(2): 103–110. <https://doi.org/10.12933/therya-11-25>.
- Walker, C. C. (2000) *Agave attenuata* and some new cultivars. *Brit. Cact. Succ. J.* 18(2): 95–98, ill. <http://www.jstor.org/stable/42793657>
- Walker, C. C. (2017) *Agave victoriae-reginae* and its close relatives. *CactusWorld* 35(3): 159–166, ill.
- Walker, C. C. (2018) Presidential potted plants. *Agave* × *leopoldii*. *CactusWorld* 36(1): 62, ill.
- Walters, M. [et al. 2011], Figueiredo, E., Crouch, N. R., Winter, P. J. D., Smith, G. F., Zimmermann, H. G. & Mashope, B. K. (2011) Naturalised and invasive succulents of southern Africa. *Abc-Taxa* 11: x + 359 pp., ill., maps, keys.
- Watson, W. (1895) New or little known garden plants. An Arizona *Agave*. *Gard. & Forest* 8: 184–185, ill.
- Watson, W. (1899a) Kew notes. *Bravoa kewensis* W. Watson. *Gard. Chron.*, ser. 3, 26: 112. <http://www.biodiversitylibrary.org/item/83204#page/132/>
- Watson, W. (1899b) Kew notes [*Agave woodrowii*, *Aloe somaliensis*]. *Gard. Chron.*, ser. 3, 26: 430. <http://biodiversitylibrary.org/page/25771514>
- Watson, W. (1902) New and rare plants. *Agave bakeri*. *Garden* (London, 1871–1927) 61: 240–241. <http://biodiversitylibrary.org/page/24621456>
- Watson, W. (1912) *Agave leopoldii*: A protest. *Gard. Chron.*, ser. 3, 52: 414. <http://biodiversitylibrary.org/page/26111648>
- Webb, R. H. & Salazar-Ceseña, J. M. (2011) *Agave turneri* (*Agavaceae*), a new species from northeastern Baja California, Mexico. *Brittonia* 63(2): 203–210, map, ill. <https://doi.org/10.1007/s12228-010-9151-3>.
- Webb, R. H. & Starr, G. (2014a) *Agave azurea* (*Agavaceae*), a new species from Baja California Sur, México, with notes on other agaves on the Vizcaino Peninsula. *Haseltonia* 19: 89–96, ill., map. <https://doi.org/10.2985/026.019.0101>.
- Webb, R. H. & Starr, G. (2014b) The real *Agave gignantensis* in Baja California Sur, Mexico. *Cact. Succ. J. (US)* 86(1): 4–11, ill., map. <https://doi.org/10.2985/015.086.0103>.
- Webb, R. H. & Starr, G. (2015) Gentry revisited: The Agaves of the peninsula of Baja California, México. *Haseltonia* 20: 64–108, ill., keys, maps. <https://doi.org/10.2985/026.020.0101>.
- Weber, J. H. (1965) Distribution notes on *Agave toumeyana* Trel. *Saguaroland Bull.* 19(4): 47–48, ill. <http://biodiversitylibrary.org/page/54640136>
- Wercklé, C. (1907) Columbianische Agaven. *Monatsschr. Kakt.-kunde* 17(8): 121–123. <http://biodiversitylibrary.org/page/14172104>
- Werner, M. (2016) *Agave (Manfreda) virginica*—Kulturerfahrungen einer echten Liebhaberpflanze von der Aussaat bis zur Blüte. *Wüstengarten* 6: 47–52, ill.
- Whitaker, J. W. (1934) Chromosome constitution in certain Monocotyledons. *J. Arnold Arbor.* 15: 135–143, ill. <http://www.biodiversitylibrary.org/item/33591#page/149>
- Wijnands, D. O. (1983) The botany of the Commelins. A taxonomical, nomenclatural and historical account of the plants depicted in the Moninckx Atlas and in the four books by Jan and Caspar Commelin on the plants in the Hortus Medicus Amstelodamensis 1682–1710. Rotterdam (NL): A. A. Balkema. <http://edepot.wur.nl/205789>

- Wilder, B. T. [& al. 2008], Felger, R. S. & Romero-Morales, H. (2008) Succulent plant diversity of the Sonoran Islands, Gulf of California, Mexico. *Haseltonia* 14: 127–160, ills, map. <https://doi.org/10.2985/1070-0048-14.1.127>.
- Williams, R. O. (1924) Notes on the plants of Patos. *Bull. Misc. Inform. Kew* 1924(7): 273–280. <https://doi.org/10.2307/4118507>.
- Wilson, K. L. (2017a) Report of the General Committee: 16. *Taxon* 66(1): 189–190. <https://doi.org/10.12705/661.15>.
- Wilson, K. L. (2017b) Report of the General Committee: 17. *Taxon* 66(2): 478–480. <https://doi.org/10.12705/662.13>.
- Wolf, S. J. (1988) George Engelmann type specimens in the herbarium of the Missouri Botanical Garden. *Ann. Missouri Bot. Gard.* 75(4): 1608–1636. <https://doi.org/10.2307/2399304>.
- Wootton, E. O. & Standley, P. C. (1913) Descriptions of new plants preliminary to a report upon the flora of New Mexico. *Contr. US Nation. Herb.* 16: 109–196, tt. 48–50. <https://biodiversitylibrary.org/page/371953>
- Worsley, A. (1911) The genus *Polianthes* (including *Prochnyanthes* and *Bravoa*). *J. Roy. Hort. Soc.* 36 (3): 603–605. <http://biodiversitylibrary.org/page/46404564>
- Xhonneux, G. (2004) *Agave cundinamarcensis* Berger. *Cact.-Avent.* 61: 25–27, ills. (excl. ill. p. 25).
- Yépez, L. [& al. 2008], Dávila, M. & Barraza, A. (2008) Discriminación de poblaciones geográficas de *Agave cocui* Trelease mediante AFLP. *Bol. Centro Invest. Biol. Univ. Zulia* 42(4): 507–519.
- Zamudio, S. & Galván Villanueva, R. (2011) La diversidad vegetal del estado de Guanajuato, México. In: *Flora del Bajío y regiones adyacentes, Fascículo Complementario 27. Pátzcuaro (MX): Instituto de Ecología.*
- Zimer, E. (2014) New first records for New Zealand naturalized and casual succulent flora. *Xerophilia* 4(1): 95–106, ills.
- Zizumbo-Villarreal, D. [& al. 2013], Rosales-Adame, J. J. & Colunga-García Marín, P. (2013) Sustainability of the traditional management of *Agave* genetic resources in the elaboration of mezcal and tequila spirits in western Mexico. *Genet. Resources Crop Evol.* 60(1): 33–47, ills., maps. <https://doi.org/10.1007/s10722-012-9812-z>.
- Zona, S. (2002) *Agave decipiens*, endemic to Florida. *Haseltonia* 8: 24–29, ills., map.
- Zona, S. (2018) The repeat-flowering *Agave* is a botanical bigfoot. *Cact. Succ. J. (US)* 90(1): 64–69, ills. <https://doi.org/10.2985/015.090.0108>.
- Zonneveld, B. J. M. (2003) The systematic value of nuclear DNA content in *Agave* L. and some related genera of the *Agavaceae*. *Bradleya* 21: 121–125. <https://doi.org/10.25223/brad.n21.2003.a17>.
- Zonneveld, B. J. M. (2007) Verklaring voor bladkleuren in *Agave americana*. *Succulenta* 86(1): 15–20, ills.
- Zuccarini, J. G. (1833) Über einige neue Pflanzen aus den Gattungen *Agave* und *Fourcroya*. *Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur.* 16: 659–679, tt. 48–51 [t. 49 used twice]. <http://biodiversitylibrary.org/page/38634697>
- Zuijlen, A. van (2008) Op de vindplaats van ... (3) *Mammillaria schiedeana* (Ehrenberg). *Succulenta* 87(2): 76–82, ills.





## Beschorneria AGAVACEAE

J. Thiede

**Beschorneria** Kunth (Enum. Pl. 5: 844, 1850). **Type:** *Furcraea tubiflora* Kunth & C. D. Bouché. — **Agavoideae—Agaveae** — **Lit:** García-Mendoza (1987: monograph); Maunder (1989: synopsis); García-Mendoza (2003: partial synopsis); Jankalski (2005: synopsis). **Distr:** Mexico, Guatemala, Belize, Honduras; dry rocky woodlands to cloud forests. **Etym:** For Friedrich W. C. Beschorner (1806–1873), German physician and botanist, director of the Institute of Public Assistance and the Lunatic Asylum at Owinsk, Poland.

Perennial rosette plants, mostly acaulescent or short-caulescent (*B. wrightii*) to caulescent-arborescent (*B. albiflora*), rhizomatous, caespitose with age; **R** fibrous to fleshy, contractile; **L** erect or recurved,  $\pm$  linear-lanceolate or oblanceolate, ascending, narrowed at the base, base broadened to form a sheath, lamina tough, carinate-canaliculate, mostly glabrous or sometimes papillose above and/or scabrous below, green to glaucous, sometimes pruinose, midrib fleshy, tip a long soft point, margins entire or minutely denticulate; **Inf** racemes or few-branched panicles, straight or arching over, peduncle greenish, rose or reddish; **Bra** red, pink or yellow, broad and long, lanceolate to ovate, conspicuous, deciduous or persistent; **Ped** articulated at the tip; **Fl** pendulous, actinomorphic,

hermaphrodite or rarely functionally unisexual (*B. yuccoides*), single or 2–5 together in remote clusters; **Tep** lanceolate, subequal, free but connivent to form a tube-like corolla, greenish, yellowish, rose or red, apical part slightly spreading and green, whitish or yellowish; **ITep** carinate on the outside, papillose or puberulous on the inside and overlapping parts; **Fil** filiform, slightly thickened at the base, papillose,  $\pm$  as long as the tepals, whitish or greenish; **Anth**  $\pm$  oblong, dorsifixed, versatile, greenish or yellowish, pollen released in monads or tetrads; **Ov** inferior, oblong, trigonous, 6-sulcate, 3-locular, glabrous or puberulent, with 3 septal nectaries; **Sty** filiform, papillose, as long as or exceeding the stamens, basally swollen into 3 ridges; **Sti** obscurely 3-lobed, papillose, occasionally ciliate; **Fr** erect or pendulous,  $\pm$  cylindrical loculicidal capsules, subglobose or subclavate, trigonous, rostrate, with persistent tepals; **Se** planoconvex, flat, shining black to blackish. — **Cytology:**  $x = 30$  (Satô 1935, Watkins 1936, Cave 1964).

With its long and soft leaves and the inflorescences with large colourful bracts, the genus is atypical for the family and might be mistaken as belonging to the *Bromeliaceae*, with some similarity to, e.g., *Billbergia*. According to recent molecular and morphological phylogenies, *Beschorneria* is closest to *Furcraea*, and they are sister groups in most analyses (Bogler & Simpson 1995, Bogler & al. 1995, Bogler & Simpson 1996, Bogler & al. 2006, Good-Avila & al. 2006), sharing the following putative synapomorphies:

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Filaments slightly to distinctly thickened, ovary basally ribbed, and pollen in monads, dyads or tetrads. *Furcraea* differs consistently from *Beschorneria* in habit and in having hard leaves mostly with denticles or teeth, inconspicuously coloured bracts, and spreading tepals.

García-Mendoza (1987) produced a full taxonomic revision of the genus, but this remained unpublished. *Beschorneria* can be divided into 2 well characterized informal species groups (Jankalski 2005):

- [1] *Beschorneria tubiflora* group: **L** linear-lanceolate to linear, 30–65 (–70) cm, relatively narrow, often rigid, rough on both faces or on the lower face only; **Inf** unbranched racemes, sometimes with 1 or few short branches at the base. — 3 spp. from Mexico. Compact-growing small plants most amenable to growing in pots.
- [2] *Beschorneria yuccoides* group: **Ros** much larger; **L** lanceolate to oblanceolate, (35–) 50–100 (–150) cm, broad, smooth on both faces or rough on the lower face only; **Inf** many-branched panicles. — 4 spp. from Mexico, Guatemala and Honduras. Very showy landscape plants, especially when in full bloom.

**Pollination ecology:** No studies are available. Hummingbirds have been suggested as the primary pollinators for most species, given the reddish colour and the tubular shape of the flowers, but at least some species may be hawkmoth-pollinated (Rocha & al. 2006). Blooming plants cultivated in the S USA indeed attract hummingbirds according to casual reports in the Web.

**Ethnobotany and uses:** Apart from the widespread use as ornamental plants the genus has little economic value. The leaves of some species are used as a soap substitute while the fresh flowers are sometimes eaten fried with egg (Matuda 1966). The leaves and flowers of *B. yuccoides* are used as drop infusion against catarrh in sheep (specimen notes for *García Mendoza* 1418, MEXU).

**Cultivation:** In warmer regions, plants in good condition may flower each year from previous years' suckers, whereas flowering of greenhouse plants in northern regions may occur at long intervals only. Seedlings grown under glass may attain flowering size in 4–6 years (Maunder 1989). For cultivation in the S USA see Irish & Irish (2000) and Symon (2005), and in C Europe Maunder (1989) and Boeuf (2007). The plants are winterhardy in the warmest parts of the British Isles such as Cornwall (Senior 1968).

The following names are of unresolved application but are referred to this genus: *Beschorneria galeottii* Jacobi (1864) (*nom. inval.*, ICN Art. 38.1); *Beschorneria pumila* Jacobi (1864) (*nom. inval.*, ICN Art. 38.1); *Beschorneria schlechtendalii* Jacobi (1864) (*nom. inval.*, ICN Art. 38.1); *Beschorneria verlindeniana* Jacobi (1864) (*nom. inval.*, ICN Art. 38.1).

**B. albiflora** Matuda (Anales Inst. Biol. UNAM, Ser. Bot. 43(1): 52–54, 1974). **Type:** Mexico, Oaxaca (*MacDougall* 359-A [MEXU, IEB]). — **Lit:** Maunder (1989); Lott & García-Mendoza (1994); García-Mendoza (2003: online version with ill.); Jankalski (2006). **Distr:** Mexico (Oaxaca, Chiapas), Guatemala, Honduras, Belize?; sclerophyllous scrub, pine-oak and cloud forests, moist and shaded places in rich soils derived from limestone, 1900–3000 m; flowers March to June or November to February. **I:** Anonymus (2005); Symon (2005: as *B. yuccoides*).

**Incl.** *Beschorneria chiapensis* Matuda (1986) (*nom. inval.*, ICN Art. 32.1c).

[2] Caulescent-arborescent, stems 0.5–3 (–8) m, 10–12 cm Ø, erect, sometimes prostrate, single in habitat, clustering in cultivation; **Ros** 1–3 (–5) at the stem tip, dense, with 15–50 leaves; **L** erect, elliptic-lanceolate or lanceolate to linear-lanceolate, chartaceous, canaliculate, gradually narrowed towards the broadened base, smooth, (35–) 50–80 (–125) × 5.5–7 (–10) cm, green to glaucous, tip acuminate, not hardened, margins entire with a yellowish or cartilaginous band, rarely denticulate; **Inf** paniculate or rarely racemose, 1.5–3 (–3.5) m, peduncle and **Bra** reddish (brilliant green according to Matuda (1974)),

glabrous, fertile part with (20–) 50–200 flowers; **Ped** 10–35 mm, reddish, glabrous, with ovate bracteoles 10–22 × 5–7 mm; **Fl** (50–) 60–70 (–85) mm, single or in clusters of up to 4 (–7); **Tep** connivent, nearly equal, 25–35 (–45) × 2–5 mm; **OTep** white with green midstripe, linear-spatulate, slightly broader than the inner tepals; **ITep** white on both faces, linear-oblong, all tepals turning bright pink at anthesis and red in age, tips yellowish or cream, glabrous outside, papillose inside; **St** erect, equal, as long as the tepals or slightly longer; **Fil** dilated, 1.7 mm broad, apex subulate, white; **Anth** oblong-elliptic, 5–7 mm; **Ov** oblong-cylindrical to semicylindrical, 25–40 × 3–6 mm, intensely red or rose, glabrous; **Sty** filiform, 27 mm; **Sti** 1–1.2 mm Ø, papillose; **Fr** pendent, oblong, 45–70 × 20–30 mm, bright pink or reddish when young; **Se** plano-convex, 9–12 × 5–8 mm.

This is the S-most and the only arborescent species. The protologue gives the flowers as white only, but these turn bright pink at anthesis and red in age. Originally described from Oaxaca (Cerro Azul) but more recently found to be widespread in Chiapas, Guatemala and Honduras (Lott & García-Mendoza 1994, Jankalski 2006). The report of *B. tonelii* for Chiapas by Breedlove (1986) most probably represents a misidentification of *B. albiflora*. The online version (accessed 2013) of Lott & García-Mendoza (1994) depicts a sterile specimen (*Davidse & al.* 36471) from S Belize that might belong here. Plants may survive temperatures down to –7 (to –9) °C.

**B. calcicola** García-Mendoza (Herbertia [ser. 3], 42: 28–30, ills., 1986). **Type:** Mexico, Oaxaca (*García-Mendoza & Lorence* 720 [MEXU, ENCB, GJ]). — **Lit:** Maunder (1989); García-Mendoza (2003: with ill.); García-Mendoza (2011: with ills.). **Distr:** Mexico (C Veracruz, SE Puebla, NW Oaxaca); sclerophyllous scrub and ecotones with pine-oak forests, in rich organic soils derived from limestone, 1900–2600 m; flowers April to September.

[1] Acaulescent; **Ros** dense, in groups of 10–15 from a short rhizome; **L** erect or sometimes ± recurved, linear, rigid, conduplicate, keeled

below, scabrous below, scabridulous above, 30–60 × 0.3–0.6 cm (0.8–1.6 cm wide at the base), glaucous (drying greenish-yellow), **L** sheath triangular, 4–6 × 1.5–2 cm, yellowish, **L** margins denticulate; **Inf** racemose, 1.15–2.3 m, peduncle 0.8–1 m, 0.5–0.8 cm Ø, pinkish or yellowish, with 7–13 pink, aristate **Bra** 3–10 × 1–1.5 cm, fertile part (20–) 40–60 cm, with 16–30 flowers; floral **Bra** deltoid, 1–2.5 × 0.3–0.6 cm; **Ped** 7–20 mm, longer than the floral bracts, glabrescent, bracteolate; **Fl** (35–) 40–50 × 6–10 mm, single or in clusters of 2 (–3); **Tep** linear to linear-spatulate, connivent to form a tubular corolla with only the tips spreading, (20–) 25–33 mm, pink or yellowish outside, white at the apex and within; **OTep** linear, 2–3 mm broad, swollen at the base; **ITep** linear-spatulate, 4–5 mm broad, with dorsal midrib, outside puberulent, within papillose; **St** as long as or slightly shorter than the tepals; **Fil** subulate, dilated at the base for 1–1.5 mm, papillose, white; **Anth** linear, 3–6 mm, pale green or greenish-yellow; **Ov** cylindrical to subglobose, 6-angled, puberulous, 13–20 × 2–4 mm, pinkish or yellowish; **Sty** dilated and trisulcate at the base, with 1 nectary per sulcus, exceeding the stamens, sometimes exceeding the tepals by 1–3 mm, papillose, white; **Sti** capitate, 0.8–1.2 mm Ø, sometimes ciliate and papillose; **Fr** erect, subglobose, 20–28 × 15–18 mm, pinkish when young, stipitate, stipe thickened, 2–3 mm Ø; **Se** crescent-shaped, plano-convex, 5–7 × 4–5 mm, shiny.

Characterized by its narrow linear and conduplicate leaves (Maunder 1989). Most closely allied to *B. tubiflora* according to the protologue, but differing in leaf, inflorescence and flower characters, and with a different habitat. First discovered E of Ciudad Oaxaca in 1973 (Lau 1993). The occurrence in Veracruz was reported by Castillo Campos & al. (1999). This is the most drought-resistant species in the genus (Jankalski 2005).

**B. rigida** Rose (Contr. US Nation. Herb. 12: 262, 1909). **Type:** Mexico, San Luis Potosí (*Palmer* 593 [US 570098]). — **Lit:** Maunder (1989). **Distr:** Mexico (Tamaulipas, San Luis Potosí, Guanajuato, Querétaro, Puebla); mountain scrub, pine-oak forests, 1800–2400 m. **I:** Curtis's

Bot. Mag. 78: t. 4642, 1852, as *B. tubiflora*; Jardin Fleuriste 4: t. 334, 1854, as *B. tubiflora*; López Martínez (2015); Nájera Quezada & al. (2015).

**Incl.** *Beschorneria roseana* Ploem (1923).

[1] Acaulescent; **L** numerous, erect, rather rigid, roughened on both faces,  $30 \times \leq 2$  cm, glaucous-green, narrowing into a long-acuminate tip; **Inf** 0.7–3 m with 24–90 flowers; peduncle 0.5–1.5 cm  $\varnothing$  at the base, pink to red; floral **Bra** large, 15–20 cm, scarious, light purple to purplish; **Ped** as long as or longer than the floral bracts; **Fl** 45 mm, in clusters of 2–4; **Tep** somewhat scabrous, dull, yellow mottled green-brown, tips green; **St** shorter than the tepals; **Fr** globose to oblong, 30 mm; **Se** black.

Insufficiently known. According to the protologue, this taxon was first regarded as belonging to *B. tubiflora*, but differs in its narrower erect and notably acuminate leaves, which are rough on both faces, pedicel length, and more numerous duller flowers (Maunder 1989). Magallán Hernández & Hernández Sandoval (2001) recorded the taxon (and genus) for the first time for Querétaro, and Hernández-Sandoval & al. (2005) provided a new record for Tamaulipas, which is corroborated by several specimens at MEXU.

**B. septentrionalis** García-Mendoza (Cact. Suc. Mex. 33(1): 3–5, ills. (2): 52 [erratum], 1988). **Type:** Mexico, Tamaulipas (*García-Mendoza & Ramos* 2903 [MEXU]). — **Distr:** Mexico (Tamaulipas, Nuevo León); cloud and pine-oak forests, rich organic soil on stony slopes, >1400 m.

[2] Acaulescent, rhizomatous; **Ros** caespitose; **L** 10–20, recurved, oblanceolate, basis dilated, smooth on both faces,  $70\text{--}90$  ( $-105$ )  $\times$   $(5\text{--})$   $6\text{--}9$  ( $-13$ ) cm,  $1.8\text{--}2.5$  ( $-3.3$ ) cm broad at the basal constriction, brilliant green, tip shortly acuminate, margins finely denticulate with 1–3 ( $-4$ ) denticles per mm; **Inf** cymose-paniculate, 1.5–2.5 m, with 4–7 part-**Inf** 9–25 ( $-50$ ) cm long, overall with 90–130 flowers, peduncle carmine-red, peduncular **Bra** 4–5, oblanceolate, to 30 cm, carmine-red; floral **Bra** 12–30, 1.5–4 cm, lanceolate to deltoid, reddish to translucent; **Ped** (10–) 35–45 ( $-60$ ) mm, longer than the floral bracts; **Fl** (50–) 55–60 ( $-65$ ) mm, in clusters of 2–4; **Tep**  $25\text{--}30 \times 2\text{--}8$  mm, carmine-red, tip and margins

yellowish, inside papillose, outside glabrous; **OTep** linear-oblong, 2–5 mm broad; **ITep** oblong to oblong-spatulate, 4–8 mm broad; **St** 2–4 mm shorter than the tepals; **Fil** subulate, papillose; **Anth** oblong, 5–7 mm; **Ov** slightly 6-sulcate,  $25\text{--}30$  ( $-33$ )  $\times$   $2\text{--}8$  mm, carmine-red; **Sty** as long as or slightly longer than the stamens, papillose; **Sti** slightly 3-lobate; **Fr** ovoid,  $35\text{--}50$  ( $-65$ )  $\times$   $25\text{--}35$  mm, green (?), stipitate for 7 cm; **Se** (8–)  $9\text{--}11 \times (5\text{--})$   $6\text{--}8$  mm, shining.

This is the N-most species of the genus, easily recognized by its glossy green leaves and showy deep red flowers on very long pedicels. It is closest to *B. yuccoides* according to the protologue.

The species is fairly tolerant to short periods of freezing (Jankalski 2005). It was hybridized with *B. yuccoides* ssp. *dekosteriana* in the 1990s, and selections were marketed under several cultivar names (Jankalski 2005, Guillot Ortiz 2010).

**B. tubiflora** (Kunth & C. D. Bouché) Kunth (Enum. Pl. 5: 844, 1850). **Type:** B. — **Lit:** Regel (1875: with ill.); Maunder (1989); García-Mendoza (2003: with ills.). **Distr:** Mexico (San Luis Potosí, Querétaro, Hidalgo, Veracruz); pine-oak and cloud forests, shady or semi-open mountain tops and rocky slopes, in wet, deep soils rich in organic matter, 1830–2440 m; flowers April to May. **I:** Curtis's Bot. Mag. 100: t. 6091, 1874, as *B. tonelii*.

≡ *Furcroya tubiflora* Kunth & C. D. Bouché (1845); **incl.** *Beschorneria cohniana* Jacobi (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Beschorneria tonelii* Jacobi *ex* Hooker *fil.* (1874); **incl.** *Beschorneria toneliana* Baker (1888) (*nom. inval.*, ICN Art. 61.1).

[1] Acaulescent to very shortly caulescent, with short conical caudex; **L** 18–30, semi-erect, arcuate-recurved, narrowly-linear to linear-lanceolate, carinate-canaliculate, base much broadened, semi-amplexicaul, triangular, above the base soon narrowing and contracted into a flat thick pseudo-petiole to 2.5 cm broad, with fine longitudinal stripes, keeled below towards the tip, apex narrowly acuminate, rough below, with very small denticles not visible to the naked eye, smooth above,  $45\text{--}65$  ( $-70$ )  $\times$   $(0.6\text{--})$   $0.9\text{--}1.6$

(–3) (in the middle) cm, green (yellow-green in dry specimens), waxy, tip sharp, obtuse, long narrowly-subulate, soon drying, margins rigid, opaque, bright green, finely papillose to denticulate, denticles not visible to the naked eye, texture papery; **Inf** racemose, (0.7–) 1–1.5 (–1.8) m, slightly inclined, brownish-red to reddish-purple, glabrous, peduncle to 2.5 cm  $\varnothing$  at the base, with membranous, lanceolate to ovate-lanceolate, remote, pendent **Bra**, fertile part  $\pm$  80 cm, lax, in strong specimens sometimes with a short branch with 2 or more flowers at the base, unbranched above, inclined or pendent above, with 23–80 (–150) flowers; **Ped** 6–25 mm, ascending-erect, with reddish-brown bracteoles 18–25  $\times$  6 mm; **Fl** 35–45 (–50)  $\times$   $\pm$  38 mm, single or in clusters of 2–3; **Tep**  $\pm$  33 mm, narrowly linear, slightly dilated at the spreading acute tip, tubularly connivent, greenish to light red in the lower  $\frac{3}{4}$ , yellow-green to green at the apex, obtuse, dorsally with a broad midrib, puberulent or glabrous outside, papillose inside; **OTep** linear-spatulate, acutish; **ITep** much broader; **St** slightly shorter than the tepals; **Fil** subulate, as long as or much shorter than the tepals, papillose below the middle, slightly thickened at the base, white, glabrous; **Anth** linear-lanceolate, sagittate, green; **Ov** oblong to subglobose, obtusely trigonous, 6-grooved, 8–15  $\times$  4–6 mm, greenish to reddish, puberulent to glabrescent, with a conical, trilobate neck; **Sty** erect,  $\pm$  30 mm, as long as or much longer than the stamens, base thickened and 3-sulcate, white, papillose; **Sti** obscurely 3-lobed, slightly papillose, white; **Fr** globose, 12–15 (–18)  $\times$  11–15 mm, green with reddish tinge; **Se** plano-convex, 4–6  $\times$  3–5 mm, shiny. — *Cytology*:  $2n = 60$  (Satô 1935).

Closest to *B. rigida*. The report of the synonymous *B. tonellii* for Chiapas (Breedlove 1986) is most certainly a misidentification of *B. albiflora*. The occurrence in Querétaro and Veracruz is based on specimens at MEXU. In cultivation, the name is often misapplied to the much larger growing *B. yuccoides* ssp. *dekosteriana* (Jankalski 2005).

**B. wrightii** Hooker fil. (Curtis's Bot. Mag. 127: t. 7779 + text, 1901). **Type**: not typified. —

**Lit**: Berger (1906: with ill.); Berger (1907); both as *B. pubescens*; Maunder (1989); García-Mendoza (2003). **Distr**: Mexico (México: Sierra de Temascaltepec); exposed rock cracks in pine-oak forests, igneous and rocky substrates rich in organic matter; 2000–2580 m; flowers February to April.

**Incl.** *Beschorneria pubescens* A. Berger (1906).

[2] Plants to 1.5 m tall; stems to 60–90 cm, with a conical caudex to 15 cm  $\varnothing$ ; **Ros** with 18–30 leaves; **L** large, densely crowded, erect, linear-lanceolate, ensiform, carinate, fleshy, subcoriaceous, base broadened, very thick and biconvex, rather stiff and fleshy along the midrib, scabridulous on the nerves below, smooth above, 70–100 (–150)  $\times$  3–5 cm in the middle, glaucous-green, tip narrowed into a long brown stiff point, margins very narrowly scarious, finely and deeply denticulate; **Inf** paniculate, 1.7–3 m, peduncle 0.8–2 cm  $\varnothing$  at the base, waxy, bright pink or cherry- to coral-red, laxly bracteate, with deltoid-lanceolate acuminate **Bra** 8–10 cm long, upper shorter, glabrous, white streaked with red, fertile part lax, pyramidal, rather slender, with 6–27 spreading or recurved part-**Inf** with 150–180 flowers in total; **Bra** ovate, white, streaked with red; **Ped** 20–40 mm, pendent, glabrous; **Fl** 45–55 (–60) mm, in clusters of 2–3 (–4), (weakly) pubescent; **Tep** greenish, with broad yellow margins, yellow within, with tips obtuse, spreading, fading to yellow; **OTep** oblong to slightly spatulate; **ITep** oblong, canescent, papillose inside; **Fil** thickened at the base, whitish, at the beginning of the anthesis shorter but finally longer than the tepals; **Anth** linear, 12 mm, tips exerted; **Ov** cylindrical to conical-cylindrical, 17–28  $\times$  3–7 mm, green to reddish, puberulent or glabrescent in mature flowers; **Sty** as long as the filaments and slightly longer than the tepals, thickened at the base, papillose; **Sti** globose, 3-lobed, papillose, sometimes ciliate; **Fr** subglobose to somewhat conical, 35–40  $\times$  17–20 mm; **Se** plano-convex, 7–8  $\times$  5–6 mm.

The pubescent flowers are characteristic of the species (*B. calcicola* has merely puberulent flowers). Closely allied to "*B. dekosteriana*" (=



*B. yuccoides* ssp. *yuccoides*) (with glabrous flowers) according to the protologue.

**B. yuccoides** K. Koch (Wochenschr. Gärtnerei Pflanzenk. 2: 337, 1859). **Type:** not typified. — **Distr:** Mexico (Hidalgo, Puebla, Veracruz, Chiapas); 2700–3000 m.

Differs from the other members of the *B. yuccoides* group in its stemless habit (vs. caulescent, to arborescent in *B. albiflora*), its leaves scabrous below and its pedicels shorter than or about as long as the bracts (vs. leaves smooth below and pedicels longer than the bracts in *B. septentrionalis*), and its glabrous flowers (vs. pubescent flowers in *B. wrightii*).

**B. yuccoides** ssp. **dekosteriana** (K. Koch) García-Mendoza (Monocot. Mexic. Syn. Florist. 1(1): 30, 1993). **Type:** not typified. — **Lit:** Maun-der (1989); Ullrich (1991: with ill.); Irish & Irish (2000: with ill.); Calderón de Rzedowski & Rzedowski (2005); Cházaro Basáñez & Vazquez-Ramírez (2015); all as *B. yuccoides*. **Distr:** Mexico (Hidalgo, Puebla, Veracruz, Chiapas); mesic woodlands, pine, pine-oak and fir forests, 2600–3400 m; flowering April to May. **I:** Hooker (1860: as *B. yuccoides*); Baker (1884: as *B. bracteata*). — Fig. 1.

≡ *Beschorneria dekosteriana* K. Koch (1864); **incl.** *Beschorneria californica* Troubetzkoy (1877); **incl.** *Beschorneria dubia* Carrière (1877); **incl.** *Beschorneria mexicana* Troubetzkoy (1877); **incl.** *Beschorneria bracteata* Jacobi ex Baker (1882); **incl.** *Beschorneria decosteriana* Baker (1884) (*nom. inval.*, ICN Art. 61.1); **incl.** *Beschorneria superba* Hort. Hanbury ex Baker (1888) (*nom. inval.*, ICN Art. 32.1c?); **incl.** *Beschorneria argyrophylla* hort. ex W. Watson (1889) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Beschorneria viridiflora* Hort. Hanbury ex Baker (1892); **incl.** *Beschorneria glauca* hort. ex Gumbleton (1898); **incl.** *Beschorneria hidalgorupicola* Matuda (1967).

[2] Overall **Ros** size not recorded; **L** (10–) 20–35, inner erect, outer arching, linear-lanceolate to lanceolate, base broadened to 4–7 cm, then narrowed above the base, broadly attenuate, (sub-) coriaceous, scabrous below, papillose on



**Fig. 1** *Beschorneria yuccoides* ssp. *dekosteriana*. (Copyright: J. Trager)

the nerves, glabrous above, (40–) 60–90 (–100) × 3.3–3.5 (–5.5, to 10 in cult.) cm, grey-green to (brilliant-) green, glaucous, tip acuminate, margins finely denticulate; **Inf** 1–1.8 (–3.2 in cult.) m, peduncle ±1–1.25 m, 1.5–3.5 cm Ø at the base, bright red, reddish to dark red, fertile part with tip overhanging at first, later erect, with up to 20 part-**Inf** in the upper ⅔, drooping, red to reddish-brown, with 130–250 flowers; **Bra** broadly ovate, 0.4–3 cm, reddish, pilose; **Ped** 4–35 mm, shorter than the subtending bracts; **Fl** 40–50 mm, glabrous to glabrescent, in clusters of (2–) 3–5 (–7), glabrous to glabrescent, (always?) functionally unisexual; **Tep** 33–40 × 3.5–7 mm, free but narrowly connivent to form a tube-like corolla, red or yellowish-green and with reddish tinge, tip green, upper ±10 mm somewhat spreading and slightly pilose; **OTep** linear-oblong to oblong, 3.5–5 mm broad, acute; **ITep** oblong to spatulate, 5–7 mm broad; **Fil** filiform, 35 mm, included; **Anth** oblong, 3.5–6 mm, greenish; **Ov**



cylindrical, 20 × 5 mm, dark red, neck slightly constricted; **Sty** filiform; **Sti** slightly pilose; **Fr** oblong to subglobose or subclavate, 30–40 × 15–25 mm; **Se** flat, 7–8 × 3.5–5 mm. — **Cytology**: 2n = 60 (Watkins 1936: as *B. superba*).

According to the protologue differing from ssp. *yuccoides* (as *B. yuccoides*) especially in its more luxuriant growth and its larger, at first overhanging inflorescences with reddish peduncles and reddish bracts (vs. straight inflorescences with greenish peduncles and reddish-greenish bracts). The long-standing confusion between the two taxa goes back to Hooker (1860), who, under the name *B. yuccoides*, figured what was subsequently published as *B. dekosteriana*, and ever since, almost all descriptions of “*B. yuccoides*” refer to the reddish peduncles and bracts of what is ssp. *dekosteriana*. To make matters worse, Baker (1884) figured plants of the true *B. yuccoides* under the misapplied name *B. dekosteriana*. — *B. superba* belongs here according to Oliver & Bailey (1927) and Berger (1906) (both under *B. yuccoides*).

This subspecies is more variable and widespread than ssp. *yuccoides* and by far the most commonly cultivated *Beschorneria* (Jankalski 2005). Its leaves are used as soap substitute for washing clothes, and the plant is used as living fence, as ornamental and for its edible flowers (Matuda 1966, Reyes & Rosado 2000; both as *B. bracteata*). Maunder (1989) provided a first record for Chiapas, based on *MacDougall*

377 from Cerro Tres Picos. The taxon is naturalized in New Zealand and N Argentina (Zimer 2014, Cantero & al. 2016; both as *B. yuccoides*).

According to Symon (2005), and based on experience in cultivation in Australia, this taxon (as *B. yuccoides*) produces flowers which are functionally unisexual: The plants (monoecious or male) produce either functionally male green flowers only, or many functionally male pink flowers as well as few functionally female pale green flowers. The plant is hardy outdoors in the Mediterranean or even in S England (Ullrich 1991). In the USA, it may survive temperatures down to –12 °C for short periods (Irish & Irish 2000). ‘Flamingo Glow’ is a variegated cultivar, and ‘Quick Silver’ a cultivar with silvery leaves; both are sold as *B. yuccoides*.

**B. yuccoides** ssp. **yuccoides** — **Lit**: Maunder (1989: with ill.). **Distr**: Mexico (Hidalgo: Sierra de Pachuca); woodland and *Abies-Juniper* forests, 2700–3000 m. **I**: Baker (1884: as *B. dekosteriana*). — Fig. 2.

**Incl.** *Beschorneria yuccoides* hort. ex Hooker (1860) (*nom. illeg.*, ICN Art. 53.1).

[2] Differs from ssp. *dekosteriana*: **L** erect, 45–65 cm, coriaceous; **Inf** peduncle 1–2 m, green(ish) to light brown, **Inf** with 100–120 flowers; **Bra** greenish to light brown; **Fl** in clusters of 2–4; **Fr** oblong. — **Cytology**: 2n = 60 (Watkins 1936, Cave 1964, both most probably referring to ssp. *dekosteriana*).

**Fig. 2** *Beschorneria yuccoides* ssp. *yuccoides*. (Copyright: U. Eggli)



The typical subspecies of *B. yuccoides* remains incompletely known, and unfortunately, no modern complete description is available. The leaves and flowers are used as drop infusion against catarrh in sheep according to the annotation of a herbarium specimen (*García-Mendoza* 1418, MEXU).

## References

- Anonymus (2005) *Beschorneria albiflora*. Cact. Succ. J. (US) 77(3): 115, ill. (front cover). [https://doi.org/10.2985/0007-9367\(2005\)77\[115a:E\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[115a:E]2.0.CO;2)
- Baker, J. G. (1884) *Beschorneria decosteriana*. Curtis's Bot. Mag. 110: t. 6768 + text. <http://biodiversitylibrary.org/page/437231>
- Berger, A. (1906) *Beschorneria pubescens* Berger. Gard. Chron., ser. 3, 40: 350–351, ill. <http://biodiversitylibrary.org/page/25911044>
- Berger, A. (1907) *Beschorneria pubescens* Berger n. sp. Monatsschr. Kakt.-kunde 17(1): 1–3. <https://biodiversitylibrary.org/page/14171984>
- Boeuf, T. (2007) *Yucca* & Co. Winterharte Wüstengärten in Mitteleuropa anlegen und pflegen. Berlin (DE): Medemia.
- Bogler, D. J. & Simpson, B. B. (1995) A chloroplast DNA study of the *Agavaceae*. Syst. Bot. 20(2): 191–205. <http://www.jstor.org/stable/2419449>
- Bogler, D. J. & Simpson, B. B. (1996) Phylogeny of *Agavaceae* based on ITS rDNA sequence variation. Amer. J. Bot. 83(9): 1225–1235. <http://www.jstor.org/stable/2446206>
- Bogler, D. J. [et al. 1995], Neff, J. L. & Simpson, B. B. (1995) Multiple origins of the *Yucca* — *Yucca* Moth association. Proc. Nation. Acad. Sci. USA 92(15): 6864–6867, ills. <http://www.pnas.org/content/92/15/6864.full.pdf+html>
- Bogler, D. J. [et al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on *ndhF*, *rbcL*, and ITS sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): Monocots. Comparative biology and evolution excluding Poales. Aliso 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>
- Breedlove, D. E. (1986) Flora de Chiapas. Listados florísticos de México IV. México (MX): Instituto de Biología, UNAM. <http://www.ibiologia.unam.mx/BIBLIO68/fulltext/lfl4.html>
- Calderón de Rzedowski, G. & Rzedowski, J. (eds.) (2005) Flora Fanerogámica del Valle de México; ed. 2, 1. reimpression. Pátzcuaro (MX): Instituto de Ecología / Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.
- Cantero, J. J. [et al. 2016], Barboza, G. E., Chiarini, F. E., Deanna, R., Espinar, L. A., Giorgis, M. A., Nuñez, C. O. & Bernardello, G. (2016) Novedades para la flora de la Argentina. Bol. Soc. Argent. Bot. 51(1): 183–207.
- Castillo Campos, G. [et al. 1999], Vovides, A. P. & Avendaño-Reyes, S. (1999) *Garrya ovata* Benth. ssp. *goldmanii* (Wooton et Standl.) Dahling (*Garryaceae*) and *Beschorneria calcicola* García Mendoza (*Agavaceae*): Two new reports from Veracruz, Mexico. Polibotánica 8: 65–68. <http://polibotanica.mx/pages/en/index/01-10/num.-8.php>
- Cave, M. S. (1964) Cytological observations on some genera of the *Agavaceae*. Madroño 17: 163–170. <http://biodiversitylibrary.org/page/47826625>
- Cházaro Basáñez, M. J. & Vazquez-Ramirez, J. (2015) Introducing the succulent flora of Mexico: *Beschorneria yuccoides* (*Agavaceae*). Cact. Succ. J. (US) 87(6): 271–272, ills. <https://doi.org/10.2985/015.087.0608>
- García-Mendoza, A. J. (1987) Monografía del género *Beschorneria* Kunth (*Agavaceae*). México (MX): UNAM, unpublished M.Sc. thesis.
- García-Mendoza, A. J. (2003) Revisión de las *Agavaceae* (sensu stricto), *Crassulaceae* y *Liliaceae* incluidas en el PROY-NOM-059-ECOL-2000. Mexico (MX): Jardín Botánico, Instituto de Biología, UNAM, Proyecto W020, bases de datos SNIB-CONABIO.
- García-Mendoza, A. J. (2011) Flora del Valle de Tehuacán-Cuicatlán. 88. *Agavaceae*. Mexico (MX): Instituto de Biología, UNAM.
- Good-Avila, S. V. [et al. 2006], Souza, V., Gaut, B. S. & Eguiarte, L. E. (2006) Timing and rate of speciation in *Agave* (*Agavaceae*). Proc. Nation. Acad. Sci. USA 103(24): 9124–9129. <https://doi.org/10.1073/pnas.0603312103>
- Guillot Ortiz, D. (2010) The first cultivar database in Spain. J. Hort. Forest. 2(8): 196–213.
- Hernández-Sandoval, L. G. [et al. 2005], Treviño Carreón, J., Mora-Olivo, A. & Martínez y Díaz, M. (2005) Diversidad florística y endemismos. In: Sánchez-Ramos, G. & al. (eds.): Historia Natural de la Reserva de la Biosfera El Cielo, Tamaulipas, México. Ciudad Victoria (MX): Universidad Autónoma de Tamaulipas.
- Hooker, W. J. (1860) *Beschorneria yuccoides*. Curtis's Bot. Mag. 86: t. 5203 + text. <http://biodiversitylibrary.org/page/432237>
- Irish, M. & Irish, G. (2000) Agaves, Yuccas and related plants. A gardener's guide. Portland (US): Timber Press.
- Jankalski, S. (2005) *Beschorneria*. Baltimore Areole 2005 (Nov.): [].
- Jankalski, S. (2006) Regarding *Beschorneria chiapensis*. Cact. Succ. J. (US) 78(1): 29–30. [https://doi.org/10.2985/0007-9367\(2006\)78\[29:RBC\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[29:RBC]2.0.CO;2)
- Lau, A. B. (1993) The discovery of *Pinguicula laeana*. Int. Pinguicula Study Group Newslett. 2: 9–10.
- López Martínez, C. (2015) Sierra de Santa Bárbara. The southernmost region of “El Gran Tunal”. Xerophilia 4(1): 37–52, map, ills.
- Lott, E. J. & García-Mendoza, A. (1994) *Agavaceae*. In: Davidse, G. & al. (eds.): Flora Mesoamericana, Volumen 6, *Alismataceae* a *Cyperaceae*; pp. 35–47, keys. México (MX): UNAM, Instituto de Biología / St. Louis (US): Missouri Botanical Garden/London

- (GB): Natural History Museum. <http://www.tropicos.org/Project/FM>
- Magallán Hernández, F. & Hernández Sandoval, L. (2001) La familia *Agavaceae* en el Estado de Querétaro, México. *Bol. Soc. Bot. México* 66: 103–112, maps. <http://www.redalyc.org/pdf/577/57706610.pdf>
- Matuda, E. (1966) *Beschorneria bracteata*, *Cact. Suc. Mex.* 6(3): 65.
- Matuda, E. (1974) *Beschorneria albiflora* Matuda sp. nov. *Anales Inst. Biol. UNAM, Ser. Bot.* 43(1): 51–53.
- Maunder, M. (1989) A survey of the genus *Beschorneria* in cultivation. *Plantsman* 10: 193–199, 1 t.
- Nájera Quezada, P. [ & al. 2015], Hernández, J. J., López Martínez, C. & Neri Cardona, S. K. (2015) Sierra de San Miguelito. A preliminary regional ecological analysis. *Xerophilia* 4(1): 4–24, map, ills.
- Oliver, G. W. & Bailey, L. H. (1927) *Beschorneria*. In: Bailey, L. H. (ed.): *The Standard Cyclopaedia of Horticulture*, new edition; pp. 495–496. New York (US): MacMillan Co.
- Regel, E. (1875) *Beschorneria tubiflora* Kunth. *Gartenflora* 24: 355–356, t. 851. <https://biodiversitylibrary.org/page/40102700>
- Reyes, S. A. & Rosado, I. C. (2000) Plantas utilizadas como cercas vivas en el estado de Veracruz. *Madera & Bosques* 6(1): 55–71.
- Rocha, M. [ & al. 2006], Good-Ávila, S. V., Molina-Freaner, F., Arita, H. T., Castillo, A., García-Mendoza, A., Silva-Montellano, A., Gaut, B. S., Souza, V. & Eguiarte, L. E. (2006) Pollination biology and adaptive radiation of *Agavaceae*, with special emphasis on the genus *Agave*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 329–344, maps. <https://doi.org/10.5642/aliso.20062201.27>
- Satô, D. (1935) Analysis of the karyotypes in *Yucca*, *Agave* and the related genera with special reference to the phylogenetic significance. *Jap. J. Genet.* 1: 272–278.
- Senior, R. (1968) Succulents outdoors in Britain. *Nation. Cact. Succ. J.* 23(3): 73–75. <https://www.jstor.org/stable/42788855>
- Symon, D. (2005) A note on the sexuality of *Beschorneria yuccoides* and comments on the horticulture of this uncommon garden subject. *Cact. Succ. J. (US)* 77(3): 144–145, ill., (4): 177 [erratum]. [https://doi.org/10.2985/0007-9367\(2005\)77\[144:ANOTSO\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[144:ANOTSO]2.0.CO;2)
- Ullrich, B. (1991) *Beschorneria yuccoides* W. J. Hooker. *Kakt. and Sukk.* 42(12): centre page pullout 1991/36, ills.
- Watkins, G. M. (1936) Chromosome numbers and species characters in *Yucca*. *Amer. J. Bot.* 23(5): 328–333. <http://www.jstor.org/stable/2436092>
- Zimer, E. (2014) A new adventiv [sic!] succulent recorded in New Zealand. *Beschorneria yuccoides*. *Xerophilia* 11: 98–101, ills.





## Furcraea AGAVACEAE

J. Thiede

**Furcraea** Ventenat (Bull. Sci. Soc. Philom. Paris 1: 65–67, 1793). **Type:** *Furcraea gigantea* Ventenat [type element according to l.c. p. 65; ING (accessed Aug. 2015) incorrectly lists *Agave cubensis* Jacquin (mentioned on p. 66 of the protologue as additional species) as lectotype designated by Britton, Fl. Bermuda, 80, 1918]. — **Agavoideae - Agaveae** — **Lit:** Baker (1879: synopsis); Baker (1888: synopsis); Drummond (1907: synopsis); Trelease (1910: taxonomic notes); Trelease (1915a: synopsis); Trelease (1915b: synopsis Guatemala); Trelease (1920: Fl. Mexico); Standley & Steyermark (1952: Fl. Guatemala); McVaugh (1989: Fl. Novo-Galiciana); Lott & García-Mendoza (1994: Flora Mesoamericana); Álvarez de Zayas (1996: synopsis Cuba); García-Mendoza (1998: revision Mexico & Guatemala); García-Mendoza (2001a: revision); García-Mendoza (2001b: revision arborescent taxa); Guillot Ortiz & Meer (2010: synopsis cultivated taxa Spain); García-Mendoza (2011: Fl. Valle Tehuacán-Cuicatlán). **Distr:** C and S Mexico, C America to Panama, Caribbean Region, Colombia, Ecuador, Venezuela, French Guiana, Guayana, Suriname, Peru, Bolivia, Brazil, Paraguay (the S American range apart from Colombia, Venezuela, Ecuador, Peru and Bolivia, as well as major parts of the Caribbean distribution might be exclusively

anthropogenic). **Etym:** For Antoine F. de Fourcroy (1755–1809), French politician and chemist, 1784 director at the Jardin des Plantes in Paris.

**Incl.** *Funium* Willemet (1796). **Type:** *Funium pitiferum* Willemet.

**Incl.** *Furcroea* De Candolle (1803) (*nom. inval.*, ICN Art. 61.1).

**Incl.** *Furcroya* Rafinesque (1814) (*nom. inval.*, ICN Art. 61.1).

**Incl.** *Fourcroya* Sprengel (1817) (*nom. inval.*, ICN Art. 61.1).

**Incl.** *Fourcroea* Haworth (1819) (*nom. inval.*, ICN Art. 61.1).

**Incl.** *Codonocrinum* Willdenow ex Schultes & Schultes *fil.* (1829). **Type:** *Codonocrinum agavoides* Schultes & Schultes *fil.*

**Incl.** *Fourcraea* Steudel (1840) (*nom. inval.*, ICN Art. 61.1).

**Incl.** *Roezlia* Laurentius (1861). **Type:** *Roezlia regia* Laurentius.

**Incl.** *Roeslia* Baillon (1894) (*nom. inval.*, ICN Art. 61.1).

Plants strictly monocarpic when unbranched or without offsets; stems none or a thick short or to 6 m long trunk; **Ros** with densely crowded leaves; **L** large, erect, coriaceous, lanceolate or linear, long and narrow, thin and flexible or rather thick and stiff, concave or flattened, keeled below, surface smooth or scabrous, rough on the veins below in some taxa, green or glaucous, tip a short mucro or corneous-hardened by the involute leaf

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margins, margins dentate, denticulate, entire or dentate-entire, teeth simple or bicuspidate, sometimes on elevated bases; **Inf** tall lax terminal panicles to 15 m but mostly shorter, peduncle short or up to 3.5 m, bracteate, fertile part pyramidal or rhomboidal to fusiform or oblong, part-**Inf** (= 1.-order branches) on long bracteate branches, with 2.- to 4.-order branches, glabrous or puberulent, often bulbiferous, bulbils conical to ovoid and sometimes with leafy bracts; **Fl** pendulous, bracteate, pedicellate, single or fasciculate in clusters of 2–5, often all or in part replaced by bulbils; **Tep** generally equal but **OTep** narrower and **ITep** with prominent dorsal midrib, ovate to elliptic, (almost) free to the base, greenish- or yellowish-white to white, sometimes with reddish tinge, overlapping marginally, glabrous to puberulent; **Fil** 3 + 3,  $\pm \frac{1}{2}$  as long as the tepals and affixed to their bases, dilated below the middle, subulate distally, papillose; **Anth** oblong, 2–8 mm, dorsifixed, centric or sometimes slightly excentric, introrse, versatile; **Ov** inferior, oblong, cylindrical or trigonous, with a short neck at the tip, glabrous or puberulent; **Sty** columnar, basally swollen and triquetrous with 3 basal ridges, papillose; **Sti** small, shortly 3-lobate; **Fr** woody capsules, oblong, subglobose or ovoid, 3-valvate, stipitate, rostrate, opening loculicidally; **Se**  $\pm$  deltoid, flattened, often (always?) narrowly to broadly winged, black. — **Cytology**:  $2n = 60$  (Whitaker 1934, Satô 1935, Fritsch 1970) (reports of  $2n = 44–46$  and  $48–50$  by Heitz (1926) are dismissed as doubtful).

The genus has not been completely studied up to the complete revision by García-Mendoza (2001a), which clarified the circumscriptions and taxonomy of many previously uncertain taxa; it is largely followed here with the exception of the taxa that have not yet been formally published. Some of the taxa recognized may, however, merely represent early anthropogenic selections, cultivars or hybrids. With a maximum length of 15 m in *F. cabuya* (García-Mendoza 2001a), the genus apparently has the largest inflorescences of any plant.

Ullrich (1991a) regards the publication of the generic name *Furcraea* as cited above as not effectively published but this was rejected in the

first edition of this handbook, and Ullrich's interpretation is also not accepted by reference works such as García-Mendoza (1998) and Govaerts (2014+).

According to recent molecular and morphological phylogenies, *Furcraea* is sister of *Beschorneria*, and both together are sister of *Agave* in most analyses (Hernández-Sandoval 1995, Bogler & Simpson 1995, Bogler & al. 1995, Bogler & Simpson 1996, Bogler & al. 2006, Rocha & al. 2006, Good-Avila & al. 2006). The two genera exhibit the following putative synapomorphies: Filaments papillose and slightly to distinctly thickened below, ovary basally ribbed and broadened, and pollen shed in tetrads (Álvarez de Zayas & Köhler 1987, Ojeda Revah & Ludlow Wiechers 1995, Hesse & al. 2009). *Beschorneria* differs conspicuously from *Furcraea* in habit and in having soft leaves without teeth, large coloured bracts, connivent tepals, and filaments  $\pm$  as long as the tepals.

*Furcraea* can (possibly artificially) be divided as follows (adapted from García-Mendoza 2001a: 71):

- [1] Sect. *Furcraea* (incl. Sect. *Spinosa* Drummond 1907, *nom. inval.*, ICN Art. 22.2): Stems mostly none or short, to 0.7–1.5 m, or rarely arborescent to 3 (–9) m; **L** margins with conspicuous  $\pm$  distant teeth (occasionally teeth few or absent), leaf tip corneous, mucronate; bulbils bracteate or foliose; seedlings with small cotyledons. — Possibly a paraphyletic hold-all.
- [2] Sect. *Serrulatae* Drummond 1907 (incl. subgen. *Roelia* (Laurentius) Baker 1888; incl. ser. *Flexiles* Baker 1879 = subgen. *Flexiles* (Baker) García-Mendoza 2001, *nom. inval.* ICN Art. 29.1): Plants mostly arborescent and stems conspicuous, 1–9 m; **L** margins closely minutely denticulate, leaf tip corneous; bulbils foliose, with chartaceous outer leaves; seedlings with large cotyledons.

Hochstätter (2016) published 3 infrageneric taxa which each includes species of both sections as recognized above; Hochstätter's names are untypified and invalidly published under ICN Art. 29.1.

**Ethnobotany:** The leaves of many species are used as source of fibres on local household or industrial scale in major parts of its area, but also outside the Americas esp. in India, Madagascar and Mauritius (García-Mendoza 1998). *Furcraea* species are also planted as hedges and living fences, and to prevent soil erosion. The flowers are eaten and used as religious Easter decoration, the inflorescences as fodder, the leaf juice as soap or to stupefy fishes, to cure gastritis, prostata inflammation, hepatitis, and for liver cleansing and increasing bile secretion (see comments for the individual species). Many species are cultivated as ornamentals worldwide in (sub-) tropical and Mediterranean climates.

For species cultivated in the open mainly in Mediterranean climates or for naturalized species, see Irish & Irish (2000) for the USA, David (2009) for Great Britain, Guillot Ortiz & Meer (2010) for Spain, Wilcox (2005) for New Zealand, and Crouch & Smith (2011) and Smith & Figueiredo (2012) for South Africa.

The following names are of unresolved application but are referred to this genus: *Agave stenophylla* Jacobi (1866); *Agave vivipara* Miller (1768) (*nom. illeg.*, ICN Art. 53.1); *Agave vivipara* Willdenow (1799) (*nom. illeg.*, ICN Art. 53.1); *Agave vivipara* Arruda (1810) (*nom. illeg.*, ICN Art. 53.1); *Furcraea cubensis* Haworth (1819) (*nom. illeg.*, ICN Art. 53.1)  $\equiv$  *Agave cubensis* (Haworth) Sprengel (1825) (*nom. illeg.*, ICN Art. 53.1); *Furcraea demouliniana* Jacobi (1867); *Furcraea rigida* Landry ex Jacobi (1867) (*nom. inval.*, ICN Art. 36.1c); *Furcraea roezlii* Eichler (1881); *Furcraea roezlii* var. *atropurpurea* Hort. De Smet (1876); *Furcraea sobolifera* Hort. J. F. Cels ex Jacobi (1867) (*nom. inval.*, ICN Art. 36.1c).

**F. acaulis** (Kunth) B. Ullrich (Quepo 6: 69, ills., 1992). **Type:** Venezuela (*Bonpland & Humboldt* 633 [†]). — **Lit:** Lott & García-Mendoza (1994: as *F. stratiotes*). **Distr:** N Colombia (César, Guajira, N Santander); N Venezuela (Carabobo, Cumaná, Distrito Federal, Falcón, Lara, Miranda, Sucre, Yaracuy, Zulia); Ecuador (La Loja); chiefly in well-drained limestone soils,

coastal plains, thorn scrub, montane and cloud forests, 0–1330 m; flowers July to September. **I:** Hoyos (1982: as *F. humboldtiana*).

$\equiv$  *Yucca acaulis* Kunth (1816); **incl.** *Codonocrinum agavoides* Willdenow ex Schultes & Schultes fil. (1829); **incl.** *Furcraea altissima* Todaro (1889); **incl.** *Furcraea humboldtiana* Trelease (1910); **incl.** *Furcraea stratiotes* J. B. Petersen (1922).

[1] Stems simple, arborescent to subcaulescent, to 1–3.5 m, dry leaves persisting; **Ros** 3.5 m  $\varnothing$ ; **L** 70–100, at first erect, later spreading, lanceolate to broadly lanceolate, coriaceous, at the base 3.5–5 (–9.5) cm broad and 4 cm thick, plane-concave in cross-section, almost flat, concave towards the apex, acute, rough below, smooth above, or also rough on the lower part of the upper face (Dewey 1943), (1–) 1.2–1.75 (–2) m  $\times$  (9–) 11–18 (–20) cm (in the middle), glaucous or yellowish-green to dark green or greyish, margins dentate, sometimes corneous-dentate to the base; **marginal teeth** geminate or doubly geminate, reflexed in opposite directions near the leaf base, further up sometimes single and upcurved, intervening margin concave, or rarely teeth nearly all simple and mostly upcurved and intervening margin nearly straight, teeth strong, 3–10 mm, 4–6 (–7) mm broad at the base, reddish to orange, becoming garnet-red with darkened tips, or at last dark chestnut-brown, on broadly deltoid or semi-circular herbaceous decurrent bases, or sometimes decurrent along the intervening margin, (1.5–) 2–4.5 (–6 (–8)) cm apart at mid-leaf, 1–3 cm at the base; **terminal Sp** acute, partially involute, mucronate, small, robust, channelled below, 3–7 (–10)  $\times$  2 mm, dark reddish to garnet-red or chestnut-brown, slightly decurrent; **Inf** 7–9 (–12) m, peduncle 5–6 m, green, with short bracts, fertile part in the upper  $\frac{1}{2}$  or  $\frac{1}{3}$ , with  $\pm 40$  part-**Inf**, 40–70 (–100) cm, glabrous, with 20–30 2.-order branches, 5–17 cm, green, glabrous or pilose, bulbiferous, bulbils conical, 23–30  $\times$  7–8 mm, bracteate, green, covered with 2 scarious bracts; **Ped** 3–5 mm, glabrous; **Fl** 37–40 mm, geminate; **Te** 20–23 mm,  $\pm$  obtuse, yellowish-green to light yellow, with white margins, glabrous; **OTep** narrowly elliptic, (4–) 5–7 mm broad; **ITep** elliptic, (6–) 8–10 mm broad; **Fil** subulate, 12–14 mm,

1–2 mm wide at the broadened base; **Anth** oblong, 2 mm, yellow; **Ov** cylindrical, triquetrous, 17–20 × 3–4 mm; **Sty** triquetrous, (15–) 18–20 mm, 2–3 mm wide at the broadened base; **Sti** trifid; **Fr** subsphaerical, 35–40 × 30–40 mm, stipitate for 10 mm; **Se** winged for 2–3 mm, 13–15 × 8–9 mm, shiny.

Insufficiently known before the first full description was published by García-Mendoza (2001a). The type collection does not seem to be extant (Stauffer & al. 2012).

After Trelease (1915a) wrongly listed the much older *Yucca acaulis* in the synonymy of his *F. humboldtiana*, Ullrich (1992) was the first to notice the error, which he rectified by publishing the necessary new combination.

First collected by Bonpland and Humboldt in Venezuela where the species is native. The distribution in Colombia appears to be natural, and several fragmentary specimens from Grenada, the Virgin Islands and Trinidad may belong here (García-Mendoza 2001a). Spineless plants placed here by Hoyos (1982) appear to belong to *F. foetida*. *F. stratiotes* (described from material collected in Nicaragua in 1848 that flowered in cultivation in Copenhagen in 1921; never recollected in Nicaragua and the only known occurrence is in the Virgin Islands according to Proctor & Acevedo-Rodríguez 2005) differs in having smaller flowers and compressed bulbils.

Olivares & Medina (1984) argue that the flowers are sterile and that the plants propagate only through bulbils, but the description of fruits and seeds by García-Mendoza (2001a) shows that this is not universally true.

*F. acaulis* is widely cultivated in Venezuela for fibre (Dewey 1943), and Giraldo & al. (2009) report that the leaves are used against various illnesses.

**F. antillana** A. Álvarez (Anales Inst. Biol. UNAM, Ser. Bot. 67(2): 331–335, ill., 1996). **Type:** Cuba, La Habana (Álvarez 63654 [HJJB, MEXU]). — **Lit:** Proctor & Acevedo-Rodríguez (2005). **Distr:** Greater Antilles: Cuba, Hispaniola, Puerto Rico (cultivated); mainly semideciduous forests or dry coastal scrub or thornscrub, also in pine forests and secondary formations, on

limestone or serpentine, 0–200 m; flowers July to September. **I:** García-Mendoza (2001a).

[1] Stems none or short, to 0.5 m, not rhizomatous; **L** 90–110, erect, straight, coriaceous, narrowly lanceolate or narrowly elliptic, base narrowed to 2–3 cm, nearly flat to slightly canaliculate, long-acuminate, slightly folded towards the tip, rigidly coriaceous, often asperous on both faces, (0.6–) 0.9–1.2 (–2) m × (3–) 5–8 (–10) cm, light green to somewhat yellowish, opaque, margins straight between the teeth; **marginal teeth** triangular, straight or normally somewhat upcurved, 1.5–5 (–7) mm, 1–3 mm broad at the base, chestnut-brown to nearly black, on small deltoid bases, decurrent, 0.8–2 (–5) cm (0.4–1 (–1.5) cm at the leaf base) apart, lacking in the upper  $\frac{1}{3}$  –  $\frac{1}{4}$  of the leaf, **L** tip acute, not or inconspicuously mucronate for 1 mm; **Inf** 4–6 (–8) m, peduncle 3–4 m, glabrous, green, with triangular green **Bra** 20–30 cm long, fertile part narrowly fusiform, part-**Inf** 50–80, (20–) 40–70 (–120) cm, glabrous or pilose, ascending, in the upper  $\frac{1}{2}$  –  $\frac{2}{3}$  of the inflorescence, with 5–10 2.-order branches 10–25 (–30) cm long, rarely with 3.-order branches to 5 cm long, bulbiferous, bulbils conical, narrowly fusiform, bracteate to somewhat leafy, with leaves to 25–35 (–50) × 5–8 (–12) mm; **Ped** 2–6 (–10) mm; **Fl** single or 2–3 grouped together, campanulate, (25–) 32–40 (–47) mm; **Tep** elliptic, (12–) 14–20 (–27) mm, glabrous, whitish-green; **OTep** 3–7 mm broad; **ITep** 5–10 mm broad; **Fil** 8–12 (–20) mm, 1.5–2 mm broad at the base; **Anth** oblong, 2–4 mm, yellowish; **Ov** cylindrical, triquetrous, (13–) 18–20 × 3–4 mm; **Sty** (10–) 12–15 (–20) mm, 4–5 mm wide at the broadened base; **Sti** 3-lobate; **Fr** oblong, (25–) 30–35 (–50) × (16–) 25–30 mm, rostrate, base constricted, stipitate for 10 mm; **Se** winged for 1–2 mm, (8–) 9–11 (–12) × 5–7 (–9) mm, shiny.

Often confused with *F. hexapetala* and similar to the Mexican *F. cahum*, but differing from the latter in being smaller in all parts, including more and shorter leaves with smaller and fewer marginal spines, as well as glabrous inflorescence branches and flowers (Álvarez de Zayas 1996, García-Mendoza 2001a). Variable in leaf and flower characters, caused mainly by different

edaphic conditions. Reproduction is mainly asexual by bulbils (Álvarez de Zayas 1996).

**F. boliviensis** Ravenna (Pl. Life (Stanford) 34: 151–153, ill., 1978). **Type:** Bolivia, Cochabamba (Ravenna 2305 [Herb. Ravenna]). — **Lit:** Ullrich (1992). **Distr:** W & C Bolivia (Cochabamba, La Paz, Santa Cruz); infrequent on open rocky slopes in arid woodland, xeromorphic forests, and anthropogenic savannas, in partial shade, 1100–3500 m; flowers March to June.

[1] Stems short, stout, sometimes prostrate, 30–40 × 10–15 cm; **Ros** 0.9–1 (incl. stem) × 1–1.4 m; **L** numerous, linear-lanceolate, erect, often spreading, thick, rigid, narrowed near the base to 3.5–5.5 cm, moderately channelled, smooth, (45–) 60–95 × 8–9 (–11) cm, opaquely ash-green, margins dentate throughout; **marginal teeth** small, simple, uncinat, upcurved, fragile, 2–4 mm, 1–3 mm broad at the base, reddish, on small deltoid bases, 1.5–2 (–2.5) cm apart, near the base 1 cm; **terminal Sp** none, with weak, acute, reddish mucro 1–1.5 mm long; **Inf** 4–7.5 m, peduncle pale green to yellowish-green, velutinous, fertile part with velutinous part-**Inf** 30–40 cm long, with 1–3 green, velutinous 2.-order branches 10–15 cm long, bulbilliferous, bulbils conical, leafy, (20–) 40–50 × (8–) 12–18 mm, with 4–6 dentate small leaves; **Ped** 3–7 mm, velutinous; **Fl** single or geminate, 45–55 mm; **Tep** 25–30 mm, velutinous, whitish-green; **OTep** narrowly elliptic, 7–8 mm broad; **ITep** elliptic, 9–11 mm broad; **Fil** 13–14 mm, 3–4 mm wide at the broadened base; **Anth** oblong, 4 mm, yellow; **Ov** 20–25 × 3–5 mm; **Sty** 18 mm, 4 mm wide at the broadened base; **Fr** and **Se** unknown.

For long known from the sterile type specimen only, but meanwhile documented by further collections. The first complete description was provided by García-Mendoza (2001a). The species is characterized by leaves with small teeth, and velutinous peduncles, inflorescence branches and flowers, and leafy bulbils with dentate small leaves.

According to the protologue related to the Mexican *F. pubescens* and the Peruvian *F. andina* (here treated as synonym of *F. hexapetala*). Apart from *F. occidentalis* (with much smaller teeth)

*F. boliviensis* is the only native Bolivian species. Pino (2006) speculates that the species might also occur on the Peruvian altiplano.

**F. cabuya** Trelease (Ann. Jard. Bot. Buitenzorg 3(Suppl. 2): 906, tt. 36–37, 1910). **Type:** Costa Rica (Worthen & Dewey s.n. [MO]). — **Lit:** Lott & García-Mendoza (1994: online version with ills.); García-Mendoza (1998); Robbins (2001: online version with ills.). **Distr:** Honduras, W Nicaragua, Costa Rica, Panama; cultivated or naturalized in Mexico (Yucatán), Colombia and Venezuela; disturbed thorn forests, savannas and pine forests, (50–) 300–1800 m; flowers July to October.

[1] Stems none or to 0.5 (–1) m, covered with old leaves; **Ros** 2–3.5 m Ø; **L** 40, lanceolate, erect, coriaceous, semisucculent, abruptly narrowed above the base to ±5–8 cm, 4–6 cm thick at the base, openly concave, long acuminate, rough below, smooth above, (1–) 1.5–2 (–3) m × (10–) 15–20 (–22) cm, green, glaucous when young, above slightly glossy and rather pale-lined, margins often subrevolute, crenate, nearly straight between the teeth, sometimes with a corneous band from mid-leaf towards the base, **marginal teeth** deltoid, strong, upcurved, straight or recurved, 5–8 (–11) mm, 3–5 mm broad at the base, reddish chestnut-brown to blackish, decurrent on distinct deltoid herbaceous bases nearly 10 mm wide, (2.5–) 3–5 (–6) cm apart (2–4 cm near the leaf base), along the whole margin; **terminal Sp** conical, minute, 1–3 (–5) × 1–1.3 mm, chestnut- or dark brown; **Inf** 4–8 (–10 (–15)) m, peduncle much shorter than the fertile part, glabrous, green, with triangular or rhomboidal **Bra** 20–50 (–70) cm long, fertile part open, with part-**Inf** 45–70 (–100) cm long, with 8–13 2.-order branches (4–) 10–25 cm long, both glabrous or puberulent, rarely with 3.-order branches <2.5 cm long, sometimes bulbilliferous, bulbils ovoid to ovoid-conical, (20–) 60 × (15–) 50 mm, with 2–3 scarios green bracts; floral **Bra** 2–3 mm, puberulent; **Ped** glabrous, 3–7 (–12) mm, glabrous or pilose; **Fl** (37–) 40–55 (–62) mm, single or 2–3 (–6) grouped together; **Tep** (20–) 25–30 (–35) mm, whitish- to yellowish-green to white, glabrous, overlapping parts papillose; **OTep**

narrowly elliptic, 7–10 (–15) mm broad; **ITep** elliptic, 10–15 (–18) mm broad; **Fil** 11–16 mm, 1.5–3 mm wide at the broadened base; **Anth** oblong, 3–4.5 mm, yellowish; **Ov** cylindrical, 20–25 (–30) × 3–5 mm, glabrous, with a neck 9–10 mm long; **Sty** 15–22 mm, 4–5 mm wide at the broadened base; **Sti** papillose, 3-lobate; **Fr** oblong, shortly stipitate, 55–60 (–75) × (35–) 40–45 mm; **Se** winged for 3 mm, 15–17 × 9–10 mm, shiny.

Characterized by (20–) 30–50 widely separated teeth along the whole leaf margin, and flowers with an ovary 3–10 mm shorter than the tepal lobes. Similar to *F. hexapetala* in leaf size, the number of the widely separated teeth, and the diffusely branched inflorescence, but differing in its larger flowers, fruits and seeds (García-Mendoza 2001a). *F. cabuya* var. *integra* is placed in the synonymy of *F. foetida*.

The widely cultivated plant and its fibre are called “cabuya”, “cabuia”, or “cabulla”. Propagation is especially by rhizomatous offsets, and also by bulbils. In Costa Rica, the fibres were used to make twines, ropes, saddlebags, cinches, halters, and hammocks, often as household industry (Dewey 1943). Its inflorescence is the largest of any flowering plant.

**F. cahum** Trelease (Ann. Jard. Bot. Buitenzorg 3(Suppl. 2): 908, t. 39, 1910). **Type** [lecto]: Mexico, Yucatán (*Schott* 809 [F, BM, ILT, MO, US]). — **Lit**: Lott & García-Mendoza (1994: online version with ills.); García-Mendoza (1998). **Distr**: Mexico (Yucatán peninsula: Campeche, Quintana Róo, Yucatán); tropical semideciduous forests, to 150 m.

[1] Stems none or short, to 0.5 (–1) m; **Ros** 2–4 m Ø; **L** 60–80, erect, linear-lanceolate, coriaceous, narrowed to 2.5–3.5 cm above the base and 1.5–2.5 cm thick, long acuminate, flat below, concave, keeled, with prominent venation, smooth, (1.3–) 1.6–2.2 (–2.5) m × (5–) 6–10 (–11.5) cm, bright to brilliant green, margins ± straight between the teeth, dentate to dentate-corneous below, yellowish to dark reddish; **marginal teeth** rather strong, upcurved or straight, rarely geminate, 2–4 (–5) mm, 2–3 (–4) mm wide at the base, reddish, brown or dark brown to black,

decurent on small deltoid bases, 1.5–3 (–4 (–6)) cm apart at mid-leaf, 0.5–1 (–2) cm near the base, absent for the upper ¼ – ½; **terminal Sp** conical, corneous, acute, 1.5–6 × 1.5–2.5 mm, blackish chestnut-brown or reddish; **Inf** (4–) 5–8 (–11) m, peduncle to (3.5–) 5–8 m, green, glabrous, with long triangular, green, puberulent to pilose **Bra** 30–65 cm long, fertile part oblong, in the upper ¼ – ½, with 40–50 part-**Inf** 50–80 cm long, with 5–8 2.-order branches 5–30 cm long, lower rarely with 3.-order branches to 12 cm long, all puberulent to pilose, freely bulbiferous, bulbils bracteate to somewhat foliose, conical, (15–) 20–28 (–40) × 4–8 (–13) mm, with (2–) 3 deltoid green bracts, small leaves 1–3 cm; floral **Bra** deltoid, 3 mm, puberulent, brown; **Ped** 4–6 (–10) mm, puberulent; **FI** (35–) 40–45 (–52) mm, single or 2–3 (–4) grouped together, minutely papillose-puberulent; **Tep** 17–20 (–25) mm; **OTep** lanceolate-elliptic, (3–) 7–9 mm broad, glabrescent to glabrous; **ITep** elliptic, (4–) 8–12 mm broad, pilose to glabrescent on the midrib, papillose in the area of overlap, yellowish-green on the outer face, whitish within; **Fil** 10–14 mm, 2.5–4 mm wide at the broadened base, somewhat papillose; **Anth** oblong, centric, sagittate, 3.5–3.7 mm, yellow; **Ov** cylindrical, 20–27 × 3–6 mm, puberulent, neck 5–10 mm; **Sty** 14–19 mm, 7–8 mm wide at the broadened base, 3-sulcate, somewhat papillose; **Sti** 3-lobate; **Fr** oblong, stipitate for 10–13 mm, beaked for 5–8 mm, pilose, (35–) 40–50 × (25–) 30–35 mm; **Se** broadly winged for 2–4 mm, 9–12 (–13) × 5–8 mm, shiny.

The species (vernacular names: “cahum”, “cajum”, “cahun” and “cajum-ci”) was widely cultivated for fibre, but has now apparently been abandoned (García-Mendoza 2001a). It is characterized by large, linear-lanceolate leaves, small and closely spaced teeth absent in the upper ¼ or ½ of the leaves, oblong inflorescences with long peduncles occupying ⅔ of its length, and flowers which are puberulent when young, becoming glabrescent when maturing (García-Mendoza 1998, García-Mendoza 2001a).

**F. depauperata** Jacobi (Hamburg. Gart.- & Blumenzeit. 22: 411, 1866). **Type**: not typified. — **Distr**: Cultivated only.



**Incl.** *Furcraea macra* Hort. Parmentier ex Jacobi (1866) (*nom. inval.*, ICN Art. 36.1, 38.1).

[1] Stems none; **L** 15–20, lanceolate, apparently ascending, thin, coriaceous, moderately firm, 33–46 × 5–5.7 cm, dull green, much narrowed towards the base and there ±1.3 cm broad, narrowed towards the apex into a terete, fleshy tip later drying off, both faces smooth or also scabrous, lower ½ longitudinally grooved and below angularly arched and roundly keeled, towards the apex slightly arched, with several keels, with imprints of the next older leaves, margins wavy curved in the lower part, straight in the upper part, continuous, very thin and somewhat remotely toothed; **marginal teeth** small, on deltoid cartilaginous whitish-green bases, with chestnut-brown upcurved tip, 1–1.5 cm apart; **Inf** with peduncle 0.9–1.5 m, smooth, fertile part rhomboid, with spreading, somewhat flattened, 10 cm long part-**Inf**, bulbiferous; **Ped** short, articulated; **Fl** (25–) 30–35 × 32 mm, single; **OTep** lanceolate, 35 × 9–10 mm, tip nearly cucullate and with a tuft of white hairs within, finely puberulent on both faces, whitish-green; **ITep** ovate-elliptic, 38 × 12–16 mm, finely puberulent on both faces, light green turning whitish towards the margins; **Fil** 15–18 mm, 4 mm wide at the broadened base; **Ov** cylindrical, inconspicuously trigonous, with 6 flat furrows, 25 mm, whitish-puberulent, pale green; **Fr** and **Se** unknown.

This long-forgotten name was re-established by Govaerts (2014+), while García-Mendoza (2001a) lists it among the insufficiently known species. Jacobi obtained his material from the Belgian nurseryman Bedinghaus as *F. tuberosa* and noted that it was cultivated in gardens under the unpublished name *F. macra*. *F. depauperata* is only known from its protologue but appears well characterized, and cannot be reliably equated with any other presently known species. It might, however, represent a depauperate pot-cultivated *F. undulata* which likewise has wavy leaf margins and pubescent tepals and ovaries. Depauperate cultivated *F. undulata* are indeed similar in their dimensions (Baker 1892: as *F. pubescens*).

**F. foetida** (Linné) Haworth (Synops. Pl. Succ., 73, 1812). **Type:** [lecto — icono]: Commelin,

Hort. Med. Amstelod. Pl. Rar. 2: 35, t. 18, 1701. — **Lit:** Verhoek & Hess (2002); Guillot Ortiz & Meer (2010); Crouch & Smith (2011); all with ills. **Distr:** USA (Florida), Mexico (Yucatán), C America (Costa Rica, Panama?), Greater and Lesser Antilles, Trinidad, N South America (Colombia, Venezuela, Bolivia, French Guiana, Guyana, Suriname, Brazil); cultivated or naturalized; widely cultivated and naturalized in Africa, Asia and the Pacific and Indian Ocean Islands, to 2000 m; flowers any time but mainly July to September. **I:** Curtis's Bot. Mag. 48: t. 2250, 1821, as *F. gigantea*; Curtis's Bot. Mag. 107: t. 6543, 1881, as *F. cubensis* var. *inermis*; Trelease (1910: tt. 35, 46–48); Irish & Irish (2000: tt. 61–62); Wilcox (2005).

≡ *Agave foetida* Linné (1753) ≡ *Aloe foetida* (Linné) Crantz (1766); **incl.** *Agave foetida* Aublet (1775) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave foetida* Lamarck (1784) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea gigantea* Ventenat (1793) ≡ *Agave gigantea* (Ventenat) D. Dietrich (1840) (*nom. illeg.*, ICN Art. 53.1) ≡ *Furcroya gigantea* (Ventenat) Hooker (1860); **incl.** *Funium pitiferum* Willemet (1796); **incl.** *Furcraea madagascariensis* Haworth (1819) ≡ *Agave madagascariensis* (Haworth) Salm-Dyck (1822); **incl.** *Furcraea tuberosa* Hasskarl (1856) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea tuberosa* Hort. Belg. (1860) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea atroviridis* Jacobi & Goeppert (1866); **incl.** *Furcraea barillettii* Jacobi (1869); **incl.** *Agave bulbosa* W. Bull (1871); **incl.** *Agave bulbosa* K. Koch (1871) (*incorrect name*, ICN Art. 6.3); **incl.** *Furcraea cubensis* var. *inermis* Baker (1881); **incl.** *Furcraea viridis* Hemsley (1884) (*nom. inval.*, ICN Art. 61.1); **incl.** *Furcraea watsoniana* Hort. Sander (1898) ≡ *Furcraea gigantea* var. *watsoniana* (Hort. Sander) Drummond (1907) (*nom. inval.*, ICN Art. 11.4); **incl.** *Furcraea altissima* Franceschi & al. (1900) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea cabuya* var. *integra* Trelease (1910); **incl.** *Furcraea gigantea* [?] *mediopicta* Trelease (1910); **incl.** *Furcraea gigantea* [?] *variegata* hort. ex Trelease (1910); **incl.** *Furcraea gigantea* var. *mediopicta* Trelease (1915); **incl.** *Furcraea variegata* hort. ex Trelease (1915); **incl.** *Furcraea foetida* 'Mediopicta'

Trelease *ex* L. H. Bailey & E. Z. Bailey (1976); **incl.** *Furcraea foetida* ‘Striata’ Piens (1996).

[1] Stems none or short, to 0.5–1 m × 20–30 cm; **Ros** 2.5–3.5 m Ø; **L** to 50 cm (75–150 cm in aged plants), broadly lanceolate or linear-lanceolate to oblanceolate, erect, outermost sometimes recurving, thick, rigid, firm, narrowing distinctly in the lower ½ to about 10 cm near the base, ± flat, keeled, concave towards the base, at the base (4–) 6–10 cm broad, smooth or obsolescently striate, 1.5–2 (–2.5) m × (9–) 14–21 (–25) cm, shiny to verdant green to yellow-green, apex channelled dorsally, hardened, flattened and folded, sometimes corneous, conical, 1–2 (–3) mm, reddish, margins hard, smooth, usually entire at least in the distal ½, straight or somewhat wavy, sometimes basally with 4–7 trigonous upcurved teeth 1–3 mm long, otherwise unarmed; **Inf** (4–) 8–10 (–12) m, peduncle 1–1.5 m, green, glabrous, with rhomboidal **Bra** 30–40 cm long, fertile part ± rhomboidal to broadly pyramidal, rather narrow, lax, occupying most of the inflorescence, with 40–60 part-**Inf** 1–2 m long, the lower richly branched, glabrous, with 4–13 2.-order branches 15–30 cm long, glabrous or somewhat pilose, scarcely to freely bulbiferous, bulbils foliose, ovoid, sometimes conical, 25–30 (–45) × 5–10 (–15) mm, with 3–5 papyraceous or chartaceous bracts and 3–4 (–5) small leaves; **Ped** 3–7 (–12) mm, glabrous; **Fl** (35–) 40–45 (–50 (–57)) mm, single or 2–3 (–5) grouped together, scented; **Tep** 20–25 (–30) mm, glabrous, whitish-green, yellowish-green, or pale blue-green; **OTep** narrowly elliptic, 5–10 mm broad; **ITep** broadly elliptic, (8–) 10–15 mm broad; **Fil** 11–14 mm, 2–4 mm wide at the broadened base; **Anth** oblong, 2–3 mm; **Ov** cylindrical, glabrous, (12–) 15–25 (–30) × 2–3 (–5) mm; **Sty** 15–16 mm, 2–4 mm wide at the broadened base, 3-lobed up to the middle; **Sti** 3-lobed; **Fr** and **Se** not described (but “infrequently produced” according to Crouch & Smith 2011); **Se** “usually not formed” (l.c.). — **Cytology**: 2n = 60 (Whitaker 1934, Satô 1935: as *F. gigantea*).

Cultivated worldwide in (sub-) tropical regions for fibre (Dewey 1943) and often naturalized. Vernacular names: “cañamo” (Bolivia), “piteira”

(Brazil), “cabuya cimarrona” (Colombia), “cabuya blanca”, “cabuya olancho”, “cabuya sin espinas”, “cabulla” (Costa Rica), “cocuiza”, “cocuiza mansa” (Venezuela) (García-Mendoza 2001a). Characterized by solid green, slightly glossy leaves with a smooth, unarmed and often wavy margin, and a soft tip. It differs from *F. selloana* in its smooth leaves with margins unarmed or only armed up to mid-leaf. According to Lott & García-Mendoza (1994) not reliably known from Mesoamerica, but García-Mendoza (2001a) later cited specimens from the Mesoamerican countries as given above.

The synonym *F. viridis* is a spelling error for *F. atroviridis*. *F. cubensis* var. *inermis* and *F. cabuya* var. *integra* refer to variants with (nearly) completely toothless leaf margins placed here by García-Mendoza (2001a). *Furcraea* ‘Castilla’, a cultivar with toothless leaf margins cultivated in Colombia esp. around Antioquia (Pérez Mejía 1974), likewise appears to belong here. *F. watsoniana*, *F. variegata*, ‘Mediopicta’, and ‘Striata’ are variegated forms grown as ornamentals.

*F. nana* (Hochstätter 2016) is an invalidly published species that appears closely related to *F. foetida*, differing by smaller size and entire leaf margins.

**F. geminispina** Jacobi (Hamburg. Gart.- & Blumenzeit. 22: 358–359, 1866). **Type**: not typified. — **Lit**: Álvarez de Zayas (1996: with ill., as *F. tuberosa*). **Dist**: Bahamas (Acklins, Cat Island, Inagua), Turks and Caicos Islands (South Caicos), Cuba (Camagüey, Holguín, Guantánamo), C & N Haiti, Dominican Republic (?); frequent in secondary habitats near roads or settlements, 700–900 m (Cuba); flowers July to September.

≡ *Furcraea tuberosa* var. *geminispina* (Jacobi) Trelease (1927); **incl.** *Agave tuberosa* var. *β spinis duplicibus* Aiton (1789) (*nom. inval.*, ICN Art. 23.1).

[1] Stems none or short, to 0.3 m; **L** up to 60, lanceolate, erect, subcoriaceous, moderately flat, 2.5 cm broad at the base, scabrous below, smooth above, 1–1.6 (–1.8) m × (7–) 10–15 (–17) cm, shiny green, margins straight, dentate, sometimes corneous towards the base; **marginal teeth** simple, upcurved, 5–10 of them geminate, uncinat,

large, strong, 5–8 (–10) mm, 3–5 (–7) mm broad at the base, on small bases, 3.5–6 cm apart, reddish, **L** tip an acute mucro 2–5 mm long, chestnut-brown; **Inf** 5–7 m, peduncle short, green, **Bra** unknown, fertile part fusiform, lax, in the upper  $\frac{3}{4}$  of the inflorescence, part-**Inf** 30, 50–80 cm, with 2–4 2.-order branches (6–) 15–30 cm long, both pilose, green, bulbiferous, bulbils ovoid, bracteate or rarely foliose, 20–30 (–45)  $\times$  10–15 (–20) mm, with 2–3 scarious green bracts; **Ped** 5–10 mm, somewhat pilose; **Fl** 45–55 (–60) mm, single or 2 grouped together; **Tep** 25–30 (–33) mm, glabrous, whitish-greenish; **OTep** narrowly elliptic, (6–) 8–10 mm; **ITep** (9–) 11–13 mm; **Fil** 11–13 mm, 1.5–2 mm wide at the broadened base; **Anth** oblong, 2.5–3 mm, yellow; **Ov** cylindrical, 20–25  $\times$  3–4 mm; **Sty** 16–18 mm, 4–5 mm wide at the broadened base; **Fr** and **Se** unknown.

The first edition of this handbook and many authors placed this name in the synonymy of *F. tuberosa* (Drummond 1907, Álvarez de Zayas 1996, Smith & Figueiredo 2012), or *F. acaulis* (Dewey 1943, Pérez Mejía 1974, Ullrich 1992), while García-Mendoza (2001a) choose to re-establish the taxon as separate species for Caribbean material with geminate leaf margin teeth (as opposed to *F. tuberosa* with single teeth). *F. geminispina* is similar to *F. hexapetala* in size and armature of the leaves as well as the size of flowers and bulbils.

**F. guatemalensis** Trelease (Trans. Acad. Sci. St. Louis 23(3): 149, t. 32, 1915b). **Type:** Guatemala (Trelease 23 [ILL]). — **Lit:** Trelease (1915b: t. 35, as *F. melanodonta*); Standley & Steyermark (1952: with ill., as *F. melanodonta*); Lott & García-Mendoza (1994: online version with ill.); García-Mendoza (1998). **Dist:** Guatemala (Alta Verapaz, Baja Verapaz, Guatemala, El Progreso, Quetzaltenango, Sololá), Honduras (Comayagua, El Paraíso, Intibucá, Morazán), Nicaragua, El Salvador (Ahuachapán, Santa Ana, San Salvador, San Vicente); open hillsides, dry rocky hills and slopes, in ecotones of pine-oak forests to tropical deciduous forests, commonly planted in hedges or fence rows, 700–2750 m; flowers late June to August. **I:** Meer (2014a).

**Incl.** *Furcraea melanodonta* Trelease (1915).

[1] Stems short, 0.7–1.2  $\times$  0.3–0.6 m, simple; **Ros** 2–3 m  $\varnothing$ ; **L** 60–100, lanceolate, erect, coriaceous, narrowed at the base to 6.5–8.5 cm, base 5–10 cm thick, tip acute, moderately concave, keeled, rough below, mostly smooth or occasionally rough above, (1.5–) 2–2.5 m  $\times$  15–20 (–25) cm, dark green, margins dentate, crenate, sometimes forming a corneous band towards the base; **marginal teeth** simple, upcurved or straight, strong, (4–) 6–10 mm, 3–6 mm broad at the base, chestnut-brown, dark reddish or blackish, 1.5–3 (–5) cm apart (1–2 (–4) cm low down), uppermost 10–30 cm toothless, decurrent on deltoid bases; **terminal Sp** conical, mucronate, 0.5–1 (–4) mm, chestnut-brown; **Inf** 5–8 m, peduncle 1–2 m, green, glabrous, with narrowly triangular, toothed, mucronate, green **Bra** 40–80 cm long, fertile part dense, pyramidal to rhomboidal, glabrous, in the upper  $\frac{3}{4}$  of the inflorescence, part-**Inf** 40–90, 1.5–2 m, 2.-order branches (15–) 20–40 (–60) cm, sometimes with 3.-order branches 3–19 cm long, all with rapidly deciduous bracts, bulbiferous, bulbils broadly ovate, 25–30  $\times$  20–25 (–30) mm, green, covered with 3–5 bracts; fertile **Bra** much shorter than the pedicels; **Ped** 4–10 mm, glabrous; **Fl** (40–) 45–50 (–55) mm, single or 2–3 grouped together; **Tep** elliptic, yellowish-green with whitish margins, glabrous; **OTep** 22–25 (–30)  $\times$  6–9 (–12) mm; **ITep** 24–30 (–35)  $\times$  10–15 (–20) mm; **Fil** 10–15 mm, 3–4 mm wide at the broadened base, papillose, yellowish; **Anth** oblong, base sagittate, 2–4 mm, yellow; **Ov** cylindrical, 20–25  $\times$  3–5 mm, greenish, glabrous, neck not mentioned; **Sty** 17–20 mm, 4–6 mm wide at the broadened base, 3-sulcate; **Sti** papillose, 3-lobate; **Fr** pear-shaped, stipitate for 12–15 mm, beaked, (40–) 50–70  $\times$  35–50 mm; **Se** winged for 4–6 mm, 16–18  $\times$  8–10 mm, shiny.

The species is characterized by its stems <1.2 m high, its large leaves which are rough below, its large, massive, dense, glabrous inflorescences with glabrous flowers and broadly ovate bulbils (García-Mendoza 1998, García-Mendoza 2001a). Vernacular names: “ikaj”, “kaq ik’e”, “maguey rojo”, “maguey”, “churr”, “pita”, or “kima” (Guatemala), “maguey” or “magueyón

macho" (El Salvador), "maguey" (Honduras) (García-Mendoza 2001a). More widely used in the past when it was planted as hedges for harvesting fibres for making ropes and backpacks. Currently, plants survive near houses where they are used apparently at low levels.

Standley & Steyermark (1952) expressed doubts whether *F. melanodonta* can be separated from *F. guatemalensis*, and Lott & García-Mendoza (1994) and subsequent authors treat the name as a straightforward synonym. Material from Mexico (Chiapas) is no longer thought to belong here by García-Mendoza (2001a) but was tentatively assigned to 2 species new to describe.

**F. hexapetala** (Jacquin) Urban (Symb. Antill., 4: 152, 1903). **Type** [neo]: Cuba, La Habana (Jacquin s.n. [BM]). — **Lit**: Britton & Millspaugh (1920: as *F. macrophylla*); Correll & Correll (1982: with ills., as *F. macrophylla*); Álvarez de Zayas (1996: with ills.); Proctor (2012). **Distr**: Bermuda, Bahamas, W Cuba (Cienfuegos, Ciudad Habana, Habana, Matanzas, Pinar del Río), Jamaica, Cayman Islands, Peru; on Cuba in semi-deciduous forests and xeromorphic scrub on serpentine, esp. abundant at anthropogenic sites, to 750 (–1250) m; flowers any time of the year but mainly August to January. **I**: Hooker's Icon. Pl. 26: t. 2501, 1899, as *F. macrophylla*; Trelease (1910: t. 37, as *F. macrophylla*; t. 41, as *F. cubensis*); Curtis's Bot. Mag. 138: t. 8461, 1912, as *F. elegans*.

≡ *Agave hexapetala* Jacquin (1760); **incl.** *Agave aspera* Jacquin (1762) ≡ *Furcraea aspera* (Jacquin) M. Roemer (1847); **incl.** *Agave cubensis* Jacquin (1763) ≡ *Furcraea cubensis* (Jacquin) Ventenat (1793) ≡ *Furcroya cubensis* (Jacquin) Ventenat (1796) (*incorrect name*, ICN Art. 11.4); **incl.** *Agave odorata* Persoon (1805); **incl.** *Furcraea agavephylla* Brotero ex Schultes (1829); **incl.** *Furcraea valleculeata* Jacobi (1867); **incl.** *Furcraea elegans* Todaro (1876); **incl.** *Furcraea ghiesbreghtii* Hort. Verschaffelt ex Todaro (1876) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Furcraea pugioniformis* Hort. Verschaffelt ex Todaro (1876) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Furcraea macrophylla* Baker (1899); **incl.** *Furcraea deledevantii* Rivière (1902); **incl.**

*Furcraea deledevantii* Rivière (1902) (*nom. inval.*, ICN Art. 61.1); **incl.** *Furcraea altissima* Todaro ex Borzi (1909) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea andina* Trelease (1915); **incl.** *Furcraea altissima* hort. ex Trelease (1915) (*nom. illeg.*, ICN Art. 53.1).

[1] Stems none or short, to 0.5 m; **L** 60–80, lanceolate, erect, straight, coriaceous, gradually narrowed to 2–7 cm above the broadened base, flat or slightly canaliculate, slightly scabrous below, smooth above, 1–1.6 (–2) m × (5.5–) 8–12 (–20) cm, bright green, lustrous, margins dentate, crenate, sometimes corneous towards the base; **marginal teeth** simple, straight or upcurved, sometimes with some recurved smaller teeth near the base, 5–8 (–11) mm, (3–) 4–7 mm broad at the base, decurrent on small deltoid bases, 3–6 (–10) cm apart, blackish to reddish, **terminal Sp** canaliculate, acute, mucronate, 2–3 mm, sometimes lacking, chestnut-brown; **Inf** 6–8 m, peduncle 1–1.5 (–2) m, glabrous, green, with triangular, green **Bra** 15 cm long, fertile part rhomboidal, diffusely branched, open, in the upper  $\frac{3}{4}$  to nearly the whole inflorescence, with 30–40 part-**Inf** (0.5–) 1–1.5 (–2) m long, pilose or glabrous, with 3–9 (–15) 2.-order branches 10–40 cm long, pilose, green, rarely with 3.-order branches <1 cm long, glabrous, bulbiferous, bulbils ovoid, 20–35 (–50) × 15–20 (–25) mm, green, with 2–3 scarious bracts; **Ped** 3–7 mm, pilose; **Fl** 40–50 (–55) mm, single or 2–3 grouped together; **Tep** 25–30 mm, glabrous, whitish or whitish-greenish; **OTep** narrowly elliptic, 7–10 mm broad; **ITep** elliptic, 9–13 mm broad; **Fil** 10–13 mm, 1.5–2 mm wide at the broadened base; **Anth** oblong, 2–3 mm, yellow; **Ov** cylindrical, 17–20 × 3–4 mm; **Sty** 15–18 mm, 4–5 mm wide at the broadened base; **Sti** minute, 3-lobate; **Fr** ovoid to oblong, 30–50 × 25–40 mm, base constricted and deeply sulcate, tip beaked; **Se** flat, winged for 2 mm, 11–13 × 6–7 mm, shiny. — **Cytology**: 2n = 60 (Cave 1964: as *F. andina*, Fritsch 1970).

Characterized by large and remote teeth along the whole leaf margin, rhomboidal inflorescences with few part-inflorescences in the upper  $\frac{3}{4}$  to nearly the whole inflorescence, flowers with very narrow tepals and a very short ovary much shorter

than the tepals (García-Mendoza 2001a). Older literature mostly uses the names *F. cubensis* (described from Cuba) or *F. macrophylla* (described from the Bahamas). The occurrence in places not given above, e.g. Colombia, needs verification. *F. andina* from Peru is considered to be native to that country by the majority of authors, and is cultivated for fibre as “Fique” in Ecuador, Peru and Colombia, where it represents the Colombian national fibre (Kluge 2016). It is here included in the synonymy by García-Mendoza (2001a) due to the lack of clear morphological differences. ‘Marginata’ is a cultivar with yellow-margined variegated leaves (Meer 2014b).

**F. longaeva** Karwinsky & Zuccarini (Flora 15: 2 (Beiblatt 2): 94–95, 1832). **Type:** [neo — icono]: Acta Acad. Leop.-Carol. Nat. Cur. 16(2): t. 48, 1833. — **Lit:** Ullrich (1991b); García-Mendoza (2001b); David (2009); Guillot Ortiz & Meer (2010); García-Mendoza (2011); all with ills. **Distr:** Mexico (S Puebla, Oaxaca); open mountain slopes in rosette scrub on stony igneous soils, 2200–3100 m; flowers February to May, but also August. **I:** Curtis’s Bot. Mag. 91: t. 5519, 1865; Trelease (1915b: t. 28); Phillips (2013).

**Incl.** *Furcraea longa* J. J. Smith (1897) (*nom. inval.*, ICN Art. 61.1?).

[2] Arborescent, stems erect, thick, simple, 3–6 (–9) × 0.4–0.7 m, bark violet-red, with a single terminal **Ros** with 150–300 leaves; spent leaves forming a dry skirt below the rosette, other **L** erect, linear-lanceolate, concave, keeled below, long acuminate, narrowed at the base to 5–8 (–11) cm, base 5–7 cm thick, smooth on both faces or below at the apex slightly scabrous, 1.2–1.6 m × 10–14 (–17) cm, dark green, margin finely denticulate, 12–27 denticles per cm, on a yellowish-green band, leaf tip hardened from the involute leaf margin, dry, deciduous; **Inf** erect, 3–6 (–9 (–13)) m, peduncle 0.3–1 m, green, glabrous, with deltoid brown-violet **Bra** 50–90 cm long, fertile part pyramidal, part-**Inf** 60–100, horizontal, 0.8–1 m, glabrous or pilose, yellowish-green, 2.-order branches 30–50, 10–30 cm, pendent, pilose or glabrous, 3.-order branches 5–15 cm, pilose, rarely with 4.-order branches to 4 cm, without bulbils; floral **Bra** inconspicuous,

much shorter than the pedicels; **Ped** 2–5 (–10) mm, pilose or glabrous; **Fl** (25–) 30–35 mm, 3–6 grouped together; **Tep** 15–20 mm; **OTep** narrowly elliptic, 4–6 mm broad, pubescent outside; **ITep** elliptic, 5–10 mm broad, pubescent on the midrib in the area of overlap, whitish-yellowish or yellowish-orange during senescence; **Fil** 8–11 mm, 1.5–3.5 mm wide at the broadened papillose base, whitish; **Anth** linear-oblong, slightly excentric, 2.2–6 mm, yellow-orange; **Ov** cylindrical, (10–) 15–20 × 2–5 mm, green, puberulent, neck 1–2 mm; **Sty** 10–17 mm, 2.5–4.5 mm wide at the broadened base, deeply 3-lobed, papillose, whitish; **Sti** 3-lobate, ciliate; **Fr** subglobose or oblong, rostrate, (35–) 40–50 × 25–30 (–35) mm, yellowish-green, rostrate for 3–6 (–10) mm, stipitate for up to 15 mm, tepals persisting; **Se** winged for 1 mm, 9–10 × 7–8 mm, shiny.

Easy to recognize by the large, linear-lanceolate, dark green leaves and the inflorescence without bulbils and with 3.- and 4.-order branches (García-Mendoza 2001b). Differs from its closest relative *F. parmentieri* in being larger in all parts except its flowers, in having inflorescences without bulbils, and in occurring in drier habitats (García-Mendoza 1998). The place of valid publication (usually thought to be in 1833) was clarified by Ullrich (1991b) who also selected a neotype (as ‘lectotype’).

Vernacular names: “pescadillo”, “tehuizote”, “palma”, “palmita”, “palmilla”, “yacktobiyack”, “yahuindayasi”, “la-fo-má-é”, and “pita”. The foam from crushed and washed fresh leaves is used for washing clothes, the dry leaves for making ropes, the flowers as fodder, and the dry stems for bee-keeping (García-Mendoza 1998, García-Mendoza 2001a, García-Mendoza 2001b).

The species was attributed to Guatemala by Skinner in Bateman (1837–1843: t. 16), but this appears to be a confusion with *F. quicheensis* (Lott & García-Mendoza 1994). Standley & Steyermark (1952) cite a collection made from a cultivated plant in Europe by Berger with a purported origin from Guatemala. There is at present no reliable record of the species from Guatemala (Lott & García-Mendoza 1994). Records from Guerrero



(Ullrich 1991b, García-Mendoza 1998) appear to represent *F. martinezii*.

With a maximum size of 13 m, the species exhibits the largest inflorescences of any plant according to Verhoek-Williams (1998), but it is superseded by *F. cabuya*, for which Robbins (2001) mentions 15 m. An inflorescence may have more than 58'000 flowers (García-Mendoza 2001a). In habitat, according to local Indians cited in the protologue, the species needs 400 years to come into flower. A more likely time span is between 50 and 100 years (García-Mendoza 1998). In cultivation, plants may flower already after 25 (or perhaps even 7 or 8?) years (Ullrich 1991b).

**F. macdougallii** Matuda (Cact. Suc. Mex. 1 (2): 24–26, ills., 1955). **Type:** Mexico, Oaxaca (*MacDougall* 269 [MEXU, MEXU]). — **Lit:** García-Mendoza (2001b); García-Mendoza (2003b: with ill.); García-Mendoza (2011). **Distr:** Mexico (S Puebla, W & C Oaxaca); tropical deciduous and thorn forests on calcareous soils, and cultivated, 750–1800 m; flowers September to December. **I:** Irish & Irish (2000: t. 63); Meer (2014c).

[1] Arborescent, stems erect, simple but offsetting from along fallen stems or old stem bases, 6–9 m, 30–70 cm Ø, bark reddish; **Ros** single at the stem tips, 4–6 m Ø, with 80–120 leaves, with a skirt formed by dry leaves; **L** erect, linear, in young plants pointing upwards, in old plants spreading in all directions, coriaceous, keeled, narrowed at the base to 4–7 cm, base to 8 cm thick, scabrous on both faces, papillose, 1.4–1.8 (–2) m × 6–10 cm, dark green to dull olive-green or yellowish-green, tip hard, sometimes with a 1 mm long mucro, reddish or yellowish, margin dentate-corneous or dentate-denticulate; **marginal teeth** 2–4 × 3–4 mm at the base, upcurved, reddish with yellowing base or brownish, separated by (1–) 2–5 cm at mid-leaf, and by 0.5–2 cm in the lower 1/3, denticulate between the teeth; **Inf** erect, 5–9 m, peduncle 1.5–3.5 m, green, glabrous, with triangular, semi-fleshy, dentate, green **Bra** 30–65 cm long, fertile part in the upper 1/2 of the inflorescence, rhomboidal, part-**Inf** 40–70, 1–1.5 m, glabrous to somewhat puberulent, 2.-order

branches 9–20, (6–) 15–30 cm, puberulent to tomentose, rarely with 3.-order branches to 15 cm, tomentose, bulbiferous, bulbils conical, 40–70 (–85) × 12–16 mm, with 5–8 deltoid bracts, those near the base scarious and deciduous; floral **Bra** inconspicuous, scarious; **Ped** 2–6 (–10) mm, puberulent; **Fl** 35–40 mm, 2–4 grouped together; **Tep** narrowly elliptic, 15–20 mm; **OTep** 3–4 (–6) mm broad, pilose outside; **ITep** 4–6 (–8) mm broad, pilose on the midrib, papillose in the area of overlap, whitish outside, yellowish within; **Fil** 9–12 mm, 2–3 mm wide at the broadened base, papillose, yellowish; **Anth** oblong, 2–2.5 × 1.5 mm, yellow; **Ov** cylindrical, 13–23 × 2–3 mm, yellowish-green, puberulent, neck 5–8 mm, glabrescent; **Sty** 13–16 mm, 3–4 mm wide at the broadened base, 3-sulcate, papillose; **Sti** superficially 3-lobate; **Fr** oblong, stipitate for 20–23 mm, rostrate for 5 mm, 40–50 × 30–35 mm; **Se** plane-convex, winged for 1–2 mm, 11–13 × 7–9 mm, shiny.

Recognizable by linear leaves with scabrous faces and dentate-corneous or dentate-denticulate margins, and conical bulbils (García-Mendoza 2001a, García-Mendoza 2001b). The thick terminal spine mentioned in the protologue was not found in the material seen by García-Mendoza (2001a). The species is apparently extinct in nature and survives in cultivation only at the Puebla/Oaxaca border (García-Mendoza l.c.), but is also commercially available in the US-American nursery trade. García-Mendoza (2003a) reports that a single inflorescence produced >15'000 bulbils, which persisted even after the plant has died. Two sterile collections from Chiapas by Matuda first provisionally placed here by Lott & García-Mendoza (1994) and García-Mendoza (1998) were later placed in a new, apparently closely related species, *F. niquivilensis*.

**F. martinezii** García-Mendoza & L. de la Rosa (Bol. Soc. Bot. México 66: 121–123, ills., 2001b). **Type:** Mexico, Guerrero (*García-Mendoza & de la Rosa* 6526 [MEXU etc.]). — **Lit:** García-Mendoza (2003a: with ills.). **Distr:** Mexico (C Guerrero); on sandy soils derived from volcanic ash in montane pine-oak cloud forest, 2000–2650 m; flowers April to May.

[2] Arborescent, stems erect, 2–4 (–8) m, simple, 0.3–0.4 m  $\varnothing$ ; **Ros** single at the stem tip, with (100–) 150–200 leaves and a skirt formed by dry leaves; **L** linear to linear-lanceolate, narrowed at the base to 4–6 cm, base 4–5 mm thick, smooth above, below slightly scabrous at the hard deciduous tip, (0.9–) 1.2–1.6 m  $\times$  6–10 cm, dark green, margin denticulate, 15–19 denticles per cm, on a greenish-yellow band; **Inf** erect, 6–8 m, peduncle 0.5–1.5 m, green, glabrous, with deltoid, denticulate, brownish **Bra** 40  $\times$  4–7 cm, fertile part pyramidal, with 100–200 part-**Inf** 1–1.5 (–2) m long, green, glabrous, 2.-order branches 10–25 cm long, rarely with 3.-order branches 3–7 cm long, bulbiferous, bulbils leafy, ovoid, 25–45  $\times$  15–35 mm, covered with leafy reddish bracts; floral **Bra** inconspicuous, much shorter than the pedicel; **Ped** 4–6 mm, glabrous; **Fl** 25–32 mm, 3–4 grouped together; **Tep** 12–16 mm, whitish-green outside, whitish within, puberulent at the base; **OTep** narrowly elliptic, 3–4 (–6) mm broad; **ITep** elliptic, 5–7 (–8) mm broad; **Fil** 9–11 mm, 2–3 mm wide at the thickened papillose base, whitish; **Anth** oblong, 2.5–3 mm, yellow; **Ov** cylindrical, 13–15  $\times$  3–4 mm, green, puberulent, neck 1–2 mm, sometimes puberulent; **Sty** 9–12 (–16) mm, 3–4.5 mm wide at the broadened base, truncate, deeply trisulcate, papillose, whitish; **Sti** 3-lobate; **Fr** subglobose to oblong, 35–45 (–50)  $\times$  30–40 mm, yellowish-green, stipitate for up to 15 mm, rostrate for 4–6 mm; **Se** winged for 2 mm, 11–12 (–14)  $\times$  7–8 (–9) mm, shiny.

Only known from 3 populations consisting of few, mainly adult individuals (García-Mendoza 2001a). Similar to *F. longaeva* with which it shares the long stem, large rosettes and a pyramidal inflorescence with up to 3.-order branches, but differing by narrower leaves, smaller flowers, larger seeds, and leafy bulbils. Records of *F. longaeva* from Guerrero belong here. A specimen which flowered at the botanical garden of Mexico City was estimated to be 40 to 60 years old, had an annual stem growth of 4–8 cm, and the inflorescence was estimated to have  $\pm$  20'000 to 30'000 flowers (García-Mendoza 2003a).

**F. niquivilensis** Matuda ex García-Mendoza (Novon 9(1): 42–45, ills., 1999). **Type:** Mexico,

Chiapas (*García-Mendoza & al.* 6441 [MEXU, ENCB, HEM, K, MO]). — **Lit:** Lott & García-Mendoza (1994: online version with ills.); García-Mendoza (2001b). **Distr:** Mexico (SE Chiapas), probably also adjacent Guatemala; at present only known from cultivation at settlements but probably from pine-oak or montane cloud forests, 1800–2700 m; flowers April to May.

[1] Arborescent, stems 1–3  $\times$  0.3–0.4 m, unbranched, covered with old dry reflexed and persisting leaves; **Ros** 4–5 m  $\varnothing$ ; **L** 80–150, erect, lanceolate, coriaceous, narrowed at the base to 7–8.5 cm, 5–5.5 cm thick, concave, keeled, scabrous or muricate on both faces, (1.7–) 1.9–2.1 m  $\times$  12–14 cm, green, tip acuminate, mucronate, conical, 1–2 (–3)  $\times$  0.5–1 mm, dark chestnut-brown, margins straight, dentate; **marginal teeth** upcurved or straight at the base, recurved at mid-leaf, and upcurved in the upper part, 5–6 (–8)  $\times$  3–4 (at the base) mm, chestnut-brown, base yellowish, decurrent so that the margin becomes corneous, on small deltoid bases, (1.5–) 2–4 cm apart at mid-leaf, 0.6–1.5 (–2) cm at the base; **Inf** 6–9 m, peduncle 1.5 m, puberulent, green, with triangular, dentate and mucronate **Bra** 50  $\times$  5 cm, fertile part pyramidal, open, making up almost the whole inflorescence, with up to 55 puberulent part-**Inf** 2–2.3 m long, 2.-order branches 14–18, 30–60 cm, puberulent, bulbiferous, bulbils spheroidal to broadly conical, 50–70 (–110)  $\times$  (30–) 45–65 mm, bracteate, covered by 4–6 broadly ovate, brownish to green persistent bracts, sometimes tinged reddish; **Ped** 4–8 mm, puberulent; **Fl** 65–75 (–80) mm, puberulent, single or 2–3 together; **Tep** elliptic, greenish-white, tinged reddish outside, whitish inside; **OTep** (30–) 40–45  $\times$  11–13 mm, pilose, glabrescent; **ITep** 40–45  $\times$  12–14 mm, pilose, glabrescent on the prominent mid-rib, papillose in the area of overlap; **Fil** 20–25 mm, 3–5 mm wide at the broadened papillose base, greenish-yellow; **Anth** oblong, 4–6 mm, yellow; **Ov** cylindrical, 30–35 (–38)  $\times$  3–6 mm, puberulent, green; **Sty** trigonous, papillose, 20–23 mm, 4–6 mm wide at the broadened base, 3-sulcate, papillose, greenish-yellow; **Sti** entire, sometimes ciliate; **Fr** oblong, 65–70  $\times$  40 mm; **Se** winged for 4–5 mm, 18–19  $\times$  10–12 mm.

Sterile collections of this plant by Matuda were provisionally included under *F. macdougallii* (Lott & García-Mendoza 1994, García-Mendoza 1998), but the clear differences such as longer leaf marginal teeth, a pyramidal inflorescence with longer 1.- and 2.-order branches, much larger flowers, and larger and broader bulbils merit species status. According to the protologue, both species appear to be closely related and share arborescent growth, leaves with both faces scabrous or muricate, as well as puberulent primary and secondary inflorescence branches, pedicels and ovaries. Both taxa are apparently extinct in nature and only survive in cultivation (García-Mendoza 2001a). *F. niquivilensis* is commonly planted as fence and to prevent soil erosion, and the fibres of the leaves are used to make baskets and ropes; this use was more common in the past and is presently restricted to a very small scale (García-Mendoza 1998). The flowers emit a lemon-like odour during night and are visited by hummingbirds at day when no nectar is produced (García-Mendoza 2001a).

**F. occidentalis** Trelease (Bot. Jahrb. Syst. 50 (Beiblatt 111): 5, 1913). **Type:** Peru, Lima (Weberbauer 1687 [B, G, GH, MEXU, NY]). — **Lit:** Macbride (1936); Ullrich (1992); Pino (2006). **Distr:** Peru (Ancash, Cajamarca, Cuzco, Huallaga, Huánuco, Lima, Loreto); NW Bolivia (La Paz); dry rocky slopes in scrubland, 2200–3860 m; flowers April to May and November to December. **I:** Pino (1996); García-Mendoza (2001a).

[1] Stems none or short; **Ros** 2.5 m Ø; **L** erect, linear-lanceolate, coriaceous, narrowed at the base to 3–5 cm, smooth on both faces, 60–70 (–100) × (4.5–) 8–10 cm, margins crenate, ± corneous, minutely aculeate; **marginal teeth** ± deltoid, simple, straight or upcurved, 1–2 mm, 0.5–1 (–2) mm broad at the base, on small bases, absent at the leaf tip, 0.2–0.8 (–1) cm apart, 0.4–0.6 cm at the base, yellowish; **terminal Sp** mucronate, obtuse and semiglobose, minute, weak, 0.5–1 × 1 mm, reddish-brown; **Inf** 4–6 (–12) m, peduncle green, glabrous, with triangular toothless **Bra** 10–23 cm long, fertile part to 2 m broad, part-**Inf** 50–80 cm, with 8–17 2.-order

branches 10–30 cm long, both glabrous, freely bulbiferous, bulbils conical, (25–) 30–40 × 6–10 (–13) mm, green, bracteate, with 2–4 scarious bracts; **Ped** (5–) 10–18 mm, glabrous; **Fl** (50–) 55–68 mm, single or 2 (–4) grouped together; **Tep** 30–33 (–38) mm, glabrous, with apiculate apex, whitish-green, creamy-white or green with white margins; **OTep** narrowly elliptic, 8–10 mm broad; **ITep** elliptic, 10–15 mm broad; **Fil** (14–) 16–20 mm, 3–4 mm wide at the broadened base, yellow-green; **Anth** oblong, 3–4 mm, yellow; **Ov** 25–30 × 5–6 mm; **Sty** 20–25 mm, 4–5 mm wide at the broadened base, yellow-green; **Fr** and **Se** unknown.

For long insufficiently known, until García-Mendoza (2001a) provided the first complete description. It is characterized by short leaves with small teeth to 2 mm, and absent at the tip, large glabrous flowers with apiculate tepals, and conical and bracteate bulbils. With its very small teeth, this species is closest to *F. longaeva* and other species of Sect. *Serrulatae* (García-Mendoza 2001a). It differs from the second Peruvian species *F. hexapetala* by narrower, less rigid and largely toothless leaves (Pino 1996: as *F. andina*).

The vernacular name in Peru is “champa qara” (Pino 2006). The leaves are used as detergent, for fibres and for extracting chemical constituents, and the peduncles for constructions (García-Mendoza 2001a). The sap of half-roasted leaves is used for curing bronchitis by rubbing it on the chest and back during night (De-la-Cruz & al. 2007). The flowers are visited by hummingbirds (García-Mendoza 2001a).

**F. parmentieri** (Roezl ex Ortgies) García-Mendoza (Bol. Soc. Bot. México 66: 115, ill. (p. 116), 2001b). **Type** [neo]: Ex cult. BG Berlin (Koch s.n. [B]). — **Lit:** McVaugh (1989: 198–200, with ill.); Ullrich (1991b: with ill.); García-Mendoza (2001b); Guillot Ortiz & Meer (2010: with ill.); all as *F. beddinghausii*; González-Martínez (2016: neophyte in Spain). **Distr:** Mexico (Jalisco, Guanajuato, Hidalgo, Veracruz, Michoacán, México, Distrito Federal, Morelos); volcanic soils derived from andesite, basalt or lava flows, mountain slopes and summits, in pine-oak cloud forests, 2300–3500 m;

**Fig. 1** *Furcraea parmentieri*. (Copyright: U. Eggli)



flowers June to September; neophyte in Spain. **I:** Curtis's Bot. Mag. 117: t. 7170, 1891, as *F. bedinghausii*; Sánchez Mejorada (1966: as *F. bedinghausii*); Benítez B. (1986: 62, as *F. bedinghausii*); Etter & Kristen (2007). – Fig. 1.

≡ *Yucca parmentieri* Roezl ex Ortgies (1859) ≡ *Beschorneria parmentieri* (Roezl ex Ortgies) Jacobi (1864); **incl.** *Furcraea flaccida* Hort. Panorm. ex Hort. Kew (s.a.); **incl.** *Beschorneria floribunda* K. Koch (1859); **incl.** *Beschorneria multiflora* K. Koch (1859); **incl.** *Beschorneria multiflora* hort. ex K. Koch (1860) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Roezlia regia* Laurentius (1861); **incl.** *Agave argyrophylla* Hort. Tonel ex K. Koch (1862) (*nom. inval.*, ICN Art. 36.1c) ≡ *Yucca argyrophylla* (K. Koch) Lemaire (1863); **incl.** *Yucca toneliana* K. Koch (1862) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Furcraea bedinghausii* K. Koch (1863) ≡ *Fourcroya bedinghausii* (K. Koch) André (1895) (*incorrect name*, ICN Art. 11.4) ≡ *Furcraea longaeva* ssp. *bedinghausii* (K. Koch) B. Ullrich (1991) (*nom. inval.*, ICN Art. 41.5); **incl.** *Agave toneliana* Hort. ex E. Morren (1863) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Roezlia regia* Lemaire (1863) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Roezlia bulbifera* Roezl (1881); **incl.** *Fourcroya roezlii* André (1887) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Roezlia regia* André (1887) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca pringlei* Greenman (1898) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Roezlia regina* Trelease (1915) (*nom. inval.*, ICN Art. 61.1); **incl.** *Yucca*

*argyraea* Trelease (1915) (*nom. inval.*, ICN Art. 61.1?).

[2] Arborescent, stems erect, thick, simple, 1.5–4 (–8) × 0.2–0.5 m; **Ros** 1 (–4) at the stem tip, 2–2.5 m Ø, with 100–150 leaves; **L** first ascending-spreading, later spreading to pendent, forming a dry skirt along the entire stem or just below the rosette, lanceolate to linear-lanceolate, stiff, ensiform, coriaceous, narrowed below the middle, base narrowed to 2–4 (–5) cm, 2–3 cm thick, long-attenuate, flat to concave or plicate, keeled, above striate and roughened by projections from the longitudinal veins, below asperous towards the tip, muricate above the veins, above scabrous, 60–90 (–120) × 5–8 (–10) cm, somewhat glaucous, margins straight, marginal teeth none, finely denticulate, denticles minute, irregularly spaced, pale, deltoid, 14–20 per cm, on a yellowish cartilaginous band, tip formed by hardened involute margins, < 1 mm; **Inf** erect, (2.5–) 4–6 (–9) m, peduncle 0.5–1 (–1.5) m, greenish, pubescent, with deltoid to lanceolate **Bra** 20–75 × 3.5–8 cm, brown or purple, fertile part narrowly pyramidal, greenish, pubescent, occupying nearly the whole inflorescence, with (50–) 80–130 part-**Inf** 1–1.5 (–2) m long, tips pendent, pubescent to glabrescent with age, 2.-order branches 0.3–0.6 (–0.9) m, pendent, pubescent, all branches with purple bracts, freely bulbiferous, bulbils leafy, conical to ovoid, 15–20 (–30) × (7–) 10–20 mm, covered with deltoid, scarious, deciduous bracts; floral **Bra** deltoid, scarious, <



10 mm, pubescent; **Ped** 5–10 (–15) mm, puberulent; **Fl** (35–) 45–55 mm, 2–4 grouped together; **Tep** elliptic or oblong-elliptic, (15–) 20–24 (–27) mm, green-white outside, whitish within, yellowish after anthesis; **OTep** narrowly elliptic, 4–6 (–8) mm broad, pubescent outside; **ITep** elliptic, 6–9 (–12) mm, pubescent on the prominent midrib, papillose in the area of overlap; **Fil** 10–14 mm, 2–4 mm wide at the broadened base, papillose, whitish; **Anth** oblong, 2–3 mm, yellow; **Ov** cylindrical, (15–) 20–25 (–30) × 2–7 mm, puberulent, in bud nearly lanate, green, neck 3–5 mm; **Sty** 13–18 mm, 2.5–5 mm wide at the broadened base, truncate, deeply 3-sulcate, somewhat papillose, yellowish; **Sti** shallowly 3-lobate; **Fr** oblong-ovoid to ovoid, 40–45 (–60) × (25–) 30–35 mm, rostrate for 4 mm, stipitate for up to 20 mm; **Se** plane-convex, winged for 2 mm, 9–11 × 6–8 mm, shiny. — **Cytology**:  $2n = 60$  (Whitaker 1934: as *F. bedinghausii*).

This is the species common in the Trans-Mexican Volcanic Belt, easy to recognize by its short glaucous leaves rough below and with minute denticles, its narrowly pyramidal inflorescence with pendent 1.- and 2.-order branches, a short trunk and puberulent branches and flowers (García-Mendoza 1998). It is closely related to *F. longaeva*, but smaller in all its parts except the flowers (García-Mendoza 1998). Vernacular names: “Shishi” (“xixi”), “large sishi”, “tacamba”, “palma”, “palmilla”, “palmito”, “magueyito”,

“izote”. The leaves and flowers are used as Easter decoration, the dried leaf fibres for binding sheaves of grain, and the whole plants as living fences (García-Mendoza 1998, García-Mendoza 2001a).

The *F. parmentieri* plant community on Pelado volcano (Mexico City) was studied by Almeida-Leñero & al. (2013), who found declining conditions due to repeated fires. According to Valverde & Hernández-Pedrero (2017), germination rate under field conditions reaches 40%, and the presence of nurse plants does not positively influence establishment rates. This is the only species of the genus at present widely grown outside in the UK (David 2009).

**F. pubescens** Todaro (Index Seminum [Palermo] 1877: 38, 1877). **Type**: not typified. — **Lit**: Todaro (1879: with ills.); McVaugh (1989: as *F. guerrensis*); García-Mendoza (1998: as *F. guerrensis*). **Distr**: México (S Nayarit, W Jalisco, Colima, Michoacán, México, Guerrero, Oaxaca); in calcareous, sandy or clayey soils or soils derived from volcanic rocks, in ecotones of tropical deciduous forests with pine-oak forests, subdeciduous tropical forests, and oak and pine-oak forests, rarely in montane cloud forests, 650–1900 m; flowers July to November, also in February, March and December. **I**: Matuda (1966: as *F. guerrensis*). — Fig. 2.

**Incl.** *Furcraea guerrensis* Matuda (1966).

**Fig. 2** *Furcraea pubescens*. (Copyright: U. Eggli)





[1] Stems mostly none, rarely short, 0.3–0.7 m, simple; **Ros** 1.5–2 × 3–4 m; **L** 40–80 (–120), lanceolate, erect, coriaceous, narrowed at the base to 3–6.5 cm, 4–5.5 cm thick, keeled, apex acuminate, nearly flat in the lower part, concave in the upper part, smooth on both faces, 1.2–1.8 (–3) m × 10–15 cm, dark green, margins crenate, somewhat corneous esp. towards the base; **marginal teeth** deltoid, upcurved or straight, sometimes hooked, strong, 3–6 (–8) mm, 2–4 (–5) mm broad at the base, brown to dark-reddish, with yellowish bases, mostly with teeth throughout, sometimes toothless for 10–15 cm below the leaf apex, (2–) 3–5 (–7) cm apart at mid-leaf, 1–2 (–4) cm at the base, decurrent on prominent deltoid bases; **terminal Sp** conical, 1–4 (–8) mm, brown; **Inf** (3–) 5–8.5 m, peduncle short, 0.5–2 m, green, puberulent, with linear-lanceolate, toothed, green **Bra** (15–) 40–70 × 4–7.5 cm, fertile part pyramidal or ellipsoid, open, in the upper  $\frac{3}{4}$  –  $\frac{1}{2}$  of the inflorescence, **part-Inf** 40–80, (60–) 100–150 cm, longest at mid-inflorescence, puberulent to tomentose, green, with 5–12 (–25) 2.-order branches 10–30 cm long, puberulent, tomentose or velutinous, green, with reddish tinge, bulbiferous, bulbils ovoid to conical-ovoid, (20–) 25–30 (–45) × 15–20 (–25) mm, green, covered with 3–4 suborbicular bracts, brownish; **Bra** at the base of the flower clusters <3 mm, deciduous; **Ped** 5–10 (–15) mm, puberulent to velutinous; **Fl** (50–) 55–65 (–70) mm, single or 2–3 (–4) grouped together; **Tep** (23–) 25–30 (–35) mm, whitish-green to yellowish, sometimes with reddish tinge outside; **OTep** narrowly elliptic to lanceolate, 6–10 (–13) mm, puberulent to glabrescent; **ITep** elliptic, 10–15 (–21) mm, puberulent on the midrib; **Fil** 15–18 mm, 3–4 mm wide at the broadened papillose base, yellowish-white; **Anth** oblong, base sagittate, 3–4 (–7) × 1–2 mm, yellow; **Ov** cylindrical, (20–) 25–30 (–35) × (2–) 3–4 mm, puberulent to tomentose, green, neck 5–7 mm; **Sty** (18–) 20–25 mm, 4–6 (–10) mm wide at the broadened base; **Sti** papillose; **Fr** ovoid to pyriform, 60–80 (–95) × 35–50 (–55) mm, rostrate, base and rostrum puberulent, stipitate for 10–20 (–25) mm, stipe glabrescent; **Se** plane-convex, with broad wing 5–6 (–8) mm, 15–20 (–22) × (7–) 8–10 (–12) mm, shiny. —

**Cytology:**  $2n = 60$  (Satô 1935: as *F. pubescens*), but uncertain whether applying to this taxon, or to *F. pubescens* Baker = *F. undulata*.

*F. pubescens* is based on material flowering 1877 at Palermo. Baker (1888) and Baker (1892) misnamed plants cultivated in the UK and attributable to *F. undulata* as *F. pubescens* (Drummond 1907). García-Mendoza (1998) attributes the name to plants from the state of México and adds *F. guerrerensis* as synonym. As now circumscribed, *F. pubescens* is characterized by its usually acaulescent habit, leaves smooth on both faces with large teeth, open pyramidal or ellipsoid inflorescences with short peduncles and puberulent flowers, peduncles and branches, ovoid to conical-ovoid bulbils, and seeds with broad wings. Vernacular names: “maguey de pita”, “maguey” (“wechi en triqui”), “maguey de ixtli”, “maguey de zopilote”, and “yú-gua oo yuwa”. Locally used (formerly more wide-spread) for fibre and as living fence, the flowers are eaten, and the leaf juice is used to stupefy fishes (García-Mendoza 1998, García-Mendoza 2001a).

**F. quicheensis** Trelease (Trans. Acad. Sci. St. Louis 23(3): 148, t. 29, 1915). **Type:** Guatemala, Quiché (Cook 421 [US]). — **Lit:** Standley & Steyermark (1952); Lott and García-Mendoza (1994: online version with ills.); García-Mendoza (2001b: with ills.). **Distr:** Mexico (E Chiapas), W Guatemala (Huehuetenango, San Marcos, Totonicapan, Quetzaltenango, Solola, Quiché), Honduras; oak forests, sometimes on exposed sites in montane pine-oak cloud forests, on soils derived from volcanic ash, cultivated or escaped from cultivation, 2000–3300 m; flowers April to August. **I:** Schröter (1992).

[2] Arborescent, stems erect, thick, naked, simple or 4–5 × branched, 1–2 × 0.2–0.4 m; **Ros** at the stem tip, 2–3 m Ø; **L** 60–100, erect, forming a dry skirt below the rosette, lanceolate, erect, spreading or reflexed, gradually narrowed towards the base, base 4–7 cm broad, 3–6 cm thick, broadly attenuate, flat or slightly channelled, subcoriaceous, smooth, below with prominent venation, 80–120 (–150) × 7–10 (–14) cm, glaucous to glaucous-green, margin narrow, minutely denticulate, denticles 8–10 per cm, yellow, on a

cartilaginous band, **L** tip hardened by the involute margins, narrowly rounded, obtuse, without terminal spine; **Inf** erect, 2–5 m, peduncle 1–2 m, green, often red, glabrous, with triangular **Bra** 20–60 × 5–12 cm, fertile part narrow, oblong, in the upper  $\frac{2}{3}$  –  $\frac{3}{4}$  of the inflorescence, part-**Inf** 50–80, (15–) 50–70 (–100) cm, sometimes with 2.-order branches to 10 cm, green, glabrous, without bulbils; **Bra** at the base of the flower clusters deltoid, 4–8 cm, much larger than the pedicels, reddish, bracteoles deltoid, scarious, <1.5 cm; **Ped** (10–) 20–35 mm, reddish, glabrous; **Fl** (50–) 55–65 (–70) mm, 3–5 grouped together; **Tep** elliptic, suberect or somewhat spreading, (20–) 25–30 (–35) mm; **OTep** 4–7 (–9) mm broad; **ITep** 6–9 (–12) mm broad, with prominent midrib, (pale) green with brownish tinge outside, greenish-whitish or greenish-yellow within, glabrous; **Fil** 10–14 mm, 2–4 mm wide at the broadened base, somewhat papillose, whitish; **Anth** oblong, 2–2.5 mm, yellow; **Ov** cylindrical, 25–30 (–39) × 3–5 (–7) mm, dark green to brown-green, glabrous, neck <2 mm; **Sty** 13–17 mm, 2–4 mm wide at the broadened base, papillose; **Sti** shallowly 3-lobate; **Fr** oblong, 50–70 (–80) × 20–30 (–35) mm, somewhat lustrous, contracted at the base, rostrate for 5 mm, stipitate for 20–30 mm; **Se** winged for 1 mm, 8–10 × 5–7 mm, shiny.

The above description largely follows García-Mendoza (2001a) and García-Mendoza (2001b); morphological measurements in Lott & García-Mendoza (1994) and García-Mendoza (1998) partly differ.

Characterized by the narrow inflorescences without bulbils, large, glabrous flowers, oblong fruits and glaucous leaves (García-Mendoza 2001b). Common on the W Guatemalan highland where it often is a conspicuous feature of the landscape (Standley & Steyermark 1952). The species apparently reproduces by seeds, since no bulbils were seen or reported. Vernacular names: “Mecate”, “mecatl”, “cheche”, “palma”, “chijute”, “maguey”, and “micato”. The plants are used as ornamentals and to prevent soil erosion, the leaves to extract fibres and as religious Easter decoration, which relates to its abundance near settlements, at the borders of agricultural land, or around houses

(García-Mendoza 1998, García-Mendoza 2001a). Nelson (2008) provides a new record for Honduras. Ullrich (1991b) placed the species in the *F. longaeva*-complex.

**F. samalana** Trelease (Trans. Acad. Sci. St. Louis 23(3): 149, tt. 30–31, 1915). **Type:** Guatemala, Quetzaltenango (Trelease 20 [ILL]). — **Lit:** Standley & Steyermark (1952); Lott & García-Mendoza (1994: online version with ills.). **Distr:** Mexico (Chiapas), Guatemala (Quetzaltenango, Retalhuleu, Suchitupéquez), El Salvador?, generally cultivated only; in flat and brown stony soils, disturbed sites on rocky slopes in scrub or pine-oak forests, often in moist thickets or more often in dry places, 400–2000 m; flowers July to September.

[1] Stems none, simple; **Ros** 2–3 × 4–6 m; **L** 150–200, broadly lanceolate, erect, cartilaginous, tapering at the base to 6–9 cm, 4–6 cm thick, apex long acuminate, convex below, channelled above, smooth on both faces, (1.3–) 1.8–2.6 m × (12–) 20–25 cm, green, margins straight to somewhat crenate; **marginal teeth** upcurved or straight, (2–) 3–5 (–7) × 2–4 mm, brownish to blackish, 2.5–4.5 (–6) cm apart at mid-leaf, 1.5–2 cm below, lacking in the upper  $\frac{1}{2}$  –  $\frac{2}{3}$  of the leaf, decurrent on low fleshy bases, sometimes forming a corneous band down to the base; **terminal Sp** normally lacking, or mucronate, conical, 1–2 mm, reddish; **Inf** 5–8 m, peduncle 2.5–3 m, green, glabrous, with deltoid, dentate, mucronate, green **Bra** 50 × 7.5 cm, margin entire or with few denticles near the constricted base, fertile part lax, narrow, oblong, with 25–35 part-**Inf** in the upper  $\frac{3}{4}$  of the inflorescence, <75 cm, glabrous, 2.-order branches (5–) 10–30 cm, glabrous, bulbiferous, bulbils 50–65 × 20 mm, leafy, with dull grey-green scales and 6–8 small leaves, green, conical-ovoid; floral **Bra** much shorter than the pedicels; **Ped** 3–9 mm, glabrous; **Fl** (45–) 50–55 (–57) mm, single or 2–3 grouped together; **Tep** 25–35 mm, greenish-white outside, yellowish-green within, glabrous; **OTep** elliptic, 10–13 mm broad; **ITep** broadly elliptic, 13–18 mm broad; **Fil** dorsiventrally flattened, 12–14 mm, 2–3 mm wide at the broadened base, papillose, yellowish; **Anth** oblong, 4–6 mm, yellow; **Ov** cylindrical, 20–25

(–27) × 2–4 mm, glabrous, greenish-white; **Sty** 19–22 mm, 4.5 mm wide at the broadened base; **Sti** papillose; **Fr** and **Se** not known.

Standley & Steyermark (1952) and Lott & García-Mendoza (1994) record the species from El Salvador (*Villacorta* 787, MO), but this view is not shared by García-Mendoza (2001a). Vernacular names: “ixtle”, “mecate”, “pita”, “jasite”, “maguey”, and “maguey ixtle”. The leaf fibres are used for making ropes for backpacks, hammocks and nets.

**F. selloana** K. Koch (Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 3: 22, 1860). **Type**: not typified. — **Lit**: Verhoek & Hess (2002); Wilcox (2005); Guillot Ortiz & Meer (2010); Aedo (2013); Smith & Figueiredo (2016: neophyte in RSA); Guillot Ortiz & al. (2016: neophyte in Spain); **Distr**: Colombia (Antioquia, Cauca, Cundinamarca, Huila, Magdalena, Santander, Tolima, Valle), Ecuador (Chimborazo, El Oro, Loja, Los Rios, Islas Galápagos); cultivated or as escape at anthropogenic and disturbed sites, wild possibly in dry river valleys and lowlands, 1000–2600 m; cultivated and naturalized in many parts of the world (e.g. RSA, Spain); flowers June to October. **I**: Curtis’s Bot. Mag. 86: t. 5163, 1860, as *F. flavoviridis*; Curtis’s Bot. Mag. 101: t. 6148, 1875; Irish & Irish (2000); Smith & Figueiredo (2012).

**Incl.** *Agave cubensis* var. *striata* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Furcraea selloa* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1); **incl.** *Furcraea flavoviridis* Hooker (1860); **incl.** *Furcraea lindenbergii* Jacobi ex Anonymus (1869); **incl.** *Furcraea albispina* Hort. Panorm. ex Baker (1893); **incl.** *Furcraea tuberosa* Franceschi (1900) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea selloana* var. *edentata* Trelease (1915a) ≡ *Furcraea selloana* fa. *edentata* (Trelease) H. Jacobsen (1954) (*nom. inval.*, ICN Art. 41.5); **incl.** *Furcraea selloana* var. *marginata* Trelease (1915a).

[1] Stems usually none or short, to 0.3 or sometimes 0.9 (–1.5) m; **Ros** 3–4 m Ø; **L** 40–60, linear-lanceolate to oblanceolate, erect, straight, coriaceous, narrowed to 4–5 cm at the base, concave, rough below (fide protologue and various authors) or smooth (fide García-Mendoza

(2001a)), (0.7–) 1–1.7 (–2.4) m × (7–) 10–15 cm, green, margins with teeth throughout; **marginal teeth** simple, upcurved, straight or recurved, rarely 1–3 bifid, 4–7 × 3–4 mm, 2.5–5 (–7) cm apart at mid-leaf, 3–4 cm below, chestnut-brown, decurrent on prominent bases, rarely forming a corneous band up to the base, leaf tip acuminate, mucro conical, 1–3 mm, deciduous, chestnut-brown; **Inf** 6–10 m, peduncle 2–3 m, green, glabrous, with oblong to lanceolate, mucronate, green, glabrous **Bra** 11–35 (–50) cm, fertile part lax, oblong, in the upper ½ of the inflorescence, part-**Inf** 40–60, patent to pendulous, (60–) 80–130 cm, green, glabrous, with 6–12 2.-order branches (5–) 10–30 cm long, green, glabrous, freely bulbiferous, bulbils ovoid to ovoid-conical, 20–50 × 15–30 mm, bracteate to somewhat foliose, with 2–4 green bracts and 3–4 small leaves; floral **Bra** small, subulate, scarious, green; **Ped** 5–10 mm, glabrous; **Fl** (37–) 45–50 (–55) mm, 1–4 grouped together; **Tep** spreading and incurved, tip rounded, (20–) 25–30 mm; **OTep** narrowly elliptic, 7–10 (–12) mm; **ITep** elliptic, 10–15 mm broad, whitish-green to greenish-yellow; **Fil** 10–14 mm, 2–4 mm wide at the broadened base, greenish-white; **Anth** oblong, 3 mm, yellow; **Ov** cylindrical, (15–) 20–25 × 3–5 mm, glabrous; **Sty** 15–20 mm, 4–5 mm wide at the broadened base; **Sti** 3-lobate; **Fr** and **Se** unknown. — **Cytology**: 2n = 60 (Whitaker 1934).

The name was published in January 1860 and thus antedates *F. flavoviridis* (publ. February 1860) (Drummond 1907). Described from material cultivated at Potsdam (Germany) and purportedly originating from Quetzaltenango, Guatemala, but neither cultivated plants nor herbarium records are known from that country (Trelease 1915b, Lott & García-Mendoza 1994, García-Mendoza 2001a). The species is at present not certainly known from C America (Lott & García-Mendoza 1994).

*F. selloana* belongs into a group with *F. cabuya* and *F. hexapetala*, sharing flowers with an ovary much shorter than the tepals and ovoid bulbils, but is separated from both by its linear-lanceolate leaves, 23–35 (–50) teeth per leaf margin and variably sized, oblong, lax inflorescences, and oblong bracts with denticles at their apex only. Specimens with bifid teeth might indicate

hybridization with *F. acaulis* (García-Mendoza 2001a). Vernacular names: “fique”, “cabuya”, “penca” and “mión-kei-úvi” (“maguey”). Planted as fence or hedge or ornamental (esp. the variegated forms). The leaf fibres are used for making bags and sacks (García-Mendoza 2001a).

The variegated form was introduced in 1867 from the Cauca valley in Colombia by the botanical traveller Wallis and published by Jacobi (1870: 79–80) as *F. lindenii*. Several variegated or toothless horticultural variants have been described. The variegated form (var. *marginata*) with creamy-yellow stripes along the leaf margin and sometimes light creamy streaks on the lamina is much more common in cultivation than normal green forms (Irish & Irish 2000). Reported as local neophyte from C Portugal by Silva & al. (2015).

[Editorial note by U. Eggli:] The name was originally published with the spelling ‘selloa’, which is sometimes amended to ‘selloi’. Since the epithet honours Hermann Sello, the name must be corrected to ‘selloana’ under ICN (2018) Art. 60.8c (see Figueiredo & Smith (2016)).

**F. stricta** Jacobi (Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss. 1869: 171, 1869). **Type:** not typified. — **Distr:** Not known to be extant.

[1] Acaulescent; **Ros** rather regular, 0.9 m Ø; **L** ± 30, linear-lanceolate, straight, rigid, coriaceous, spreading to all directions, narrowed to 3.8 cm above the base, gradually narrowed from mid-leaf towards the tip, convex below and subacutely keeled, above below the base flat or concave, so deeply channelled as to be almost triquetrous in section above mid-leaf, scabrous below, smooth and somewhat shiny above, 60–76 × 5–6.3 cm, vivid light green to bright green, margins straight, narrow, somewhat reddish; **marginal teeth** strong, rigid, distant, tip corneous, uncinat, reddish chestnut-brown on broad deltoid reddish bases, leaf tip straight, upper end soon drying; **Inf** erect, 2.43–2.74 m, green, glabrous, peduncle very short, ± 0.45 m, with lanceolate appressed **Bra** to 12.5 cm long below, fertile part 2 to 2.3 m, with part-**Inf** longest at mid-inflorescence, ascending-spreading, somewhat incurved above the middle, 30–35 cm, 2.-order branches very short, to 1 cm, bulbiferous,

bulbils many, partly somewhat laterally flattened, partly inconspicuously obtusely trigonous; **Ped** very short; **Fl** not known whether single or in groups, ovoid; **Tep** incurved, whitish-green; **OTep** lanceolate, tip somewhat thickened, 25 × 8 mm; **ITep** elliptic, with fleshy midrib, 25 × 10 mm; **Fl** 10 mm, 2.5 mm wide at the broadened base; **Anth** elliptic, sagittate, 4 mm, golden-yellow; **Ov** clavate, bluntly trigonous, 15 × 4 mm, papillose; **Sty** longer than the stamens, 15–17 mm, 4 mm wide at the broadened base; **Sti** slightly thickened, capitate; **Fr** and **Se** unknown.

Insufficiently known, and first described from a plant that flowered in the Demoulin garden in Mons (Belgium) in 1868, later also grown at Kew from material from the Berlin Botanical Garden (Baker 1888). Characterized by deeply channelled leaves scabrous below, inflorescences with a very short peduncle, and esp. by the laterally somewhat compressed bulbils (terete in all other species except *F. stratiotes*, here included in *F. acaulis*). The name was for long considered as unresolved (e.g. in the first edition of this handbook and in the revision of García-Mendoza (2001a), but was recently re-established by Govaerts (2014+). Govaerts places *F. elegans* in the synonymy here, whereas García-Mendoza (2001a) is followed here, to treat it as synonym of *F. hexapetala*. Modern records of *F. stricta* possibly refer to *F. hexapetala*.

**F. tuberosa** (Miller) W. T. Aiton (Hort. Kew., ed. 2, 2: 303, 1811). **Type:** [icono]: Plukenet, Almag., 19, 1700. — **Lit:** Drummond (1907); Álvarez de Zayas (1996); Proctor & Acevedo-Rodríguez (2005); Smith & Figueiredo (2012); all with ills. **Distr:** Lesser Antilles, Bahamas, Haiti, Puerto Rico, Dominican Republic, French Guiana, Guyana & Suriname (natural?), Brazil, Paraguay (?), cultivated worldwide; in Guyana and Suriname in tropical lowland forests, otherwise mostly in secondary anthropogenic habitats near roads or settlements, 50–400 m; flowers July to August in Guyana & Suriname, in the Caribbean January to October.

≡ *Agave tuberosa* Miller (1768) ≡ *Fourcroya tuberosa* (Miller) Hooker (1860) (*incorrect name*, ICN Art. 11.4); **incl.** *Agave tuberosa* Lamarck (1784) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave*

*tuberosa* Aiton (1789) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave tuberosa* var. *β spinis solitariis* Aiton (1789) (*nom. inval.*, ICN Art. 23.1); **incl.** *Furcraea spinosa* O. Targioni Tozzetti (1808) ≡ *Agave spinosa* (O. Targioni Tozzetti) Steudel (1840); **incl.** *Yucca superba* Roxburgh (1814) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Agave gigantea* Tussac (1818); **incl.** *Agave vivipara* Maycock (1830) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave commelynii* Salm-Dyck (1834) ≡ *Furcraea commelynii* (Salm-Dyck) Kunth (1850); **incl.** *Agave angustifolia* Hort. Par. ex Steudel (1840) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea gigantea* var. *willemetiana* M. Roemer (1847); **incl.** *Agave cubensis* Hasskarl (1856) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Furcraea interrupta* Hort. van Houtte ex Jacobi (1869); **incl.** *Furcraea lipsiensis* Jacobi (1869); **incl.** *Fourcroya vivipara* hort. (1869) (*incorrect name*, ICN Art. 11.4); **incl.** *Furcraea tuberosa* Fenzl ex Baker (1879) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave gigantea* Baker (1888) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Agave campanulata* Sessé & Moçño (1894).

[1] Stems none or short, hardly 30 cm, moderately rhizomatous; **Ros** semiglobose in outline, 1.5–2 × 2–3 m; **L** 50–70, oblong-elliptic, erect, coriaceous or cartilaginous, semi-concave, 4.5–6 (–10) cm broad at the base, keeled below, smooth, 1–1.5 (–2) m × (10–) 15–20 cm, yellowish-green, glossy, margins between the teeth crenate, sometimes with a corneous band towards the base; **marginal teeth** simple, small, straight or recurved, 1–3 (–4) × (1–) 2–3 mm, decurrent on prominent deltoid bases, 1–2.5 (–3) cm apart at mid-leaf, 1–3 cm below, lacking in the upper ½ – ⅔, brown-reddish or blackish, with yellow base, **L** tip broadly acuminate, canaliculate, mucro thickened, flattened and folded, sometimes horny, (1–) 2–4 mm, reddish; **Inf** 4–7 m, peduncle 2–3 m, green, glabrous, with deltoid, mucronate, entire, pilose, green **Bra** 6 cm long, fertile part lax, oblong to rhomboidal, in the upper ½ of the inflorescence, part-**Inf** 30–40, 45–100 (–150) cm, glabrous, with 4–15 2.-order branches 10–30 cm long, glabrous, freely bulbiferous, bulbils conical to conical-ovoid, (20–) 30–50 (–70) × 10–20 (–25) mm, with 3–5 bracts and 3–4 broadly lanceolate small leaves 3–7 (–10) cm long; floral

**Bra** deltoid, 4–7 mm, deciduous; **Ped** 5–10 (–15) mm, glabrous; **Fl** (47–) 50–55 (–57) mm, single or 2–3 grouped together; **Tep** 25–30 mm, glabrous, whitish-green to greenish-yellow; **OTep** narrowly elliptic, 6–10 mm broad; **ITep** broadly elliptic, 10–15 mm broad; **Fil** dorsiventrally flattened, 10–15 mm, 2–4 mm wide at the broadened base, yellow; **Anth** oblong, 2–3 (–6) mm, yellow; **Ov** cylindrical, (22–) 25–30 × 3–4 mm, glabrous, “perhaps not functional” fide Proctor & Acevedo-Rodríguez (2005); **Sty** 15–20 (–22) mm, 3–4 (–5) mm wide at the broadened base; **Sti** papillose; **Fr** and **Se** unknown.

The typification of this name remains unresolved: Howard & Thompson-Mills (1979) designate a Plukenet plate (Almagestum, 19, 1700, showing an unarmed plant) as type, but this is in conflict with the protologue, which describes an armed plant. García-Mendoza (2001a) selected a neotype (Commelin, Horti Med. Amstelod. 2: 35, 5. 19, 1701), but since García-Mendoza’s thesis was not formally published, the selection remains inoperative.

Characterized by oblong-elliptic or broadly lanceolate leaves with a very narrow base, small, prominent teeth placed close together in the lower ½ or ⅔ of the leaves, a canaliculate tip with thickened and flattened mucro, and an ovary as long as the tepals (García-Mendoza 2001a). The species is cultivated since earliest times in the Americas and later worldwide as “Mauritius hemp”, esp. in the 19. and 20. century on Mauritius. The occurrence in Guyana and Suriname is natural (García-Mendoza 2001a). It reproduces entirely by bulbils (Proctor & Acevedo-Rodríguez 2005).

*F. samalana* is very close and García-Mendoza (2001a) treats it as a mere variety of *F. tuberosa*, but the combination is not validly published. *F. tuberosa* is also similar to *F. hexapetala* (Álvarez de Zayas 1996, Smith & Figueiredo 2012), but differs in its oblong-elliptic, mostly broader leaves smooth on both faces with brown-reddish teeth and larger flowers (vs. narrower, lanceolate leaves scabrous below with blackish to reddish teeth and smaller flowers).

Vernacular names: “guassu” (Brazil), “karata” or “carata” (Guadalupe), “pite” (Haiti), “maguey”, “maguey criollo” or “female karata” (Puerto



Rico), “langue boeuf” (Trinidad), “aloés créole” (“sábila criolla”) (Mauritius), and “shikwenga” (Moçambique) (García-Mendoza 2001a).

**F. undulata** Jacobi (Abh. Schles. Ges. Vaterl. Cult., Abth. Naturwiss. 1869: 170, 1869). **Type:** not typified. — **Distr:** Mexico (?). **I:** Curtis’s Bot. Mag. 100: t. 6160, 1874; Curtis’s Bot. Mag. 118: t. 7250, as *F. pubescens*;

**Incl.** *Furcraea aitonii* Jacobi (1869); **incl.** *Furcraea pubescens* Baker (1892) (*nom. illeg.*, ICN Art. 53.1).

[1] **Ros** (almost) acaulescent, small, to 0.9 m Ø; **L** few, (12–) 20–30, younger leaves somewhat erect-recurved, older leaves spreading-recurved or strict, partly nearly horizontal, (narrowly) lanceolate to ensiform, coriaceous but not rigid, narrowed towards the broadened semi-amplexicaul base, base to 10 cm broad, above the base 1.9–3.8 cm broad, at mid-leaf ±3 mm thick, long-acuminate, below sharply keeled in the lower ⅓, obscurely keeled in the middle, asperous, channelled above, at mid-leaf very shallowly grooved, smooth, 40–45 × 5–10 cm, fresh to dull dark olive-green, not glaucous, margins strongly wavyly curved; **marginal teeth** stout, triangular, upcurved, regular along the whole margin, or reduced in the upper ⅓, 2–3 mm, brown, on small deltoid bases; **terminal Sp** straight, (scarcely) pungent, 2.5 mm, obtusely conical, corneous, chestnut-brown; **Inf** ± 3 m, peduncle green, with few subulate bracts, fertile part elongate, slender, narrow, pubescent, in the upper ⅓, with ascending, more erect than spreading, simple, strict part-**Inf** to 30 cm, tips pendent, bulbils not mentioned; floral **Bra** minute; **Ped** ± 6 mm; **Fl** usually geminate, 50–63 mm Ø; **Tep** narrowly oblong to oblong-lanceolate, obtuse, obtusely keeled down the centre, 10–13 mm broad, pale green to greenish-white; **Fil** ½ as long as the tepals, subulate above, broadened base deltoid; **Anth** short, yellow; **Ov** cylindrical, ± 25 mm, green, pubescent (but glabrous according to Baker (1879)); **Sty** deeply 3-lobed below, subulate above, about as long as the filaments; **Fr** and **Se** unknown. — **Cytology:** 2n = 60 (Satô 1935), as *F. pubescens*, but undecidable whether applying to *F. pubescens* Baker (and thus belonging here), or to *F. pubescens* Todaro.

Introduced by Ghiesbreght for the nursery Verschaffelt (Gand, Belgium). Differs from all other species except *F. depauperata* in its wavyly curved leaf margins. It was published from sterile plants allegedly from Chiapas and Tabasco (Mexico) where Ghiesbreght mainly travelled the years before. *F. undulata* is at present unknown in habitat or cultivation; no material from S Mexico matches the description (Lott & García-Mendoza 1994), and records for El Salvador (Standley & Calderón 1941: 52), the Lesser Antilles or Puerto Rico and cultivated plants labelled *F. undulata* are all doubtful. A specimen from the Bahamas doubtfully placed here (Drummond 1907) is placed in *F. hexapetala* by Britton & Millspaugh (1920: 77, as *F. macrophylla*). Baker (1892) misnamed plants with a wavy margin and thus attributable here as *F. pubescens*. See also under *F. depauperata*.

## References

- Aedo, C. (2013) *Furcraea*. In: Castroviejo, S. & al. (eds.): Flora Iberica, Vol. XX. *Liliaceae-Agavaceae*; pp. 498–500. Madrid (ES): Real Jardín Botánico, Consejo Superior de Investigaciones Científicas.
- Almeida-Leñero, L. [& al. 2013]. Mondragón, A. M., Ludlow-Wiechers, B. & Aguilar-Zamora, V. (2013) The community of *Furcraea parmentieri*, a threatened species, Central Mexico. *Polibotánica* 37: 25–46, map.
- Álvarez de Zayas, A. (1996) El género *Furcraea* (*Agavaceae*) en Cuba. *Anales Inst. Biol. UNAM, Ser. Bot.* 67(2): 329–346, ills., maps, key.
- Álvarez de Zayas, A. & Köhler, E. (1987) Morfología del polen de las *Agavaceae* y algunos géneros afines. *Grana* 26(1): 25–46. <https://doi.org/10.1080/00173138709428902>.
- Baker, J. G. (1879) The species of *Fourcroya*. *Gard. Chron.*, ser. nov. 11: 623–624. <http://biodiversitylibrary.org/page/26083863>.
- Baker, J. G. (1888) Handbook of the *Amaryllideae*, including the *Alstroemerieae* and *Agaveae*. London (UK): G. Bell & Sons. <https://doi.org/10.5962/bhl.title.15516>.
- Baker, J. G. (1892) *Furcraea pubescens*. *Curtis’s Bot. Mag.* 118: t. 7250 + text. <http://www.biodiversitylibrary.org/item/14246#page/143>.
- Bateman, J. (1837–1843) The *Orchidaceae* of Mexico and Guatemala. London (GB): J. Ridgway & Sons for the author. <https://doi.org/10.5962/bhl.title.896>.
- Benítez B., G. (1986) Árboles y flores del Ajusco. México D.F. (MX): Instituto de Ecología, Museo de Historia Natural de la Ciudad de México.
- Bogler, D. J. & Simpson, B. B. (1995) A chloroplast DNA study of the *Agavaceae*. *Syst. Bot.* 20(2): 191–205. <http://www.jstor.org/stable/2419449>.

- Bogler, D. J. & Simpson, B. B. (1996) Phylogeny of *Agavaceae* based on ITS rDNA sequence variation. *Amer. J. Bot.* 83(9): 1225–1235. <http://www.jstor.org/stable/2446206>
- Bogler, D. J. [& al. 1995], Neff, J. L. & Simpson, B. B. (1995) Multiple origins of the *Yucca* — *Yucca* Moth association. *Proc. Nation. Acad. Sci. USA* 92(15): 6864–6867, ills. <http://www.pnas.org/content/92/15/6864.full.pdf+html>
- Bogler, D. J. [& al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on ndhF, rbcL, and ITS sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>
- Britton, N. L. & Millspaugh, C. F. (1920) *The Bahama Flora*. New York (US): New York Botanical Garden. <https://doi.org/10.5962/bhl.title.54084>
- Cave, M. S. (1964) Cytological observations on some genera of the *Agavaceae*. *Madroño* 17: 163–170. <http://biodiversitylibrary.org/page/47826625>
- Correll, D. S. & Correll, H. B. (1982) *Flora of the Bahama Archipelago (including the Turks and Caicos islands)*. Vaduz (FL): J. Cramer.
- Crouch, N. R. & Smith, G. F. (2011) Notes on African plants. *Agavaceae. Furcraea foetida*: An invading alien in South Africa. *Bothalia* 41(1): 196–199, ills., map. <https://doi.org/10.4102/abc.v41i1.48>
- David, J. C. (2009) A review of trunk-forming species of *Furcraea* (*Agavaceae*) in cultivation in the UK. *Hanburyana* 4: 23–32, ills., key.
- De-la-Cruz, H. [& al. 2007], Vilcapoma, G. & Zevallos, P. A. (2007) Ethnobotanical study of medicinal plants used by the Andean people of Canta, Lima, Peru. *J. Ethnopharmacol.* 111(2): 284–294. <https://doi.org/10.1016/j.jep.2006.11.018>
- Dewey, L. H. (1943) *Fiber production in the western hemisphere*. Washington (US): US Department of Agriculture. <https://archive.org/details/fiberproductioni518dewe>
- Drummond, J. R. (1907) The literature of *Furcraea* with a synopsis of the known species. *Annual Rep. Missouri Bot. Gard.* 18: 25–75, 4 pl. <https://doi.org/10.2307/2400020>
- Etter, J. & Kristen, M. (2007) Neuigkeiten von den Fundorten. *Avonia* 25(3): 96.
- Figueiredo, E. & Smith, G. F. (2016) *Furcraea selloana* K. Koch is the correct orthography of the species name that commemorates Hermann Sello in *Furcraea* Vent. (*Asparagaceae* subfam. *Agavoideae/Agavaceae*). *Haseltonia* 22: 31–34, ills. <https://doi.org/10.2985/026.022.0106>
- Fritsch, R. (1970) Chromosomenzahlen von Pflanzen der Insel Kuba I. *Kulturpflanze* 18(1): 189–197. <https://doi.org/10.1007/BF02095592>
- García-Mendoza, A. (1998) Revisión taxonómica del género *Furcraea* (*Agavaceae*) en México y Guatemala. México D.F. (MX): UNAM, Instituto de Biología.
- García-Mendoza, A. (2001a) Revisión del género *Furcraea* (*Agavaceae*). México D.F. (MX): UNAM, Facultad de Ciencias, unpublished Ph.D. thesis.
- García-Mendoza, A. (2001b) Revisión taxonómica de las especies arborescentes de *Furcraea* (*Agavaceae*) en México y Guatemala. *Bol. Soc. Bot. México* 66: 113–129, maps, key, ills. <http://www.redalyc.org/pdf/577/57706611.pdf>
- García-Mendoza, A. J. (2003a) La floración de *Furcraea martinezii*, un espectáculo inusitado en el jardín botánico. *Ciencias (Madrid)* 72: 32–35, ill. [www.ejournal.unam.mx/cns/no72/CNS07209.pdf](http://www.ejournal.unam.mx/cns/no72/CNS07209.pdf)
- García-Mendoza, A. J. (2003b) Revisión de las *Agavaceae* (sensu stricto), *Crassulaceae* y *Liliaceae* incluidas en el PROY-NOM-059-ECOL-2000. Mexico (MX): Jardín Botánico, Instituto de Biología, UNAM, Proyecto W020, bases de datos SNIB-CONABIO.
- García-Mendoza, A. J. (2011) *Flora del Valle de Tehuacán-Cuicatlán*. 88. *Agavaceae*. Mexico (MX): Instituto de Biología, UNAM.
- Giraldo, D. [& al. 2009], Baquero, E., Bermúdez, A. & Oliveira-Miranda, M. A. (2009) Caracterización del comercio de plantas medicinales en los mercados populares de Caracas, Venezuela. *Acta Bot. Venez.* 32(2): 267–301.
- González-Martínez, X. I. (2016) *Furcraea parmentieri* (Roelz ex Ortgies) García-Mend.: Una nueva agavácea naturalizada para la Península Ibérica. *Bot. Complut.* 40: 131–134, ills. <https://doi.org/10.5209/BOCM.53205>
- Good-Avila, S. V. [& al. 2006], Souza, V., Gaut, B. S. & Eguiarte, L. E. (2006) Timing and rate of speciation in *Agave* (*Agavaceae*). *Proc. Nation. Acad. Sci. USA* 103(24): 9124–9129. <https://doi.org/10.1073/pnas.0603312103>
- Govaerts, R. H. A. (comp.) (2014+) World checklist of selected plant families [continuously updated]. Richmond (GB): Trustees of the Royal Botanic Gardens, Kew. <http://apps.kew.org/wcsp>
- Guillot Ortiz, D. & Meer, P. van der (2010) El género *Furcraea* Ventenat (*Agavaceae*) en la provincia de Valencia: Aspectos históricos, especies y cultivares. *Bouteloua* 7: 3–14, ills.
- Guillot Ortiz, D. [& al. 2016], Meer, P. van der & López-Pujol, J. (2016) Primera cita como alóctona de *Furcraea selloa* K. Koch en España. *Bouteloua* 24: 136–138, ills.
- Heitz, E. (1926) Der Nachweis der Chromosomen. Vergleichende Studien über ihre Zahl, Größe und Form im Pflanzenreich. *I. Z. Bot.* 18(11/12): 625–681.
- Hernández-Sandoval, L. G. (1995) Análisis cladístico de la familia *Agavaceae*. *Bol. Soc. Bot. México* 56: 57–68.
- Hesse, M. [& al. 2009], Halbritter, H. & Weber, M. (2009) *Beschorneria yuccoides* and *Asimina triloba* (L.) Dun: Examples for proximal polar germinating pollen in angiosperms. *Grana* 48(3): 151–159. <https://doi.org/10.1080/00173130903024343>
- Hochstätter, F. (2016) *Furcraea* Ventenat (*Agavaceae*). Mannheim (DE): Published by the author.
- Howard, R. A. & Thompson-Mills, B. (ed.) (1979) *Flora of the Lesser Antilles. Leeward and Windward Islands. Volume 3. Monocotyledoneae*. Jamaica Plain (US): Arnold Arboretum.

- Hoyos, J. F. (1982) Plantas ornamentales de Venezuela. Caracas (VE): Sociedad de Ciencias Naturales La Salle.
- Irish, M. & Irish, G. (2000) Agaves, Yuccas and related plants. A gardener's guide. Portland (US): Timber Press.
- Kluge, E. (2016) Herkunft, Nutzung und Verbreitung von Agavengewächsen. *Kakt. and Sukk.* 67(1): 15–21, ills.
- Lott, E. J. & García-Mendoza, A. (1994) *Agavaceae*. In: Davidse, G. & al. (eds.): *Flora Mesoamericana*, Volumen 6, *Alismataceae a Cyperaceae*; pp. 35–47, keys. México (MX): UNAM, Instituto de Biología/St. Louis (US): Missouri Botanical Garden/London (GB): Natural History Museum. <http://www.tropicos.org/Project/FM>
- Macbride, J. F. (1936) Flora of Peru, part II. *Publ. Field Mus. Nat. Hist., Bot. Ser.* 13(1:3): 421–768, keys. <https://doi.org/10.5962/bhl.title.2266>.
- Matuda, E. (1966) *Furcraea guerrerensis*. *Anales Inst. Biol. UNAM* 66: 114, ills.
- McVaugh, R. (1989) Flora Novo-Galiciana. A descriptive account of the vascular plants of Western Mexico. Vol. 15: *Bromeliaceae to Dioscoreaceae*. Ann Arbor (US): University of Michigan Herbarium.
- Meer, P. van der (2014a) *Furcraea guatemalensis* Trel., una nueva especie cultivada en la Comunidad Valenciana. *Bouteloua* 18: 160, ill.
- Meer, P. van der (2014b) Primera noticia sobre el cultivo de *Furcraea hexapetala* 'Marginata' (*Agavaceae*) en la provincia de Valencia. *Bouteloua* 19: 231–232, ill.
- Meer, P. van der (2014c) *Furcraea macdougalii* Matuda cultivada en la provincia de Valencia. *Bouteloua* 17: 147–148, ill.
- Nelson, C. H. (2008) Catálogo de las plantas vasculares de Honduras. Tegucigalpa (HN): Secretaría de Recursos Naturales y Ambiente.
- Ojeda Revah, L. & Ludlow Wiechers, B. (1995) Palinología de *Agavaceae*, una contribución bio-sistemática. *Bol. Soc. Bot. México* 56: 25–43.
- Olivares, E. & Medina, E. (1984) Oscilaciones diurnas de la acidez titulable durante el desarrollo vegetativo temprano de *Fourcroya humboldtiana* Trelease. In: Medina, E. (ed.): *Temas sobre eco-fisiología de plantas CAM/Themes on physiological ecology of CAM plants*; pp. 130–144. Caracas (VE): CIET (IVIC-UNESCO).
- Pérez Mejía, J. A. (1974) El fique. Su taxonomía, cultivo y tecnología. Medellín (CO): Compañía de Empaques. Ed. 2.
- Phillips, C. (2013) "Rare and novel species". Singular words and curious plants sent by Karwinski from Oaxaca & Puebla, 1826–1832. *Cact. Succ. J. (US)* 85(4): 132–142, ills., map. <https://doi.org/10.2985/0007-9367-85.4.132>.
- Pino, G. (1996) Agaváceas cultivadas en el Perú. *Quepo* 10: 64–70, ills.
- Pino, G. (2006) Estado actual de las suculentas en el Perú. *Zonas Áridas (Lima)* 10: 155–173. <http://revistas.lamolina.edu.pe/index.php/rza/article/view/560/549>
- Proctor, G. R. (2012) Flora of the Cayman Islands. Richmond (GB): Kew Publishing.
- Proctor, G. R. & Acevedo-Rodríguez, P. (2005) *Agavaceae*. In: Acevedo-Rodríguez, P. & Strong, M. T. (eds.): *Monocotyledons and Gymnosperms of Puerto Rico and the Virgin Islands*; pp. 116–125. Washington D.C. (US): Department of Botany, National Museum of Natural History. <http://www.fs.usda.gov/treesearch/pubs/30275>
- Robbins, R. L. (2001) *Agavaceae*. In: Steven, W. D. & al. (eds.): *Flora de Nicaragua*, Introducción, Gimnospermas y Angiospermas (*Acanthaceae — Euphorbiaceae*); pp. 41–47. St. Louis (US): Missouri Botanical Garden. <http://www.tropicos.org/Project/FN>
- Rocha, M. [ & al. 2006], Good-Ávila, S. V., Molina-Freaner, F., Arita, H. T., Castillo, A., García-Mendoza, A., Silva-Montellano, A., Gaut, B. S., Souza, V. & Eguiarte, L. E. (2006) Pollination biology and adaptive radiation of *Agavaceae*, with special emphasis on the genus *Agave*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. Aliso 22: 329–344, maps. <https://doi.org/10.5642/aliso.20062201.27>.
- Sánchez Mejorada, H. (1966) *Furcraea bendinghausii* [sic!]. *Cact. Succ. Mex.* 11(3): 72–73, ill.
- Satô, D. (1935) Analysis of the karyotypes in *Yucca*, *Agave* and the related genera with special reference to the phylogenetic significance. *Jap. J. Genet.* 1: 272–278.
- Schröter, F. (1992) Aus dem Tagebuch der Guatemala-Reise. *Kaktusblüte* 1992: 43–47, ills.
- Silva, V. [ & al. 2015], Figueiredo, E. & Smith, G. F. (2015) Alien succulents naturalized and cultivated on the central west coast of Portugal. *Bradleya* 33: 58–81, map, ills. <https://doi.org/10.25223/brad.n33.2015.a10>.
- Smith, G. F. & Figueiredo, E. (2012) A second species of *Furcraea* Vent. (*Agavaceae*), *F. tuberosa* (Mill.) W. T. Aiton, naturalised in South Africa. *Bradleya* 30: 107–110, ills., key. <https://doi.org/10.25223/brad.n30.2012.a13>
- Smith, G. F. & Figueiredo, E. (2016) A further species of *Furcraea* Vent., *Furcraea selloana* K. Koch (*Asparagaceae* subfam. *Agavoideae/Agavaceae*), naturalised in South Africa. *Bradleya* 34: 15–23, ills. <https://doi.org/10.25223/brad.n34.2016.a16>
- Standley, P. C. & Calderón, S. (1941) Flora salvadoreña. Lista preliminar de plantas de El Salvador. San Salvador (SV): Imprensa Nacional.
- Standley, P. C. & Steyermark, J. A. (1952) Flora of Guatemala. Part III. *Amaryllidaceae*. *Fieldiana, Bot.* 24(3): 103–145, ills., keys. <http://www.biodiversitylibrary.org/item/19685#page/117>
- Stauffer, F. W. [ & al. 2012], Stauffer, J. & Dorr, L. J. (2012) Bonpland and Humboldt specimens, field notes and herbaria; new insights from a study of the monocotyledons collected in Venezuela. *Candollea* 67(1): 75–130, ills. <https://doi.org/10.15553/c2012v671a10>.

- Todaro, A. (1879) Sopra una nuova specie di *Fourcroya*. Giorn. Sci. Nat. Econ. Palermo 14: 213–223, tt. 5–7. <http://biodiversitylibrary.org/page/35334252>
- Trelease, W. (1910) Observations on *Furcraea*. Ann. Jard. Bot. Buitenzorg 3(Suppl. 2): 905–916.
- Trelease, W. (1915a) *Furcraea*. In: Bailey, L. H. (ed.): Standard Cyclopaedia of Horticulture; 3: 1305–1306. New York (US): Macmillan and Co.
- Trelease, W. (1915b) The *Agaveae* of Guatemala. Trans. Acad. Sci. St. Louis 23(3): 129–152, tt. 6–35. <http://biodiversitylibrary.org/page/29092583>
- Trelease, W. (1920) *Furcraea*. In: Standley, P. C. (ed.): Trees and shrubs of Mexico. Contr. US Nation. Herb. 23(1): 105–107. <https://doi.org/10.5962/bhl.title.15726>.
- Ullrich, B. (1991a) Notas sobre la publicación del género *Furcraea* Ventenat (*Agavaceae*). Cact. Suc. Mex. 36(1): 8–9.
- Ullrich, B. (1991b) El complejo *Furcraea longaevea* Karwinski et Zuccarini. Cact. Suc. Mex. 36(2): 30–36, (3): 56–61, (4): 79–83, ills., map.
- Ullrich, B. (1992) *Furcraea* (*Agavaceae*) en Sudamerica. Quepo 6: 67–75, ills.
- Valverde, T. & Hernández-Pedrero, R. (2017) Hay nodricismo en las zonas templadas? Un estudio de caso con *Furcraea parmentieri* (*Asparagaceae*) en el volcán Pelado, Ciudad de México. Cact. Suc. Mex. 62(4): 100–115, ills., map.
- Verhoek, S. & Hess, W. J. (2002) *Agavaceae*. In: Flora of North America north of Mexico; 26: 413–465, ills., keys. New York (US: NY) /Oxford (GB): Oxford University Press.
- Verhoek-Williams, S. (1998) *Agavaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 60–70, ills., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_8](https://doi.org/10.1007/978-3-662-03533-7_8).
- Whitaker, J. W. (1934) Chromosome constitution in certain Monocotyledons. J. Arnold Arbor. 15: 135–143, ills. <http://www.biodiversitylibrary.org/item/33591#page/149>
- Wilcox, M. (2005) The genus *Furcraea* (*Agavaceae*) in the Auckland region. J. Auckland Bot. Soc. 60: 159–162.







## Hesperaloe AGAVACEAE

J. Thiede

**Hesperaloe** Engelmann (in S. Watson, Bot. US Geol. Expl. 40. Parallel 5: 497, 1871). **Type:** *Aloe yuccifolia* A. Gray [*nom. illeg.*, ICN Art. 52.1;  $\equiv$  *Yucca parviflora* Torrey]. — **SHH-Clade** — **Lit:** Gentry (1972: synopsis Sonora); Starr (1995: ill. synopsis); Starr (1998: monograph); Robbins (2002: flora N America); Guillot Ortiz & Meer (2006: ill. synopsis cult. spp. Spain); Hochstätter (2009: ill. synopsis); Hochstätter (2011: ill. synopsis). **Distr:** S USA (Texas), N Mexico (Sonora, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí). **Etym:** Gr. ‘hespera’, evening; for the occurrence in North America (i.e. in the West, where the sun disappears in the evening); and for the superficial similarity to *Aloe* (*Asphodelaceae*).

Acaulescent perennials; main **R** thick and fleshy, contractile, with many additional fibrous roots; **Ros** monocarpic, caespitose with short to long rhizomes, either tightly packed or widely separated and forming large rings, or forming grass-like clumps with bulbous fibrous bases; **L** few to many, linear-elongate, succulent, fibrous, either thin, narrow and arching to recurved, or thick, broad and stiffly erect, canaliculate, leaf tip frayed or a hard spine, leaf margins narrow, brown or white, filiferous, fibres thin and tightly curled to thick and nearly straight, white, grey, or brown; **Inf** terminal, ascending, to 4.6 m but

mostly shorter, peduncle with dry lanceolate bracts, fertile part racemose to paniculate, then with 3–8 (–10) part-**Inf** in the upper  $\frac{1}{2}$ – $\frac{1}{3}$ ; **Fl** arising from indeterminate lateral spurs, either on the main stalk or on branches (part-inflorescences); **Ped** within a cluster unequal in length, persistent; **Fl** stipitate, not opening in sequence from bottom to top, 6-merous, diurnal or nocturnal; **Per** elements tubularly connivent for most of their length or upper part  $\pm$  spreading, then flowers broadly campanulate or rotate-campanulate; **Tep** with fleshy keel, about equal, essentially free but united on a fleshy nectariferous receptacle, coloured with combinations of green, white, and purplish-brown to red, pink, salmon, or coral-red to rarely yellow; **Fil** inserted on the receptacle or adnate to the base of the tepals, with the very slender apex abruptly curved inwards; **Anth** dorsifixed, sagittate, introrse, included to exerted; **Ov** superior, ovoid to oblong, trigonous, with 3 large flat septal nectaries, with 3 locules, each with numerous ovules in 2 rows; **Sty** elongate but mostly included in the perianth, sometimes exerted; **Sti** distinctly capitate, fringed with papillae; **Fr** septicidal woody capsules, transversely rugose, beaked or not, stipitate, persistent; **Se** large, black, flat, thin. — **Cytology:**  $x = 30$  (McKelvey & Sax 1933, Gómez-Pompa & al. 1971, Engard 1980, Pinkava & Baker 1985).

According to molecular and morphological phylogenies, *Hesperaloe* is closest to and the sister group of *Hesperoyucca* (Bogler & Simpson

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1995, Clary & Simpson 1995, Bogler & Simpson 1996, Rocha & al. 2006). Putative synapomorphies are leaves with papillate epidermal cells arranged over the veins, stamens adnate to the tepal base or lower part of the tepals, styles slender, and stigmas fringed with papillae. *Hesperaloe* differs from *Hesperoyucca* esp. in its coarsely grass-like habit, the filiferous leaf margins, and the flower colour (never purely whitish) and  $\pm$  connivent tepals. Differences from *Yucca* are flower colour (never pure whitish), the  $\pm$  connivent tepals, and the capitate stigma. Recent molecular studies (Halpin & Fishbein 2013, Archibald & al. 2015) unexpectedly found the non-succulent genus *Schoenolirion* of subfamily *Chlorogaloideae* as sister-group of *Hesperaloe*, and both together are in turn sister of *Hesperoyucca* (see also there).

The geographical range of *Hesperaloe* is remarkable: 2 species (*H. nocturna*, *H. tenuifolia*) are found on the W side of the Sierra Madre Occidental (which represents an important floristic continental divide), widely disjunct from the remaining 6 species, which occur E of the Sierra Madre Occidental (4 in the Chihuahuan Desert region, *H. malacophylla* in Tamaulipas, *H. engelmannii* in Texas).

**Pollination ecology:** The strictly diurnal flowers of *H. parviflora* are pollinated by hummingbirds and bees. The nocturnal, less brightly coloured, fragrant flowers of *H. funifera* and *H. nocturna* are pollinated by bats and hawkmoths. The flowers of the latter may occasionally remain open well into the morning when they are visited by bees, while visiting hummingbirds and bumblebees may merely represent nectar thieves. *H. campanulata* combines both syndromes and is pollinated by bats and hawkmoths during the night and by hummingbirds and bees the following day when the flowers close somewhat to form a tube (Engard 1980, Starr 1995, Pellmyr & Augenstein 1997, Starr 1998). While most species of *Agavaceae* are believed to be self-compatible, experimental hand-pollinations indicated that *H. parviflora* might be self-incompatible (Pellmyr & Augenstein 1997, see also Bolliger 2010).

**Ecology:** The carbohydrates stored in a *H. funifera* plant prior to flowering are sufficient to meet only about  $\frac{1}{3}$  of what is needed to produce an average inflorescence with 1–2% fruit set; accordingly all carbohydrates produced during growth are needed to support flowering and fruit production (McLaughlin & Williams 2000). *H. funifera* and *H. nocturna* both exhibit CAM photosynthesis, esp. in older leaves. These have weakly expressed mesophyll succulence closer to that of typical C3 species, and both species are characterized as non-succulent CAM-plants by Ravetta & McLaughlin (1993). Heyduk & al. (2016) found *H. funifera* and *H. parviflora* as CAM plants and characterize them as (weakly) succulent.

**Ethnobotany:** Wild populations of *H. funifera* were formerly a source of fibres used chiefly for twine and coarse sacking (Dewey 1943). McLaughlin (1996), McLaughlin (2000), Sanchez & al. (2010a), and Sanchez & al. (2010b) report about trials to use *H. funifera* leaves as raw material for producing paper and bioenergy.

**Cultivation:** *Hesperaloe* is cultivated since 1849 in England and since 1878 in the USA (Starr 1995). Cultivation advice is given by Starr (1995) and Irish & Irish (2000) for the USA, by Smith & Steyn (2002) for RSA and the Mediterranean, and by Boeuf (2007), Bolliger (2010) and Hochstätter (2011) for European regions. Plants are rather drought-tolerant and do equally well in desert, subtropical and mediterranean climates in direct or indirect sun and fast-draining soils. In a sunny place in fast-draining soil and with rain protection in the winter, plants may be hardy in C Europe (*H. campanulata* to  $-10^{\circ}\text{C}$ , *H. engelmannii* to  $-14^{\circ}\text{C}$ , *H. nocturna* to  $-15^{\circ}\text{C}$ , *H. parviflora* ssp. *parviflora* to  $-18$  (to  $-21$ )  $^{\circ}\text{C}$ ) (Boeuf 2007, Bolliger 2010, Hochstätter 2011).

**H. campanulata** G. D. Starr (Madroño 44(3): 285–286, ill., 1998). **Type:** Mexico, Nuevo León (Starr 93-001 [ARIZ, MEXU, MO, TEX]). — **Lit:** Starr (1995: as sp. nov. #1, with ill.). **Dist:** Mexico (C Nuevo León); open Chihuahuan Desert scrub, limestone slopes and hillsides,

100–600 m; flowers late March to November. **I:** Irish & Irish (2000); Guillot Ortiz & Meer (2006); Hochstätter (2011).

**Ros** moderately caespitose, forming clumps to 0.6–1.2 m Ø; **L** > 25, stiff and erect to slightly spreading, linear-lanceolate, tapering towards the tip, slightly canaliculate, 0.6–1.1 m × 1.5–2.6 cm (widest point 1/3 from the base), medium green, margins finely filiferous, fibres white, 5–7 cm, 6–8 cm apart, terminal **Sp** recurved, canaliculate, not pungent, light brown-grey; **Inf** to 3 m, peduncle green-purple, **Bra** purple, the lower 7–10 cm, fertile part unbranched racemes or usually panicles with 2–5 (–19) part-**Inf** in the upper 1/2–1/3; **Ped** recurved, 8–13 mm, rose; **Fl** tubular-campanulate to broadly campanulate, 20–25 × 20–22 (–28 in cult.) mm, in clusters of 3–8, buds rose; **Tep** strongly recurved; **OTep** linear to linear-lanceolate, 18–22 × 4–8 mm, inside white, outside pink with broad white margins; **St** included; **Fil** 14–16 mm, adnate to the tepal base for 3 mm, white; **Anth** sagittate, 3 mm, yellow-greenish; **Ov** 6–10 × 4–6 mm, white; **Sty** 9–13 mm, included; **Fr** globose or oblong, 20–30 (excl. beak) × 20–25 mm, with a sharp 4–11 mm long beak; **Se** 6–9 × 5–6 mm.

Known only from few localities. Vegetatively like a small *H. funifera*, but easily separated by the pink flower colour (vs. greenish-white). Distinguished from *H. parviflora* by more open flowers and lighter green and less channelled leaves (Starr 1995). Molecular sequence data (Archibald & al. 2015) place *H. campanulata* closest to *H. funifera*. F1 and F2 hybrids between the nocturnal *H. funifera* and the diurnal *H. parviflora* resemble *H. campanulata*, suggesting a putative hybrid origin for the latter (Archibald & al. 2015). The flowers open in the evening and are pollinated at night by bats and hawkmoths; the following day, they close somewhat forming a “tube” and are then visited by hummingbirds (Starr 1998).

**H. chiangii** (G. D. Starr) B. L. Turner (Lundellia 5: 39, 2002). **Type:** Mexico, San Luis Potosí (*Garcia Moya* s.n. [DES]). — **Lit:** Starr (1998: with ills.); Hochstätter (2009: with ills.). **Distr:** Mexico (San Luis Potosí, probably also S Nuevo León and SW Tamaulipas); locally

common in grassland on flat plateaux, open slopes and hills, 1350–1500 m. **I:** Gómez-Pompa & al. (1971: 221, as *H. funifera* from San Luis Potosí); Hochstätter (2011); Archibald & al. (2015: as *H. funifera* ssp.).

≡ *Hesperaloe funifera* ssp. *chiangii* G. D. Starr (1998).

**Ros** with long rhizomes >30 cm, forming broad clumps or fairy rings to >2 m Ø; **L** stiff and erect, lanceolate, not arching, deeply canaliculate, 1–1.5 m × 5–6 cm (from base to middle, when flattened), tapering above to the tip, medium to dark green, fibres coarse, 2–3 mm thick, white to grey near the point of attachment, straight to slightly curled; **Inf** 2–4 m, panicles with 6–8 spreading to ascending part-**Inf** in the upper 1/2; **Fl** tubular, 30 × 25 mm, nocturnal, in clusters of 3–4; **Tep** inside white, outside pinkish-red; **Fr** ovoid to rounded, 25–30 × 25 mm, with a short beak 3 mm long. — **Cytology:** x = 30 (Gómez-Pompa & al. 1971: as *H. funifera* from San Luis Potosí).

First published as a subspecies of *H. funifera*, but geographically isolated and morphologically clearly distinct. This is fully confirmed by molecular sequence data of Archibald & al. (2015), which place *H. chiangii* distant from *H. funifera* and closest to *H. nocturna* and *H. tenuifolia*. Material was already collected by C. G. Pringle in 1891, and identified as *H. funifera*. Reports of *H. funifera* for San Luis Potosí (Standley 1920–1926, Engard 1980) and S Nuevo León and SW Tamaulipas (Ullrich 1990) might refer to *H. chiangii*.

**H. engelmannii** Krauskopf (Notice Bot., [], 1878). **Type** [neo]: USA, Texas (Turner 99–367 [TEX]). — **Lit:** Trelease (1902: as *H. parviflora* var.); Turner & Turner (2002); Diggs & al. (2006); Guillot Ortiz & Meer (2006: as *H. parviflora* var.); Hochstätter (2009); all with ills. **Distr:** USA (C & S-C Texas: Edwards Plateau); sandy, silty, or rocky, usually calcareous soils, usually beneath oaks and associated shrubs and trees; flowers April to June. **I:** Hochstätter (2011).

≡ *Hesperaloe parviflora* var. *engelmannii* (Krauskopf) Trelease (1902).

**Ros** forming clumps to 0.5–1.2 Ø; **L** linear to linear-falcate, recurved, variable, to 1–1.5 m, dark

green to grey-green, tip with pungent grey to brown terminal spine, **L** margins lined purple, not markedly fibrous, fibres white to grey, irregular, 4–5 cm, 2.5–4 cm apart; **Inf** 1–2.5 m, panicles, peduncle sometimes salmon-coloured, with scarious **Bra** 4 × 1 cm, fertile part making up the upper ½, curved, with ascending part-**Inf**; **Ped** to 35 mm, rose, straight; **Fl** in clusters of 3–8, oblong-campanulate, tubular, 25–40 mm; **Tep** linear-oblong, tips slightly cucullate, 20–22 × 10 mm, pink or salmon-coloured, margins light rose; **OTep** rose; **ITep** tending to have white flaring tips; **St** included; **Fil** to 18 mm, rose; **Anth** 3–6 mm (longer than in *H. parviflora*), yellow; **Ov** 5 × 3 mm, white; **Sty** short and thick, mostly 1–2 (–3) × as long as the ovary proper, included and much shorter than the tepals; **Fr** unknown.

The author citation follows Turner & Turner (2002). Previously included in the synonymy of *H. parviflora* (e.g. Starr (1998)), but a distinct species according to Turner & Turner (2002), differing in larger and relatively narrower, somewhat flatter and darker green leaves not markedly fibrous, shorter and thicker styles, larger anthers, and inner tepals with white flaring tips (Hochstätter 2009). According to molecular sequence data (Archibald & al. 2015), *H. parviflora* ssp. *bechtoldii* is nested within *H. engelmannii*, and both place separate from *H. parviflora* s.s. Trelease (1902) describes and depicts a plant in which the first and later flowers had slightly exerted styles, similar to *H. parviflora* ssp. *bechtoldii*. Hybrids with *H. parviflora* ssp. *parviflora* are known in cultivation in the USA and Europe (Hochstätter 2009).

**H. funifera** (K. Koch) Trelease (Annual Rep. Missouri Bot. Gard. 13: 36, tt. 3–4, 1902). **Type** [neo]: Mexico, Coahuila (Engard & Gentry 23241 [ARIZ]). — **Lit**: Trelease (1902); Ullrich (1990); Starr (1995); Hochstätter (2009); all with ills. **Distr**: S USA (SW Texas: Val Verde County), N Mexico (Coahuila, N Nuevo León); calcareous lowlands and foothills in (semi-) arid regions, 350–1000 (–2100) m; flowers April to September. **I**: Irish & Irish (2000); Guillot Ortiz & Meer (2006); Hochstätter (2011).

≡ *Yucca funifera* K. Koch (1862) ≡ *Agave funifera* (K. Koch) Lemaire (1864); **incl.** *Hesperaloe davyi* Baker (1898).

**Ros** forming clumps to 1.5 m Ø, rhizomes short; **L** stiff and erect, linear-lanceolate or lanceolate, rigid, not arching, canaliculate, tapering from the middle towards the tip, 0.8–2 m × (2–) 3–4 (–6) cm (when flattened, from base to middle, to 1.5 cm wide at the base), light or yellowish-green, tip with a brown terminal spine, **L** margins brown, medium to coarsely fibrous, fibres loosely coiled, 8–15 cm, to 12 cm apart, to 1 mm thick, white or grey, or tinged purple at the base; **Inf** 2–4 (–4.6) m, paniculate, peduncle bluish-green, 1.5–1.8 m, with brown scarious **Bra**, fertile part 0.3–1.2 m, making up the upper ½, with 3–8 ascending or arching part-**Inf**; **Ped** slightly curved, 5–6 mm, green to purplish-green; **Fl** rotate-campanulate, 15–25 mm, in clusters of 3–4, opening in the morning, closing in the evening of the same day; **Tep** linear-oblong, 17–22 mm, tips cucullate, inside white; **OTep** outside green at the base, upper ⅓ reddish-purple, 6–7 mm wide; **ITep** outside green and white with a narrow mid-stripe tinged brownish-purple, 8–9 mm wide; **St** exerted; **Fil** 15–18 mm, white, at the base connate to the tepals; **Ov** (6–) 10–12 × 4–5 mm; **Sty** 6–7 × 4–5 mm, thick, included to scarcely exerted; **Fr** globose or broadly oblong, 25–35 × 25–35 mm, sharply beaked, beak 2–4 mm; **Se** 7–9 × 5–7 mm. — **Cytology**: 2n = 60 (Engard 1980; Pinkava & Baker 1985).

The largest species of the genus. Mature plants are easily recognizable by their stiff long leaves. Young plants are difficult to distinguish from *H. parviflora*, but the leaves are greener and stiffer in *H. funifera* (Starr 1995). Molecular sequence data place *H. funifera* closest to *H. campanulata*; the distributions of both taxa overlap in N Mexico where Starr observed a putative hybrid population of *H. funifera* with intermediate plant sizes and flower colours (Archibald & al. 2015).

The single collection from Texas (Butterwick & Poole 1980) is regarded as doubtful and possibly resulting from introduction (Turner & Turner 2002). Records of *H. funifera* from San Luis Potosí are *H. chiangii* (see there). Dewey (1943) reported the species from Chihuahua, but this

needs confirmation; the genus is not at present recorded from Chihuahua. A specimen from near Ciudad Victoria in Tamaulipas (*González M.*, MEXU 584975) labelled *H. funifera* would confirm earlier records of the species from that state (Dewey l.c.; Ullrich l.c.), but was collected not far from the sole locality of *H. malacophylla* and might represent that species. In cultivation, hybrids with *H. parviflora* ssp. *parviflora* and *H. tenuifolia* are known (Starr 1995).

**H. malacophylla** Hochstätter & Martínez-Ávalos (Plante Grasse 30(1): 20–22, ill., 2010). **Type:** Mexico, Tamaulipas (*Martínez-Ávalos* 898 [UAT]). — **Lit:** Hochstätter (2011: with ill.). **Distr:** Mexico (W-C Tamaulipas); open moist woodland, in the shade of oaks and pines, 800–1000 m; known from the type locality only; flowers April to May.

**Ros** in small clumps to 0.4 m Ø; **L** erect or arching, soft, flexible, 0.5–1.5 m, width not indicated, yellow-green, margins finely filiferous, fibres flexible; **Inf** usually branched panicles, 1–3 m, fertile part to 1 m making up the upper ½; **Fl** tubular-campanulate, 25–30 × 20 mm at anthesis; **Tep** white within, pink outside; **Fr** globose, 25 × 25 mm, sharply beaked, beak short; **Se** 8 × 4–7 mm, surface structured.

The short protologue lacks several floral features. Characterized by its soft and flexible, erect to arching leaves (vs. stiff, strong and ± erect in all other taxa), and notable for its occurrence in relatively moist habitats. See also under *H. funifera*.

**H. nocturna** Gentry (Madroño 19(3): 74–78, 1967). **Type:** Mexico, Sonora (*Gentry & Felger* 19988 [US, ARIZ, DES, MEX, NY]). — **Lit:** Gentry (1972); Starr (1995); Hochstätter (2009); all with ill. **Distr:** Mexico (N-C Sonora); talus slopes of basalt cliffs, 950–1150 m; flowers April to July. **I:** Hochstätter (2011); Guillot Ortiz & Meer (2016: 20–21).

**Ros** very dense, densely caespitose and forming clumps 1–2 m Ø; **L** upright and arching, narrowly linear, striate, tapering gradually from the base to the long-attenuate tip, flat towards the base, deeply canaliculate upwards, 1–1.5 m × 1–2 cm (at the base), dark green, tip an acicular

and pungent spine, fraying with age, **L** margins narrow, brown, white-filiferous, fibres irregularly wavy, white; **Inf** to 1.5–4 m, peduncle long, with lanceolate dry **Bra** 4–6 cm or less, fertile part slender racemes or panicles with 2–3 part-**Inf** in the upper ½; **Ped** 5–18 mm; **Fl** campanulate-rotate, 24–30 mm, nocturnal, in clusters of 4, 6 or 8; **Tep** reflexed at anthesis, 15–25 mm, whitish or greenish-white within, buds pruinose pink to lavender, greenish below; **OTep** 6–7 mm wide, outside reddish with greenish-brown midstripe (pink or lavender fide Gentry); **ITep** 8–9 mm wide, outside with broad reddish-purple mid-stripe (greenish-pink or greenish-lavender fide Gentry); **St** included; **Fil** 8–9 mm, as long as the style, attached to the base of the tepals for 3 mm; **Anth** sagittate, versatile, 8–9 mm; **Ov** oblong, trigonous, 10 × 4 mm, basis ringed with a nectary, roundly angled at the apex; **Sty** stout, 8 mm, included; **Sti** capitate, papillate; **Fr** depressed-ovoid or oblong, 25–40 × 25–45 mm, shortly beaked, apiculate; **Se** 11 × 8 mm. — **Cytology:** 2n = 60 (Engard 1980).

Easily identifiable by its long narrow leaves and the campanulate-rotate nocturnal flowers (Starr 1995). Molecular sequence data (Archibald & al. 2015) place *H. nocturna* closest to *H. tenuifolia*, suggesting that the Sierra Madre Occidental was traversed only once in the evolution of *Hesperaloe*.

The short but distinct flower tube mentioned by Gentry (1967) and Gentry (1972) is not mentioned by later authors and appears to be erroneous, and Gentry's drawings show the tepals free to the base as in all other species. The nocturnal flowers remain open well into the next morning on humid days. The predominant night-time pollinator is an unidentified species of bat, and a bee is a regular morning visitor, while hummingbirds are probably merely nectar thieves (Engard 1980). In cultivation, hybrids with *H. parviflora* ssp. *parviflora* are known (Starr 1995).

Hesdörfer (1904) reported that C. A. Purpus collected “*H. funifera*” in S Arizona back in 1903. If not in error or relating to cultivated plants, this might have been an early record of *H. nocturna* across the border, although *Hesperaloe* is not currently recorded from Arizona.



**H. parviflora** (Torrey) J. M. Coulter (Contr. US Nation. Herb. 2: 436, 1894). **Type** [lecto]: USA, Texas (*Wright* 1908 [GH, NY]). — **Distr**: USA (SW Texas), N Mexico (NW & N Coahuila).

≡ *Yucca parviflora* Torrey (1859); **incl.** *Aloe yuccifolia* A. Gray (1867) (*nom. illeg.*, ICN Art. 52.1) ≡ *Hesperaloe yuccifolia* (A. Gray) Engelm. (1871) (*nom. illeg.*, ICN Art. 52.1).

Molecular sequence data (Archibald & al. 2015) show the species to be polyphyletic, with *ssp. bechtoldii* nested within *H. engelmannii*, and both are placed separate from *H. parviflora ssp. parviflora*.

**H. parviflora ssp. bechtoldii** Hochstätter (CactusWorld 27(2): 103–105, ills., 2009). **Type**: Mexico, Coahuila (*Bechtold* 733 [HEID]). — **Lit**: Hochstätter (2011). **Distr**: N Mexico (N Coahuila); flat sandy desert area, 660 m; known only from the type locality; flowers April to May.

≡ *Hesperaloe bechtoldii* (Hochstätter) Hochstätter (2016) (*nom. inval.*, ICN Art. 29.1, Ex. 2).

Differs from *ssp. parviflora*: **Ros** smaller, forming irregular small clumps to 20–40 cm Ø; **L** stiff, erect, lanceolate, 20–40 cm, curving somewhat to the side, narrowly canaliculate; **Inf** unbranched racemes to 30–80 cm; **Fl** tubular, longer, 30–50 mm, not widely opening; **Sty** exserted, 12–18 mm; **Fr** 25–30 × 20–30 mm.

The protologue claims that the exserted style is characteristic, but this character is also sometimes present in the typical subspecies.

**H. parviflora ssp. parviflora** — **Lit**: Smith & Steyn (2002); Hochstätter (2009); both with ills. **Distr**: USA (SW Texas), N Mexico (NW Coahuila); creosote scrub, oak and chaparral zones, 500–2000 m; flowers March to September. **I**: Curtis's Bot. Mag. 126: t. 7723, 1900, as *H. yuccaefolia*; Hochstätter (2011). — Fig. 1.

**Incl.** *Hesperaloe yuccoides* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1/61.1).

**Ros** densely caespitose, forming clumps to 1 m Ø or more; **L** arching, linear, narrowing towards the tip, 30–60 (–125) × 0.8–1.8 (–2.5) cm (at the base), dark, shiny or bluish-green, tip pungent,



**Fig. 1** *Hesperaloe parviflora ssp. parviflora*. (Copyright: U. Eggli)

5–20 mm, brown, **L** margins finely filiferous, fibres tightly curled, 4–6 cm, 3–5 cm apart, white or grey; **Inf** panicles to 1–2.5 m, peduncle 50–75 cm, fertile part with few part-**Inf** mainly in the upper ½, rachis and part-inflorescences rose-purple; **Ped** to 25 mm, rose-purple; **Fl** tubular or oblong-campanulate, suberect, 25–35 mm, diurnal, in indeterminate clusters; **Tep** linear-oblong, pressed together at anthesis, tip ± curved outwards, obtuse, with a minute tuft of white hair-like papillae; **OTep** 15–20 × 4–7 mm, salmon-coloured, coral-red, pink, or rosy-red (also yellow or pale cream in horticultural selections); **ITep** 17–20 × 8–9 mm; **St** included; **Fil** 7–13 mm, white or rosy, attached to the tepal base for 1 mm; **Anth** 2–3 mm; **Ov** ovoid to conical-ovoid, small, very slightly 6-grooved, 4–6 × 3–4 mm; **Sty** slender, elongate, 12–13 mm, slightly tapering, included or 1–3 mm exserted, triquetrous near the base, white; **Sti** 3-lobed, somewhat fimbriate; **Fr** woody, ovoid or oblong-ovoid, 25–40 ×

25–30 mm, beaked; **Se** 9–10 × 6–8 mm. — **Cytology:** 2n = 60 (McKelvey & Sax 1933, Engard 1980).

Distinguished by the combination of narrow, mainly salmon-coloured to reddish flowers and relatively short and dark green leaves (Starr 1995). Starr (1998) and Smith & Steyn (2002) describe the style as “included”, but Trelease (1902: 30), Powell (1988: Fig. 40), Turner & Turner (2002: 41) and Diggs & al. (2006) all report that the style may also be exerted (see also ssp. *bechtoldii*). Pollination is probably exclusively by hummingbirds, and the visiting bees appear to be non-pollinating nectar thieves (Engard 1980). Hummingbird pollination was also confirmed by Pellmyr & Augenstein (1997).

In cultivation, plants with yellow (cultivar ‘Yellow’) and pale cream flowers are known from Europe (Guillot Ortiz & Meer 2006, Hochstätter 2009), and the USA (Irish & Irish 2000). The yellow-flowered plants possibly belong to *H. engelmannii* on the base of flower morphology (Guillot Ortiz & Meer 2006). ‘Perpa’ is a cultivar with scarlet-red flowers. Hybrids of cultivated origin are known with *H. funifera* and *H. nocturna* (Starr 1998). For a micropropagation protocol see Richwine & al. (1996).

**H. tenuifolia** G. D. Starr (Madroño 44(3): 293–294, ills., 1998). **Type:** Mexico, Sonora (Jenkins & Meyer 90–63 [ARIZ]). — **Lit:** Starr (1995: as sp. nov. #2); Hochstätter (2009); Hochstätter (2011); all with ills. **Distr:** NW Mexico (S Sonora: Cerro Agujudo); dry rhyolitic hilltops in pine-oak forest or woodland, 1200–1500 m; only known from the type locality; flowers April to May.

**Ros** open, sparsely caespitose and forming small clumps to 50 cm Ø; **L** few, arching, narrowly linear, tapering towards the tip, 50–100 × 0.5–1 cm (at the base), apiculate, **L** margins thin, finely filiferous, fibres not tightly curled, white; **Inf** racemes or narrow panicles with 2–3 part-**Inf**, to 1.5–2 m; **Fl** rotate, small, 13 × 10 mm, nocturnal; **OTep** linear, 13 × 5 mm, outside dark pinkish-red, inside white with reddish margin; **ITep** ovate, 15 × 8 mm, outside dark pinkish-red with white margin, inside white; **St** included;

**Fil** 9 mm, attached to the tepal base for 2 mm; **Anth** 3 mm; **Ov** 6 × 3 mm; **Sty** 4 mm; **Fr** woody, ovoid, 20–30 × 20–25 mm, beak none or 1 mm; **Se** 10 × 5–7 mm.

Very easily recognized by its long and very thin leaves with finely textured very curly marginal fibres. The very short open flowers cannot be confused with those of any other species (Starr 1995). Molecular sequence data (Archibald & al. 2015) place *H. tenuifolia* closest to *H. nocturna* (see also there). — Hybrids of cultivated origin with *H. funifera* are known (Starr 1995).

## References

- Archibald, J. K. [ & al. 2015], Kephart, S. R., Theiss, K. E., Petrosky, A. L. & Culley, T. M. (2015) Multilocus phylogenetic inference in subfamily *Chlorogaloideae* and related genera of *Agavaceae* — Informing questions in taxonomy at multiple ranks. *Molec. Phylogen. Evol.* 84: 266–283, ills., map. <https://doi.org/10.1016/j.ympev.2014.12.014>
- Boeuf, T. (2007) *Yucca* & Co. Winterharte Wüstengärten in Mitteleuropa anlegen und pflegen. Berlin (DE): Medemia.
- Bogler, D. J. & Simpson, B. B. (1995) A chloroplast DNA study of the *Agavaceae*. *Syst. Bot.* 20(2): 191–205. <http://www.jstor.org/stable/2419449>
- Bogler, D. J. & Simpson, B. B. (1996) Phylogeny of *Agavaceae* based on ITS rDNA sequence variation. *Amer. J. Bot.* 83(9): 1225–1235. <http://www.jstor.org/stable/2446206>
- Bolliger, T. (2010) *Hesperaloe parviflora* und ihre Winterhärte. *Kakt. and. Sukk.* 61(11): 290–293, ills.
- Butterwick, M. & Poole, J. M. (1980) *Hesperaloe funifera* (*Agavaceae*) in Texas. *Sida* 8(3): 314–315. <https://biodiversitylibrary.org/page/10010572>
- Clary, K. H. & Simpson, B. B. (1995) Systematics and character evolution of the genus *Yucca* L. (*Agavaceae*): Evidence from morphology and molecular analyses. *Bol. Soc. Bot. México* 56: 77–88. <https://doi.org/10.17129/botsci.1466>
- Dewey, L. H. (1943) Fiber production in the western hemisphere. Washington (US): US Department of Agriculture. <https://archive.org/details/fiberproductioni518dewe>
- Diggs, G. M. [ & al. 2006], Lipscomb, B. L., Reed, M. D. & O’Kennon, R. J. (2006) Illustrated flora of East Texas. Volume 1: Introduction, Pteridophytes, gymnosperms and monocotyledons. Fort Worth (US): Botanical Research Institute of Texas & Austin College.
- Engard, R. G. (1980) *Hesperaloe*: Potential crop for arid lands. In: Anonymus (ed.): Conferencia Internacional sobre *Yucca* 1979; pp. 115–123. Saltillo (MX): Centro de Investigación en Química Aplicada.

- Gentry, H. S. (1967) A new *Hesperaloe* from Sonora, Mexico. *Madroño* 19(3): 74–78. <http://www.jstor.org/stable/41423267>
- Gentry, H. S. (1972) *The Agave family in Sonora*. Agricultural handbook No. 399. Washington D.C. (US): US Department of Agriculture. <http://naldc.nal.usda.gov/download/CAT87209091/PDF>
- Gómez-Pompa, A. [ & al. 1971], Villalobos-Pietrini, R. & Chimal, A. (1971) Studies in the *Agavaceae* I. Chromosome morphology and number of seven species. *Madroño* 21(4): 208–221, ills. <http://www.jstor.org/stable/41423783>
- Guillot Ortiz, D. & Meer, P. van der (2006) El género *Hesperaloe* Engelm. cultivado en la Península Ibérica e Islas Baleares. *Bot. Complut.* 30: 137–145.
- Guillot Ortiz, D. & Meer, P. van der (2016) Nuevos datos sobre las especies y taxones infraespecíficos del género *Hesperaloe* Engelm. cultivados en la Península Ibérica y las Islas Baleares. *Bouteloua* 25: 13–23, ills.
- Halpin, K. M. & Fishbein, M. (2013) A chloroplast phylogeny of *Agavaceae* subfamily *Chlorogaloideae*: Implications for the tempo of evolution on serpentine soils. *Syst. Bot.* 38(4): 996–1011, ills., map. <https://doi.org/10.1600/036364413X674850>
- Hesdörfer, M. (1904) Die Reisen des Sammlers C. A. Purpus in Mexiko im Jahre 1903. *Gartenwelt* 8(32): 378–380. <http://biodiversitylibrary.org/page/6613949>
- Heyduk, K. [ & al. 2016], McKain, M. R., Lalani, F. & Leebens-Mack, J. (2016) Evolution of a CAM anatomy predates the origins of Crassulacean Acid Metabolism in the *Agavoideae* (*Asparagaceae*). *Molec. Phylogen. Evol.* 105: 102–113, ills. <https://doi.org/10.1016/j.ympev.2016.08.018>
- Hochstätter, F. (2009) The genus *Hesperaloe* (*Agavaceae*). *CactusWorld* 27(2): 97–106, ills., key. <https://www.jstor.org/stable/42795447>
- Hochstätter, F. (2011) Die Gattung *Hesperaloe*. *Kaktusblüte* 2011: 52–61, ills.
- Irish, M. & Irish, G. (2000) *Agaves, Yuccas and related plants*. A gardener's guide. Portland (US): Timber Press.
- McKelvey, S. D. & Sax, K. (1933) Taxonomic and cytological relationships of *Yucca* and *Agave*. *J. Arnold Arbor.* 14: 76–81. <https://www.jstor.org/stable/43780651>
- McLaughlin, S. P. (1996) Domestication of *Hesperaloe*: Progress, problems, and prospects. In: Janick, J. (ed.): *Progress in new crops*; pp. 395–401. Arlington (US): ASHS Press. <https://hort.purdue.edu/newcrop/proceedings1996/V3-395.html>
- McLaughlin, S. P. (2000) Properties of paper made from fibers of *Hesperaloe funifera* (*Agavaceae*). *Econ. Bot.* 54(2): 192–196. <https://doi.org/10.1007/BF02907822>
- McLaughlin, S. P. & Williams, R. R. (2000) Carbohydrates and flowering in *Hesperaloe funifera* (Koch) Trel. (Samandoque). *Bol. Soc. Bot. México* 66: 67–72. <http://www.redalyc.org/articulo.oa?id=57706606>
- Pellmyr, O. & Augenstein, E. J. (1997) Pollination biology of *Hesperaloe parviflora*. *Southw. Naturalist* 42(2): 182–187. <http://www.jstor.org/stable/30055259>
- Pinkava, D. J. & Baker, M. A. (1985) Chromosome and hybridization studies of *Agaves*. *Desert Pl.* 7(2): 93–100, ills. <http://repository.arizona.edu/handle/10150/554212>
- Powell, A. M. (1988) *Trees & Shrubs of Trans-Pecos Texas*. Terlingua (US): Big Bend Natural History Association.
- Ravetta, D. A. & McLaughlin, S. P. (1993) Photosynthetic pathways of *Hesperaloe funifera* and *H. nocturna* (*Agavaceae*): Novel sources of specialty fibers. *Amer. J. Bot.* 80(5): 524–532. <https://doi.org/10.2307/2445367>
- Richwine, A. M. [ & al. 1996], Tipton, J. L. & Thompson, G. A. (1996) Micropropagation of *Hesperaloe parviflora*. *In Vitro Cell. Developmental Biol. Plant* 32(4): 262–266. <https://doi.org/10.1007/BF02822698>
- Robbins, R. L. (2002) *Hesperaloe*. In: *Flora of North America north of Mexico*; 26: 413, 441–442. New York (US)/Oxford (GB): Oxford University Press.
- Rocha, M. [ & al. 2006], Good-Ávila, S. V., Molina-Freaner, F., Arita, H. T., Castillo, A., García-Mendoza, A., Silva-Montellano, A., Gaut, B. S., Souza, V. & Eguiarte, L. E. (2006) Pollination biology and adaptive radiation of *Agavaceae*, with special emphasis on the genus *Agave*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 329–344, maps. <https://doi.org/10.5642/aliso.20062201.27>
- Sanchez, R. [ & al. 2010a], Rodríguez, A., Navarro, E., Conesa, J. A. & Jimenez, L. (2010a) Use of *Hesperaloe funifera* for the production of paper and extraction of lignin for synthesis and fuel gases. *Biomass & Bioenergy* 34(10): 1471–1480. <https://doi.org/10.1016/j.biombioe.2010.04.019>
- Sanchez, R. [ & al. 2010b], Rodríguez, A., Requejo, A., Ferrer, A. & Navarro, E. (2010b) Soda pulp and fuel gases synthesis from *Hesperaloe funifera*. *Bioresource Technol.* 101(18): 7032–7040. <https://doi.org/10.1016/j.biortech.2010.04.008>
- Smith, G. F. & Steyn, E. M. A. (2002) The Red Yucca, *Hesperaloe parviflora*: A beautiful *Agavaceous* species. *Aloe* 39(2): 42–45, ills.
- Standley, P. C. (1920–1926) *Trees and shrubs of Mexico*. *Contr. US Nation. Herb.* 23(1–5): 1721 pp. <https://doi.org/10.5962/bhl.title.15726>
- Starr, G. (1995) *Hesperaloe*: Aloes of the West. *Desert Pl.* 11(4): 3–8, ills. <https://repository.arizona.edu/handle/10150/554092>
- Starr, G. (1998) A revision of the genus *Hesperaloe* (*Agavaceae*). *Madroño* 44(3): 282–296, map, ills., key. <http://www.jstor.org/stable/41425214>
- Trelease, W. (1902) *The Yuccaeae*. *Annual Rep. Missouri Bot. Gard.* 13: 27–133, tt. 1–99. <https://doi.org/10.5962/bhl.title.20018>
- Turner, B. L. & Turner, M. W. (2002) Natural populations of *Hesperaloe* (*Agavaceae*) in Texas. *Lundellia* 5: 34–43, ills.
- Ullrich, B. (1990) *Hesperaloe funifera* (Koch) Trelease. *Kakt. and Sukk.* 41(3): centre page pullout 1990/7, ills.



## Hesperoyucca AGAVACEAE

J. Thiede

**Hesperoyucca** (Engelmann) Trelease (Annual Rep. Missouri Bot. Gard. 4: 208, 1893). **Type:** *Yucca whipplei* Torrey. — **SHH-Clade** — **Lit:** Turner & al. (1995: ecology); Clary (2001: classification); Hochstätter (2000: 15–23, as sect. *Hesperoyucca*, ill. synopsis); Boeuf & al. (2009: 126–129, ill. synopsis); Powell (2013: summary pollination ecology). **Distr:** W USA, NW Mexico. **Etym:** Gr. ‘hespera’, evening; for the occurrence in W North America (i.e. in the West, where the sun disappears in the evening); and for the similarity to *Yucca* (*Agavaceae*).

≡ *Yucca* [?] *Hesperoyucca* Engelmann (1871).

≡ *Yucca* subgen. *Hesperoyucca* (Engelmann) Baker (1876).

Acaulescent rosette plants, monocarpic when remaining unbranched or polycarpic otherwise; **Ros** solitary or in colonies, sessile, sometimes stem rhizomatous, single or caespitose; **L** linear or rarely narrowly lanceolate, rigid and sword-like to flexible and frequently falcate, plano-convex or subtriquetrous, or keeled on both faces, 25–115 × 0.5–4 cm, ± grey-green, finely striate, base expanded to ± 4–7 × 4–7 cm, ± white to greenish, margin thin, horny, pale yellow, without fibres, mostly denticulate, terminal spine sharp;

**Inf** terminal large panicles, 1.4–8 m with a bracteate peduncle 0.9–4.5 m long, flowering part dense, cylindrical or somewhat slenderly ellipsoid; **Fl** densely arranged, usually broadly expanding, pendent, campanulate or ± globose, 3.5–5 cm, very fragrant; **Tep** broadly lanceolate, nearly equal, 3–4.5 (–6) × 0.8–2.5 cm, white or creamy white to greenish or purple-tinged, tips generally purple, free to the base; **Fil** straight, linear below, tip angled, club-like, papillose, attached to the lower part of the tepals so that the stamens are pulled away from the ovary as the flower opens; **Anth** reniform, pollen uniquely glutinous; **Ov** superior, stout, 8–12 × 6–10 mm; **Sty** short, slender, white; **Sti** distinctly capitate, green towards the centre, fringed with elongated translucent papillae; **Fr** erect, obovoid, strictly loculicidally dehiscent, 3–5 × 1.5–4 cm; **Se** flat, thin, smooth, without marginal wing, 6–7 × 8 mm, dull black. — **Cytology:** n = 30 (Halpin & Fishbein 2013: 1007).

With the exception of Trelease (1893) and indirectly also Baker (1892), most earlier authors included *Hesperoyucca* within *Yucca*. Recent molecular studies (Bogler & Simpson 1995, Bogler & al. 1995, Bogler & Simpson 1996, Bogler & al. 2006, Smith & al. 2008) and a combined morphological/molecular study (Clary & Simpson 1995) clearly revealed a position as sister group of *Hesperaloe* and thus separate from *Yucca*. In fact, the recent molecular phylogenies of Halpin & Fishbein (2013), Archibald & al. (2015) and McKain & al. (2016) all show *Hesperoyucca*

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as sister of *Hesperaloe* + *Schoenolirion*, in an *Agavaceae* subclade completely distant to that which includes *Yucca*. A closer association with *Yucca* is only evident in the molecular phylogeny of Good-Avila & al. (2006) and in the morphology-based phylogeny of Hernández-Sandoval (1995). Consequently, *Hesperoyucca* should be treated as separate genus, morphologically clearly distinct from *Yucca*, as in the first edition of this handbook and in several modern floras and checklists, while some still retain it as synonym of *Yucca*.

*Hesperoyucca* differs clearly from *Yucca* (data in brackets) in forming a definite bulb in the seedling stage (Webber 1953: t. 53) (vs. bulb absent), its capitate bright green and densely long-papillate stigma (vs. 3-lobed, white, papillose on the inner surface), its filaments basally attached to the tepals, usually longer than the pistil, finely papillate, and  $\pm$  swollen the entire length, erect or spreading outwardly from the point of attachment at anthesis, bearing tufts of papillae at the apex (vs. filaments not attached to the tepals, usually shorter than the pistil, pubescent, distally clavate and held close to the ovary and bent outwards near the swollen apex), its cordate anthers (vs. sagittate or hastate), and its strictly loculicidally dehiscent fruits (vs. indehiscent or, if dehiscent, septicidal, occasionally also septicidal and loculicidal). The often very large inflorescences of *Hesperoyucca* by far exceed the inflorescence size in *Yucca*, and unbranched plants (“ssp. *whipplei*”) are monocarpic, whereas some branched plants (“ssp. *caespitosa*”) develop new rosettes from the leaf axils of very young plants; both features are unknown in *Yucca*.

Author citation and date and place of valid publication were differently interpreted over time and have been clarified by Greenhouse & Strother (2002).

**Pollination:** Powell (2013) published a comprehensive summary of present knowledge of the pollination of *Hesperoyucca*: The *Yucca* moth *Tegeticula maculata* appears to be the only pollinator, with 3 distinct geographical races. Male moths usually stay in the same inflorescence for their whole life, while females usually translocate to other inflorescences (average 53 m distance). The plants are predominantly self-sterile.

**Ethnobotany:** According to Hodgson (2001, 43–44, ill.), *H. whipplei* was formerly used as food by the local populations in its range. The base of the inflorescence as well as the “heads” left when the leaves are pruned were roasted or baked, and then tasted like a fibrous sweet potato. Young flowers were also roasted and eaten.

**H. newberryi** (McKelvey) Clary (Sida 19(4): 845, 2001). **Type:** USA, Arizona (McKelvey 4087 [A]). — **Distr:** USA (Arizona: Mohave & Coconino Counties: W slopes of the Colorado River Canyon); rocky granite, 400–1300 m; spring-flowering. **I:** Hochstätter (2015: 3, 12, 15, as *Yucca*).

$\equiv$  *Yucca newberryi* McKelvey (1947)  $\equiv$  *Yucca whipplei* ssp. *newberryi* (McKelvey) Hochstätter (2000); **incl.** *Yucca newberryi* ssp. *mckelveyana* Hochstätter (2015).

Monocarpic; **Ros** solitary; **L** 50–60 cm, 0.7–2 cm wide at the base in narrow-leaved forms, 2–2.5 cm in broader-leaved forms; **Inf** 2.8–3.2 m, peduncle 1.4–1.6 m  $\times$  10–14 cm, floriferous part in the upper  $\frac{1}{2}$ , in outline 4–55 cm wide at the widest point; **Fr** woody capsules, at maturity with slight or inconspicuous placental wings.

**H. whipplei** (Torrey) Trelease (Annual Rep. Missouri Bot. Gard. 4: 208, 1893). **Type** [lecto]: USA, California (Schott s.n. [NY]). — **Lit:** Schaffer & Schaffer (1977: pollination ecology); Schaffer & Schaffer (1979: pollination ecology); Aker (1982: summary pollination ecology); Turner & al. (1995: 414–416, as *Yucca*); Powell (2013: summary pollination ecology). **Distr:** SW USA (SW California), NW Mexico (N Baja California, N Baja California Sur, NW Sonora: Pinacate region); coastal sage, chaparral, desert woodland, 0–1400 (–2500) m; flowers (February to) May–June. **I:** Greulich (2012); Hochstätter (2015: 5–10). – Figs. 1 and 2.

$\equiv$  *Yucca whipplei* Torrey (1859); **incl.** *Yucca californica* Groenland (1858); **incl.** *Yucca graminifolia* Alph. Wood (1868) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca engelmannii* Masters (1880); **incl.** *Yucca ortgiesiana* Roetzl (1880); **incl.** *Yucca whipplei* var. *violacea* André (1884); **incl.** *Hesperoyucca whipplei* var. *graminifolia* Trelease (1893)  $\equiv$  *Yucca whipplei* fa. *graminifolia*





**Fig. 1** *Hesperoyucca whipplei*. (Copyright: U. Eggli)



**Fig. 2** *Hesperoyucca whipplei*. (Copyright: U. Eggli)

(Trelease) Voss (1895); **incl.** *Yucca nitida* C. Wright ex W. Watson (1906); **incl.** *Yucca whipplei* var. *caespitosa* M. E. Jones (1929)  $\equiv$  *Yucca whipplei* ssp. *caespitosa* (M. E. Jones) A. L. Haines (1942); **incl.** *Yucca whipplei* var. *parishii* M. E. Jones (1929)  $\equiv$  *Yucca whipplei* ssp. *parishii* (M. E. Jones) A. L. Haines (1941); **incl.** *Yucca whipplei* ssp. *intermedia* A. L. Haines (1941)  $\equiv$

*Yucca whipplei* var. *intermedia* (A. L. Haines) J. M. Webber (1953); **incl.** *Yucca whipplei* ssp. *percursa* A. L. Haines (1941)  $\equiv$  *Yucca whipplei* var. *percursa* (A. L. Haines) J. M. Webber (1953); **incl.** *Yucca whipplei* ssp. *typica* A. L. Haines (1941) (*nom. inval.*, ICN Art. 24.3); **incl.** *Yucca peninsularis* McKelvey (1947)  $\equiv$  *Hesperoyucca peninsularis* (McKelvey) Clary (2001); **incl.** *Yucca whipplei* ssp. *eremica* Epling & A. L. Haines (1957); **incl.** *Yucca whipplei* ssp. *rigata* Afferni & Drovandi ex Afferni (2004).

Monocarpic and **Ros** solitary, or polycarpic and **Ros** caespitose and forming small to large, compact or open groups, sometimes rhizomatous, sometimes with secondary rosettes at the base or stem branching after flowering to form new rosettes; **L** 20–90 (–125)  $\times$  0.7–4 cm at the base; **Inf** 3–6 (–8) m, peduncle 0.9–3 (–4.5) m, 2.5–15 cm  $\varnothing$  near the base, floriferous part 2.5–2.8 m, 1 when rosettes are solitary, 1 to many per group when rosettes form colonies; **Fr** woody capsules, at maturity with conspicuous placental wings.

*Yucca californica* is here listed as synonym with considerable doubt and would have priority if it is indeed conspecific. Within *H. whipplei*, Trelease (1893) recognized 2 varieties, Haines (1941) and Munz & Keck (1959) each recognized 5 subspecies, and Webber (1953) recognized 4 varieties based on growth form. In contrast, McKelvey (1938) and McKelvey (1947) as well as McKinney & Hickman (1993) argued that growth form is highly variable and recognition of any infraspecific taxa in *H. whipplei* is unwarranted. Moreover, wild populations often contain plants of different “varieties” (Keeley & Tufenkian 1983), and seeds from one capsule may even produce all possible growth forms (DeMason 1984). Consequently, no infraspecific taxa are recognized here.

*H. peninsularis* from Baja California is sunk here following Govaerts (2014+, accessed Sept. 2018). The Californian and Mexican populations show a continuous distribution (Turner & al. 1995), the differences in leaf size given by Clary (2001) are contiguous, and material from Baja California (e.g. *Hodgson 9577* [DES, digital image!]) exhibits the conspicuous placental

wings present in the Californian plants but absent in *H. newberryi*.

Forms of *H. whipplei* from higher altitudes may be winterhardy in protected sites outdoors in C Europe and may reach flowering size in as little as 13 years (Bolliger 1998). The frost tolerance is given as about  $-15\text{ }^{\circ}\text{C}$  in C Europe (Boeuf 2007) and to about  $-12\text{ }^{\circ}\text{C}$  for the USA (Irish & Irish 2000). Wolf (1935) (cited from Hodgson (2001)) reports that rosettes need 6–7 years to reach flowering size.

## References

- Aker, C. L. (1982) Spatial and temporal dispersion patterns of pollinators and their relationship to the flowering strategy of *Yucca whipplei* (Agavaceae). *Oecologia* 54(2): 243–252. <https://doi.org/10.1007/BF00378399>
- Archibald, J. K. [& al. 2015], Kephart, S. R., Theiss, K. E., Petrosky, A. L. & Culley, T. M. (2015) Multilocus phylogenetic inference in subfamily *Chlorogaloideae* and related genera of *Agavaceae* — Informing questions in taxonomy at multiple ranks. *Molec. Phylogen. Evol.* 84: 266–283, ill., map. <https://doi.org/10.1016/j.ympev.2014.12.014>
- Baker, J. G. (1892) Agaves and arborescent *Liliaceae* on the Riviera. *Bull. Misc. Inform. Kew* 1892(61): 1–10. <http://www.jstor.org/stable/4102510>
- Boeuf, T. (2007) *Yucca & Co.* Winterharte Wüstengärten in Mitteleuropa anlegen und pflegen. Berlin (DE): Medemia.
- Boeuf, T. [& al. 2009], Bechtold, M. & Horn, K. (2009) Halbsträucher und Schopfbäume. *Yucca* und *Hesperoyucca*. Pforzheim (DE): Deutsche Kakteen-Gesellschaft.
- Bogler, D. J. & Simpson, B. B. (1995) A chloroplast DNA study of the *Agavaceae*. *Syst. Bot.* 20(2): 191–205. <http://www.jstor.org/stable/2419449>
- Bogler, D. J. & Simpson, B. B. (1996) Phylogeny of *Agavaceae* based on ITS rDNA sequence variation. *Amer. J. Bot.* 83(9): 1225–1235. <http://www.jstor.org/stable/2446206>
- Bogler, D. J. [& al. 1995], Neff, J. L. & Simpson, B. B. (1995) Multiple origins of the *Yucca* — *Yucca* Moth association. *Proc. Nation. Acad. Sci. USA* 92(15): 6864–6867, ill. <http://www.pnas.org/content/92/15/6864.full.pdf+html>
- Bogler, D. J. [& al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on *ndhF*, *rbcl*, and ITS sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>
- Bolliger, T. (1998) Nach 13 Jahren kam die Blüte: *Yucca whipplei* Torrey ssp. *parishii* in Mitteleuropa im Freiland gehalten. *Kakt. and. Sukk.* 49(8): 187–189, ill.
- Clary, K. H. (2001) The genus *Hesperoyucca* (Agavaceae) in the western United States and Mexico: New nomenclatural combinations. *Sida* 19(4): 839–847, ill. <https://biodiversitylibrary.org/page/9307939>
- Clary, K. H. & Simpson, B. B. (1995) Systematics and character evolution of the genus *Yucca* L. (Agavaceae): Evidence from morphology and molecular analyses. *Bol. Soc. Bot. México* 56: 77–88. <https://doi.org/10.17129/botsci.1466>
- DeMason, D. A. (1984) Offshoot variability in *Yucca whipplei* ssp. *percursa* (Agavaceae). *Madroño* 31: 197–202. <https://biodiversitylibrary.org/page/47946082>
- Good-Avila, S. V. [& al. 2006], Souza, V., Gaut, B. S. & Eguiarte, L. E. (2006) Timing and rate of speciation in *Agave* (Agavaceae). *Proc. Nation. Acad. Sci. USA* 103(24): 9124–9129. <https://doi.org/10.1073/pnas.0603312103>
- Govaerts, R. H. A. (comp.) (2014+) World checklist of selected plant families [continuously updated]. Richmond (GB): Trustees of the Royal Botanic Gardens, Kew. <http://apps.kew.org/wcsp>
- Greenhouse, J. A. & Strother, J. L. (2002) *Hesperoyucca whipplei* and *Yucca whipplei* (Agavaceae). *Madroño* 49(1): 20–21. <https://biodiversitylibrary.org/page/48190581>
- Greulich, M. (2012) *Hesperoyucca whipplei* (Torr.) Baker ex Trel. (1893) — ein Juwel der *Agavaceae*. *Berliner Kakt.-Blätt.* 12: 29–42.
- Haines, L. (1941) Variation in *Yucca whipplei*. *Madroño* 6: 33–64.
- Halpin, K. M. & Fishbein, M. (2013) A chloroplast phylogeny of *Agavaceae* subfamily *Chlorogaloideae*: Implications for the tempo of evolution on serpentine soils. *Syst. Bot.* 38(4): 996–1011, ill., map. <https://doi.org/10.1600/036364413X674850>
- Hernández-Sandoval, L. G. (1995) Análisis cladístico de la familia *Agavaceae*. *Bol. Soc. Bot. México* 56: 57–68.
- Hochstätter, F. (2000) *Yucca* I (Agavaceae) in the southwest and midwest of the USA and Canada. Mannheim (DE): Published by the author.
- Hochstätter, F. (2015) *Yucca* Section *Hesperoyucca* (Agavaceae). *Int. Cact.-Advent.* 106–107: 2–19, ill.
- Hodgson, W. C. (2001) Food plants of the Sonoran Desert. Tucson (US): University of Arizona Press.
- Irish, M. & Irish, G. (2000) Agaves, Yuccas and related plants. A gardener's guide. Portland (US): Timber Press.
- Keeley, J. E. & Tufenkian, D. A. (1983) Garden comparison of germinability and seedling growth of *Yucca whipplei* subspecies (Agavaceae). *Madroño* 31(1): 24–29.
- McKain, M. R. [& al. 2016], McNeal, J. R., Kellar, P. R., Eguiarte, L. E., Pires, J. C. & Leebens-Mack, J. (2016) Timing of rapid diversification and convergent origins of active pollination within *Agavoideae* (Asparagaceae). *Amer. J. Bot.* 103(10): 1717–1729. <https://doi.org/10.3732/ajb.1600198>

- McKelvey, S. D. (1938) *Yuccas of the Southwestern United States. Part I.* Jamaica Plain (US): Arnold Arboretum of Harvard University.
- McKelvey, S. D. (1947) *Yuccas of the Southwestern United States. Part II.* Jamaica Plain (US): Arnold Arboretum of Harvard University.
- McKinney, K. K. & Hickman, J. C. (1993) *Yucca*. In: Hickman, J. C. (ed.): *The Jepson Manual. Higher plants of California*; p. 1210. Berkeley etc. (US): University of California Press.
- Munz, P. A. & Keck, D. D. (1959) *A California flora.* Berkeley (US): University of California Press.
- Powell, J. A. (2013) Longevity and individual activity of the Yucca Moth, *Tegeticula maculata extranea* (Prodoxidae), based on mark-release monitoring. *J. Lepidopterists' Soc.* 67(3): 187–195, ills.
- Schaffer, W. M. & Schaffer, M. V. (1979) The adaptive significance of variations in reproductive habit in *Agavaceae*. II. Pollinator foraging behavior and selection for increased reproductive expenditure. *Ecology* 60: 1051–1069. <http://www.jstor.org/stable/1936872>
- Schaffer, W. M. & Schaffer, M. V. (1977) The adaptive significance of variations in reproductive habit in the *Agavaceae*. In: Stonehouse, B. (ed.): *Evolutionary Ecology*; pp. 261–276. London (GB): Macmillan.
- Smith, C. I. [& al. 2008], Pellmyr, O., Althoff, D. M., Balcázar-Lara, M., Leebens-Mack, J. & Segraves, K. A. (2008) Pattern and timing of diversification in *Yucca (Agavaceae)*: Specialized pollination does not escalate rates of diversification. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 275: 249–258. <https://doi.org/10.1098/rspb.2007.1405>
- Trelease, W. (1893) Further studies of *Yuccas* and their pollination. *Annual Rep. Missouri Bot. Gard.* 4: 181–226, tt. 1–23. <https://doi.org/10.5962/bhl.title.33385>
- Turner, R. M. [& al. 1995], Bowers, J. E. & Burgess, T. L. (1995) *Sonoran Desert plants. An ecological atlas.* Tucson (US): University of Arizona Press.
- Webber, J. M. (1953) *Yuccas of the Southwest.* Washington D.C. (US): US Department of Agriculture. <http://archive.org/details/yuccasofsouthwes17webb>
- Wolf, C. (1935) *California plant notes. Part 1.* Occas. Pap. Rancho Santa Ana Bot. Gard. 1(1): 31–43.





## Yucca AGAVACEAE

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**Yucca** Linné (Spec. Pl. [ed. 1], 319, 1753). **Type:** *Yucca aloifolia* Linné [lectotype, designated by Britton & Shafer, North Amer. Trees, 151, 1908 (fide ING)].— **Agavoideae - Yuccaceae** —**Lit:** Trelease (1902: synopsis); McKelvey (1938: monograph SW USA); McKelvey (1947: monograph SW USA); Webber (1953: synopsis SW USA); Shreve & Wiggins (1964: synopsis Sonoran Desert); Reveal (1977: Intermountain flora USA); Matuda & Piña Luján (1980: ill. synopsis Mexico); Benson & Darrow (1981: ill. synopsis SW USA); Welsh & al. (1987: synopsis Utah); Hochstätter (2000: ill. synopsis USA dehiscent fruited taxa); Irish & Irish (2000: cultivated taxa USA); Hess & Robbins (2002: flora N America); Hochstätter (2002a: ill. synopsis USA indehiscent fruited taxa); Hochstätter (2004a: ill. synopsis Mexico); Smith (2004: ill. synopsis); Pellmyr & al. (2007: molecular AFLP phylogeny); Guillot Ortiz & Meer (2008: cultivated taxa Spain); Smith & al. (2008a: molecular phylogeny, evolution); Boeuf (2007a: ill. synopsis); Boeuf & al. (2009: ill. synopsis); Hawker (2016: ill. synopsis SW USA); Ondrovic & Ondrovic (2016: ill. synopsis USA). **Distr:** S Canada, N, C and S USA, Mexico, Guatemala; cultivated worldwide. **Etym:** Name first used 1557 in a German travelogue and probably derived from a name used on

Hispaniola through Span. ‘yuca’, which is, however, used for the edible root tubers of Cassava, and that was perhaps erroneously applied to *Yucca* because of the edible flowers of some species.

**Incl.** *Iuka* Adanson (1763) (*nom. inval.*, ICN Art. 61.1). **Type:** *Yucca aloifolia* Linné.

**Incl.** *Clistoyucca* (Engelmann) Trelease (1902). **Type:** *Yucca brevifolia* Engelmann [typification by inference; only element included].

**Incl.** *Samuela* Trelease (1902). **Type:** not designated.

**Incl.** *Sarcoyucca* (Trelease) Lindinger (1933). **Type:** not designated.

Woody perennials, terrestrial (very rarely epiphytic: *Y. lacandonica*); stems none, short, or thick and arborescent, then usually  $\pm$  branched; **Ros** terminal, always monocarpic, but rosettes/stems always branched and whole plant polycarpic; **L** mostly numerous,  $\pm$  ensiform, nearly linear, thin and flexible or thicker and very rigid, margins entire or minutely denticulate, horny, often desintegrating into fibres, terminal **Sp** often present; **Inf** large panicles or racemes; **Fl** pedicellate, usually  $\pm$  pendent,  $\pm$  campanulate to globose, conspicuous, somewhat fleshy;  **Tep** 3 + 3, all similar and subequal in size, mostly white or whitish (or greenish or slightly reddish),  **Tep** tube none, short or up to  $\pm \frac{3}{10}$  of the tepal length;  **St** 3 + 3;  **Fil** fleshy, clavate, or slightly swollen beneath the small versatile  **Anth**, pubescent or at least papillose;  **Ov** superior, 3-locular;

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**Sty** very short or none, with 3 short branches with a 2-lobed **Sti** each; **Fr** many-seeded loculicidal capsules with  $\pm$  intruding dorsal false septa, more rarely septicidal, or baccate and indehiscent; **Se** flat and usually thin, black.—**Cytology**:  $x = 30$ .

The genus includes  $\pm 50$  species. Most are more xerophytic than succulent and would therefore fall mostly outside the scope of this Handbook. However, many species of *Yucca* are horticulturally important or represent dominant elements of arid vegetations, and in order to provide a complete treatment of the family *Agavaceae* s.s., the genus is dealt with in full here.

*Yucca* is easily recognizable by the flat and thin leaves typical of many species, often with filiferous leaf margins which are otherwise only found in *Hesperaloe* and a couple of *Agave* species. The mostly whitish wax-like and somewhat fleshy pendent flowers in usually compact inflorescences are another diagnostic feature of the genus. The inflorescences are either racemose, or paniculate, then distally sometimes racemose; the part-inflorescences are always unbranched and mostly decrease in length distally. Inflorescences of hybrids between species with racemose or paniculate inflorescences may be paniculate below, and racemose above, as in *Y. ×karlsruhensis* (for the inflorescence morphology, see Boeuf & al. 2008b).

**Classification:** *Yucca* (including the superficially similar but usually monocarpic *Hesperoyucca*) was historically placed in *Liliaceae* due to its superior ovary. Since the 1950s, the close relationship with *Agave* and closely related genera with inferior ovaries is universally accepted.

*Yucca* is “one of the most difficult” genera of the N American flora (Reveal 1977) due to the complex nomenclature with many old names of uncertain application, the presence of mostly poorly documented horticultural names, and the pronounced variability of many taxa, including possible hybridisation and introgression.

Carrière (1859: 389–390) published the first classification of the genus, subdividing it into unranked, artificial groups according to characters of stems (caulescent vs. acaulescent) and leaf margins (filiferous vs. non-filiferous), and in part

based on leaf size and shape. Baker (1870: 828; revised in Baker (1880: 220–221)) subdivided *Yucca* into 3 unranked, artificial groups with entire, serrulate, or filiferous leaf margins, respectively. Engelmann (1871) subdivided *Yucca* into two unranked major taxa, *Euyucca* (= *Yucca*) and *Hesperoyucca* (the latter today regarded as independent genus, see there). *Euyucca* was subdivided into 3 unranked second-order taxa, named *Sarcocarpa*, *Clistocarpa* and *Chaenocarpa*. These 3 unranked subdivisions of *Euyucca* s.l. were also used by Engelmann (1873) (publication year in dispute, said to be 1878 by TL2, but stated as 1873 in the biographical sketch included in the collective reprint of Engelmann’s works by Trelease & Gray 1887), who changed the names to *Sarcoyucca*, *Clistoyucca*, and *Chaenoyucca*, respectively, thus laying the base for the disparate use of both sets of names indiscriminately up to today. Later, Engelmann (1874: 210, 212) introduced the formal rank of section, treating the taxa as Sect. *Sarcoyucca* (*nom. inval.*,  $\equiv$  Sect. *Yucca*), Sect. *Clistoyucca*, and Sect. *Chaenoyucca*.

Trelease (1902) split *Yucca* into the segregate genera *Hesperoyucca*, *Clistoyucca* (corresponding to Sect. *Clistoyucca*), and *Samuela* (corresponding to the later Ser. *Faxonianae*). While *Hesperoyucca* is widely accepted today as separate genus being part of a separate evolutionary clade within *Agavaceae* s.l., *Clistoyucca* and *Samuela* were returned to *Yucca* by McKelvey (1938). Within *Yucca* (excl. *Clistoyucca*), Trelease (1902: 44–46) recognized three sections (rank of section explicitly used l.c. p. 82): Engelmann’s Sect. *Chaenoyucca* and Sect. *Sarcoyucca*, and the new Sect. *Heteroyucca*, split off from the latter.

McKelvey (1938, 1947) further subdivided Engelmann’s large sections *Sarcoyucca* (as *Sarcocarpa*) and *Chaenoyucca* (as *Chaenocarpa*) into a number of series, whose names were unfortunately published invalidly for lack of a Latin diagnosis (ICN Art. 39.1). Hochstätter (2002b) and subsequent publications validated most of these series names and added further new names at both sectional and series rank, but some of these were likewise published invalidly.

The first molecular phylogenetic study of *Yucca* was performed by Clary & Simpson

(1995) and Clary (1997), who found none of the traditionally recognized series to be monophyletic, and even concluded that the distinction into berry- and capsular-fruited taxa is artificial. In contrast, the much more deeply sampled studies of Pellmyr & al. (2007), Smith & al. (2008a) and Heyduk & al. (2016) (wrongly treating Engelmann's first-order divisions at the rank of subgenera) largely supported the traditional subdivision in three sections. The infrageneric classification applied here is largely based on Pellmyr & al. (2007: fig. 1) and recognizes few series only; for variable species, morphologically as well as geographically distinct infraspecific taxa are treated at subspecific rank, when names are available.

- [1] Sect. *Yucca* (incl. *Yucca* [unranked] *Sarcocarpa* Engelmann 1871 = Sect. *Sarcocarpa* Engelmann 1873, *nom. inval.*, ICN Art. 22.1; incl. Sect. *Heteroyucca* Trelease 1902, *nom. inval.*, ICN Art. 22.1; incl. Sect. *Endlichiana* Hochstätter 2008): **R** fibrous; adult plants usually stem-forming, rarely rhizomatous (*Y. endlichiana*); **L** of young plants (<6 years) few, broadened and generally reddish; **Fr** pendent, indehiscent, baccate, fleshy and edible, or pendent and soon drying; **Se** rough, unwinged.
- [1a] Ser. *Faxonianae* McKelvey ex Hochstätter 2002 (incl. Ser. *Faxonianae* McKelvey 1938, *nom. inval.* ICN Art. 39.1).
- [1b] Ser. *Baccatae* McKelvey ex Hochstätter 2002 (incl. Ser. *Baccatae* McKelvey 1938, *nom. inval.* ICN Art. 39.1; incl. Ser. *Validae* Hochstätter 2016, *nom. inval.* ICN Art. 29.1 Ex. 2).
- [1c] Ser. *Yucca* (incl. Ser. *Treculianae* McKelvey 1938, *nom. inval. & illeg.* ICN Art. 22.1 & 39.1; incl. Ser. *Treculianae* McKelvey ex Hochstätter 2003; incl. Ser. *Graclifoliae* Hochstätter 2008; incl. Ser. *Lacandonicae* Hochstätter 2016, *nom. inval.* ICN Art. 10.1 & 29.1 Ex. 2).
- [1c × 3c] Ser. *Gloriosae* Hochstätter 2002.  
Only species: *Y. gloriosa*.
- [2] Sect. *Clistoyucca* Engelmann 1873 (= *Yucca* [unranked] *Clistocarpa* Engelmann 1871 = *Clistoyucca* (Engelmann) Trelease 1902): **Fr**

capsular, indehiscent, dry and spongy; **Se** smooth, unwinged.—2 species: *Y. brevifolia*, *Y. jaegeriana*.

- [3] Sect. *Chaenoyucca* Engelmann 1873 (incl. *Yucca* [unranked] *Chaenocarpa* Engelmann 1871): **R** of young plants bulbous, adult plants rhizomatous; **L** of young plants many, thin and greenish-glaucous; **Fr** soon becoming erect, capsular, dehiscent; **Se** smooth, winged or unwinged.
- [3a] Ser. *Rupicolae* McKelvey ex Hochstätter 2002 (incl. Ser. *Rupicolae* McKelvey 1947, *nom. inval.* ICN Art. 39.1; incl. Ser. *Rostratae* Hochstätter 2016, *nom. inval.* ICN Art. 10.1 & 29.1 Ex. 2).
- [3b] Ser. *Harrimaniae* McKelvey ex Hochstätter 2002 (incl. Ser. *Harrimaniae* McKelvey 1947, *nom. inval.* ICN Art. 39.1; incl. Ser. *Elatae* McKelvey 1947, *nom. inval.* ICN Art. 39.1; incl. Ser. *Elatae* McKelvey ex Hochstätter 2016, *nom. inval.*, ICN Art. 29.1, Ex. 2).
- [3c] Ser. *Glaucae* McKelvey ex Hochstätter 2002 (incl. Ser. *Glaucae* McKelvey 1947, *nom. inval.* ICN Art. 39.1; incl. Ser. *Arkansanae* McKelvey 1947, *nom. inval.* ICN Art. 39.1; incl. Ser. *Constrictae* McKelvey 1947, *nom. inval.* ICN Art. 39.1; incl. Ser. *Filamentosae* Hochstätter 2002; incl. Ser. *Arkansanae* McKelvey ex Hochstätter 2016, *nom. inval.* ICN Art. 10.1 & 29.1 Ex. 2).

**Evolution:** Radiation in *Yucca* started in the period 18–12 mybp (Good-Avila & al. 2006; Rocha & al. 2006), and Smith & al. (2008a) found a high diversification rate of 0.33 species/mybp (in contrast to 0.15–0.2 species/mybp in the analysis of Rocha & al. 2006). The crown group age of *Yucca* (excluding *Y. queretaroensis*) is estimated at ±6 mybp. This is younger than previous estimates such as “eocene” by Pellmyr & Leebens-Mack (1999). The oldest known fossil record of *Yucca*, the arborescent *Protoyucca sadishii* from NW Nevada, dates to 14 mybp (middle miocene) (Tidwell & Parker 1990). It should be noted that the fossil *Yuccites* Martius from the Carboniferous, superficially similar to extant *Yucca*, is regarded as belonging to the

*Lycophyta*, and *Yuccites* Schimper & Mougeot (*nom. illeg.*, ICN Art. 53.1, = *Pelourdea* Seward) refers to fossil gymnospermous leaves from the Triassic (Doweld 2013).

Interestingly, *Yucca* diversification is much younger than the diversification of its pollinators, whose origin falls into a period of roughly 40–32 mybp (Smith & al. 2008a). The extremely specialist pollination syndrome has thus not led to increased speciation, i.e. the radiation of *Yucca* is not the result of the obligate mutualistic pollination system (Smith & al. 2008a). The origin of the *Yucca*/moth system is dated at  $40 \pm 11$  mybp by Pellmyr & Leebens-Mack (1999) or to 13 mybp by Smith & al. (2008a: 2680). The likely age difference of moth and *Yucca* origins and diversifications is enigmatic. Substantial host switching must have occurred in the moths, and no congruence between plant and moth evolution has been found in the case of *Y. brevifolia* (incl. *Y. jaegeriana*) and its two pollinator species (Smith & al. 2008a, contradicting Pellmyr & Segraves (2003) and Godsoe & al. (2008)). In contrast to these interpretations, Cole & al. (2017) found “a functional basis for coevolution” between the two pollinator species and *Y. brevifolia* (incl. *Y. jaegeriana*).

The *Yucca*—moth pollination syndrome evolved twice independently, once in *Hesperoyucca*, and once in *Yucca*, well after the separation of these two lineages at 27 mybp. Pollinating yucca moths have a single origin within the *Prodoxidae* (bogus yucca moths, see below) (McKain & al. 2016). The evolution of pollinating yucca moths from bogus yucca moths only necessitated minimal trait evolution (Yoder & al. 2010) since oviposition in carpels and fruit feeding larvae pre-existed in the ancestors and only the behavioural component of actively collecting and depositing pollen had to evolve, linked to modifications in the tentacular apparatus to make pollen collection possible. Pollinating moths thus evolved from a pre-existing parasitic insect—plant interaction.

A major diversification of the moths occurred at  $3.2 \pm 1.8$  mybp, coincident with the development of arid habitats. Cheating yucca moths (see below, pollination ecology) evolved twice independently as part of this radiation (Segraves &

al. 2005). Plant and moth speciation shows significant phylogenetic congruence but is likely due to shared biogeography rather than co-evolution (Althoff & al. 2012) or cospeciation (Pellmyr & Leebens-Mack 1999, Smith & al. 2008b).

**Succulence:** Most species of *Yucca* have tough, rigid, very fibrous leaves, and well-developed voluminous water storage tissue is probably restricted to *Y. endlichiana*. Nonetheless, Walter (1931: 9, 153) treated *Y. elata* as a succulent. Thickened rhizomes are present in many species, and some (e.g. *Y. guatemalensis*) have a well-developed pachycaulous trunk, whose architecture is similar to that found in the stems of *Beaucarnea* (Fisher 1975, Stevenson 1980, Carlquist 2012: 113). A thickening meristem develops in the outer cortex and produces un lignified parenchymatous conjunctive tissue with abundant vascular strands.

**Physiology:** *Yucca* is heterogenous with respect to the photosynthetic pathways employed: Heyduk & al. (2016) found the species of Sect. *Clistoyucca* and *Chaenoyucca* to be C3, and those of Sect. *Yucca* (as “subgen. *Sarcocarpa*”, etc.) to be CAM. Some species use both CAM and C3, e.g. *Y. baccata*, which is a constitutive CAM species, but with considerable C3 photosynthesis during the day (Szarek & Troughton 1976, Kemp & Gardetto 1982).

Similar as in *Agave*, roots near the stem play an important role in the rapid uptake of water after the dry season (North & Baker 2007), likely based on the fact that the internal anatomy continues to appear more reminiscent of young roots with living cortical cells, despite the suberisation of the external root tissues (North & Baker 2007). Rapid water uptake occurs close to the stem and in the distal parts of the root system, while the mid-root sections rapidly lose water uptake abilities (North & al. 2004).

Eighty-five percent of the examined species had contractile roots close to the stem (North & Baker 2007, North & al. 2008). Contraction is achieved by radial expansion and longitudinal shortening of the cells of the inner and/or middle cortex, accompanied by a lack of suberisation

(North & al. 2008). Root contraction occurs already in young seedlings, which are pulled into the soil at an average of 34.7 mm/year in the 6 species studied (North & al. 2008).

**Flowering and fruiting ecology:** Flowering and fruit production is correlated with favourably wet winter/spring periods (Campbell & Keller 1932, Smith & Ludwig 1976): In good years (“mast years”), 67–83% of all plants in *Y. elata* populations produced fruit, but only 0–8% in a dry year. In populations of *Y. brevifolia*, 66% of the inflorescences developed fruit in a high-reproduction year, and 53% of the fruits were infested with yucca moth larvae, with 19.5% of the seeds consumed. In a low-reproduction year, the majority of the fruits were infested, and  $\pm 40\%$  of the seeds were consumed (Borchert & DeFalco 2016). For *Y. baccata*, Wallen & Ludwig (1978) found flowering to occur at intervals of three years—based on a simulation model, they propose that after flowering, several years of vegetative growth would be necessary to replenish the carbohydrate reserves.

Over-exploitation of fruits by the pollinator’s larvae is counter-balanced by selective fruit-abscission of multiply infested ovaries/developing fruits (Humphries & Addicott 2000). Overall, 80–90% of all flowers of a *Yucca* inflorescence abscise (Segraves 2008). The fate of a pollinated and oviposited flower is influenced by the size of the pollen load (i.e. pollination quality), the number of deposited eggs, the number of pollinated flowers in the inflorescence, as well as by the position of the flower within the inflorescence (Humphries & Addicott 2000, Snell & Addicott 2008a). Althoff (2014) found that the ability of *Yucca* plants to selectively abscise flowers that contain pollinator eggs probably influences ovipositor length of the pollinating moths; it appears that laying the eggs more superficially near the surface of the ovary wall or style base minimizes plant reaction.

Selective abortion of fruits with multiple yucca moth eggs were observed by Pellmyr & Huth (1994). Possibly, the depth of oviposition is critical, and abortion is probably triggered when ovules are damaged by oviposition, in comparison

with more superficial oviposition not touching the ovules (Marr & Pellmyr 2003, Segraves 2008). Abscission strategies are probably variable from species to species; *Y. baccata* retains relatively more multiply infested fruits than other species such as *Y. glauca* (Addicott & Bao 1999).

The puncturing of the ovary with the ovipositor during pollination by the yucca moths locally inhibits the development of the ovary wall and ovules, thus giving rise to specific types of fruit deformations in the developing fruits (Davis 1967): Fruits with a  $\pm$  pronounced curvature result from single punctures towards the middle part of the pistil in a single locule (e.g., *Y.  $\times$ schottii*), whereas fruits with a  $\pm$  pronounced median constriction result from several ovipositor punctures towards the middle part of the pistil in each of the locules (e.g., *Y. filifera*). In species such as *Y. brevifolia*, where oviposition does not occur in the ovary but in the style, the ovary and ovules are not affected and the fruits do not show deformations (Davis 1967: 33–34). The fruit curvature or constriction thus results from the oviposition injury and is independent from larval development (Davis 1967: 33). In *Y. filifera*, besides the common fruits with median curvature, fruits with a distal constriction are also found. These result from pollination by *Tegeticula yuccasella* females with a different genital morphology (Villavicencio & Pérez-Escandón 1995).

**Pollination ecology:** There is a closely knit symbiosis between *Yucca* species and its pollinators, the yucca moths. Indeed, the *Yucca*-moth system is a well-known text-book example of an obligate mutualism between the plant and its pollinators (called “obligate nursery pollination mutualism” by Svensson & al. (2011) and specialized “brood pollination mutualism” by Althoff (2016)). The specialized pollination system was first mentioned by Riley (1872) and described in more detail by Riley (1873). Additional observations were communicated subsequently by Riley (1874, 1878, 1880, 1881, 1892). Little additional investigations of the relationships were made for the almost 70 years that follow, but esp. in the past 20 years, interest has been revived, and numerous studies on various aspects of the mutualism were

published in recent years. Detailed information on the history of knowledge of the mutualism are found in Powell & Mackie (1966) and Davis (1967).

According to the accumulated knowledge, the *Yucca*—yucca moth pollination mutualism emerges as a delicate balance between the number of developing seeds in one season and a sufficient number of larvae completing their development in order to assure pollination in the next season. A total of 25 species of yucca moths from the 2 genera *Tegeticula* (20 species; incl. *Pronuba*) and *Parategeticula* (5 species) are known today (Pellmyr & al. 2008). They evolved from bogus yucca moths (*Prodoxus*, 22 species) (Althoff 2014) that feed on plant tissue other than flowers (Pellmyr 2003, Althoff 2008). *Parategeticula* females lay eggs into pits of the inflorescences or flower pedicels, and the larvae after emergence crawl into the flower and bore into the ovary (Pellmyr & al. 2008). Females of *Tegeticula* lay eggs directly on or into the ovary. Females of the pollinator moths actively collect pollen from one or more anthers of a flower before ovipositing an egg into one of the locules of the ovary. The pollen package collected is subsequently actively deposited on the stigma of the next flower visited. Attraction of the moths to the flowers is likely via floral scent, but scent is at least for some species groups not species-specific (Svensson & al. 2005, 2006, 2011, for *Y. elata*, *Y. filamentosa* and *Y. glauca*). In *Y. reverchonii*, some of the hydrocarbons in the floral scent were shown to be perceived by the antennae of *Tegeticula cassandra* (pollinator) and *Prodoxus decipiens* (herbivore) (Tröger & al. 2019). Both sexes are equally attracted by floral scents and use the flowers as resting sites during the day, and mating usually occurs in the flowers as well at night (Snell & Addicott 2008a, Svensson & al. 2011, for *Y. glauca* and the pollinator *Tegeticula yuccasella*). Scent quality of the flowers does not appear to change after successful pollination, so that multiple visits and ovipositions are possible (Svensson & al. 2011). When larval development is completed, the larvae burrow out of the fruit and pupate and overwinter in the ground (Pellmyr 2003).

There is no 1:1 relationship between *Yucca* species and species of pollinating moths; rather, most pollinator species are shared among several *Yucca* species. The most polyphagous pollinator is *Tegeticula yuccasella*, ovipositing on 5 different *Yucca* species across its geographical range (Althoff 2016). On the other hand, more than one moth species serves the same *Yucca* species, e.g. “*Y. schottii*”, whose inflorescences are visited by 2 pollinating moth species (with radically different behaviours and different ovipositions) as well as 2 bogus moths (Powell 1984). Pellmyr (2012) found evidence for selection of female yucca moths to gather and deposit abundant pollen to assure high pollination quality (an average of 3600 pollen grains are deposited per flower of *Y. filamentosa* with 150–200 ovules per ovary). A climatic niche modelling approach for 2 co-occurring species of *Tegeticula* moths both pollinating *Y. filamentosa* suggests that moth geographic distribution is heavily influenced by climate, but the competition among pollinating congeners restricts the populations of co-occurring moth species (Darwell & Althoff 2017).

Pollinator abundance is usually greatest before peak flowering, although year-to-year variations are large (Althoff & al. 2013). At any one locality, pollinator moths are very host specific, but it remains largely unknown whether this is caused by pollination ability, or larval feeding preferences (Althoff 2016). There are some indications that even in widespread pollinating moths such as *T. yuccasella*, local preferences for the locally native *Yucca* species have developed, and larval development is reduced in non-target *Yucca* species pollinated by the same pollinator species (Althoff 2016). Changes in moth morphology and emergence times have been described in association with shifts from native *Y. filamentosa* to introduced *Y. aloifolia* (Groman & Pellmyr 2000).

The close mutualistic moth—plant interaction is not an evolutionary dead-end for *Yucca* pollination. Rentsch & Leebens-Mack (2014) describe that European honey bees “were passively but effectively pollinating” *Y. aloifolia* flowers resulting in good fruit set when nocturnal moth pollinators were excluded.



A component largely overlooked in early studies are antagonists and commensalists participating in the plant—pollinator network (Althoff 2016): Parasitoid wasps feeding on *Yucca* moth larvae are at the same time indirect mutualists of the *Yucca* plants by reducing the number of consumed seeds (Crabb & Pellmyr 2006). In addition, moth egg mortality is increased by the presence of Tenebrionid beetles: The beetles, often present in large numbers but not influencing pollinator visitation behaviour, mate and feed within *Yucca* flowers and consume esp. stylar tissue, where most oviposition events by the pollinator occur (Segraves 2008).

Two species of *Tegeticula*, *T. intermedia* and *T. corruptrix*, have evolved independently into “cheaters” (Tyre & Addicott 1993, Addicott & Tyre 1995, Althoff 2014): Females oviposit without first collecting and/or depositing pollen and place their eggs into developing fruits, i.e. after fruit crop regulation by selective abscission is complete. Successful development of their larvae is dependent on successful pollination of the flowers by pollinating moths. No negative effects of the cheating moths on the mutualism were discovered (Pellmyr & Leebens-Mack 1999).

Cheating not only occurs on the side of the pollinators, but apparently also on the *Yucca* side of the mutualism: Bao & Addicott (1998) found that *Y. baccata* has two fruit types, which appear to be specific for an individual:  $\pm 70\%$  of all individuals produce narrow fruits that taper towards the style, while the remaining plants produce shorter and more globose fruits. Oviposition occurs at the transition of the style and the ovary, and the tapered fruits have no viable ovules near that zone, causing frequent premature death of the moth larvae. In the short rounded fruits, larval mortality is much lower, and a higher proportion of the seeds are consumed. The individuals with tapered fruits are regarded to be obligate cheaters by Bao & Addicott (1998). These authors also suggest that cheating could be present in other *Yucca* species that produce apically tapered fruits.

Bogus yucca moths (*Prodoxus*) were first so named by Riley (1880). The females oviposit during the flowering period of the hosts into

(depending on the species) the inflorescence axis, fruit wall, or leaves, and their larvae feed on non-flower tissues. It appears that they do not directly reduce plant fitness or were weakly antagonistic (“parasitic”) only (Althoff & al. 2004). *Yucca* does not appear to have a defence mechanism to control *Prodoxus* activity (Snell & Addicott 2008b). *Prodoxus* larvae diapause for up to 30 years (Powell 2001) and are parasitized by the wasp *Eusandalum* sp. (Althoff 2008).

Ants and aphids are further components of the *Yucca* interaction network. Ant presence reduces the number of oviposition events of the cheating yucca moth *Tegeticula corruptrix*. Aphid presence reduces herbivory/florivory by ants since ants prefer aphid honey dew (Perry & al. 2004, Snell & Addicott 2008a).

**Seed dispersal and establishment:** For the dehiscent-fruited *Yucca* species, wind dispersal of the light-weight seeds ( $\pm 15$  mg) seems to be the primary mechanism (Waitman & al. 2012 and references there cited). For the indehiscent fruited taxa, wind speeds are insufficient to detach the fruits and move them over the ground. For these species, dispersal by scatter-hoarding rodents is postulated (Waitman & al. 2012: 7).

Scatter-hoarding rodents appear to play a major role as dispersers. Animals were observed to harvest fruits directly from the canopy of *Y. brevifolia*, with subsequent seed caching (Waitman & al. 2012). Borchert & DeFalco (2016) found that 33% of the fruit crop of *Y. brevifolia* falls to the ground and was removed within 4 months by rodents. Rodents also exploited the fruits that remained in the canopy. Fruit exploitation is more rapid when the fruit crop is small (Borchert & DeFalco 2016). Animals involved in dispersal are the White-tailed antelope squirrel, Pinyon mouse, Merriam’s kangaroo rat, and many more sporadically occurring species (Borchert & DeFalco 2016).

Seed longevity remains poorly studied. Seeds of *Y. filifera* were still germinating after 3–4 years of storage at 5 °C (Morales-Rangel & al. 2015). Cambrón-Sandoval & al. (2013) found that seeds of *Y. filifera* still germinated for  $\pm 60\%$  after

4 years of storage, but were no longer viable after 14 years. In *Y. brevifolia*, germination decreases from 50–68% after 12 months to <3% after 40 months in the ground, and no soil seed bank is present (Reynolds & al. 2012).

Successful establishment of *Yucca* species from seeds is probably an infrequent event. For *Y. brevifolia*, establishment only occurs in above-average wet years (Brittingham & Walker 2000). Survivorship of a cohort due to a rare establishment event during 1983/1984, based on above-average summer rainfall, in a Nevada population was 19% after 22 years—most seedlings succumbed to herbivory by jackrabbits in the first 2 years. Average yearly growth over the 22-year period was  $3.12 \pm 1.96$  cm (Esque & al. 2015).

**Ethnobotany:** According to Hodgson (2001: 44–51) species of *Yucca* were significant sources of food and fibre for the indigenous people of the Sonoran Desert. Flowering stalks and flowers (usually boiled and consumed as vegetables) of most species were “valuable additions” to the diet of these people, esp. when plants were locally abundant. The fruits of the berry-fruited species were also consumed (fresh, cooked or roasted and then dried, and rehydrated, with the seeds removed) and are described as being pleasantly sweet and nutritive, although with cathartic effects when eaten in large numbers (Hodgson 2001: 45). A general overview of known uses of species of *Yucca* is found in Mitich (1977). The historical importance of *Yucca* fibres is documented by artefacts 2000 years old (Webber 1953). The same author also describes that plants were used as emergency fodder for cattle during the drought of 1916–1919 in the USA. Matuda & Piña Luján (1980) describe *Yucca* usage in Mexico and esp. stress the historical importance for fibres. Fibre extraction from the leaves of *Y. carnerosana* was an important business in Zacatecas and San Luis Potosí in the early 1960s, amounting to as much as 6000 tons/year. In addition, the trunks or stems of several species were used for wall construction in rural housing. *Yucca* species were also sometimes used as living fence in Mexico (Matuda & Piña Luján 1980: 8, ill.) as well as in India (Howes 1946).

Apart from its use for food and fibres, *Yucca* spp., esp. *Y. schidigera*, are important sources of saponins with many actual and potential applications in human and animal nutrition such as antibacterial activities (review by Cheeke 2000). *Yuccas* also have manifold therapeutic attributes with antioxidant, anti-inflammation, anti-arthritis, anticancer, antidiabetic, antimicrobial, and hypocholesterolaemic properties (review by Patel 2012). Tissue culture methods for large-scale propagations of useful *Yucca* species are reviewed by López-Ramírez & al. (2018).

**Horticulture:** Many *Yucca* species are popular in horticulture, esp. for landscaping, and are known by the vernacular name “Palm Lily”. Several species have become naturalized in different parts of the world (see Guillot Ortiz & Meer (2003) for a preliminary list of species for Spain, and Walters & al. (2011) for South Africa). House plants sold as “*Yuccas*” by the horticultural trade are usually species of the genus *Cordylina* (*Laxmanniaceae*).

In cultivation, variegated cultivars of several taxa are widespread and popular, and Boeuf & al. (2008a, 2010) and Boeuf & Heim (2014) discuss the known examples. Webber (1953: 66) found that some species are self-fertile, while other are self-sterile. The same author also reports on hybridisation trials.

*Yucca* hybridisation started with Jean-Baptiste A. Deleuil at Marseille (France) who obtained seeds from 13 hybrids (Deleuil 1880); some of these and further hybrids of Deleuil were published as the earliest *Yucca* nothospecies by André (1883) (listed here among the names of unresolved application). Leopold Graebener started hybridising at BG Karlsruhe (Germany) at  $\pm 1880$  and raised the still extant *Y. \times karlsruhensis* in 1899, later followed by further hybrids, which stimulated others to start with *Yucca* hybridisations (Weissbeck 2012b). Carl Sprenger (see Sprenger 1920a, b) at Korfu (Greece) raised and named no less than 122 *Yucca* hybrids in the period 1897–1907 (Jensen 2018), many of them published under nothospecies names (not further covered here). Further *Yucca* cultivars were

brought into the trade starting in 1958 by Karl Foerster at Potsdam-Bornim (Germany), largely restricted to selections (and not hybrids) of the *Y. filamentosa/flaccida*-complex still widespread in Germany, but leading to difficulties separating both species from each other and from *Y. gloriosa* (Boeuf 2018). Recent hybridisations are carried out by a few amateur collectors (e.g., *Y. 'Anna'*, Jensen 2015).

Hochstätter (2000) indicates the following species to be hardy outdoors in C Europe: *Y. arkansana*, *Y. angustissima*, *Y. baccata*, *Y. baileyi*, *Y. elata*, *Y. filamentosa*, *Y. glauca*, *Y. gloriosa*, *Y. harrimaniae*, *Y. pallida* and *Y. recurvifolia*. The following species need additional protection from moisture: *Y. faxoniana*, *Y. rupicola*, *Y. rostrata* and *Y. thompsoniana* (Hochstätter 2000).

The following names are of unresolved application but are referred to this genus: *Yucca ×andreaana* Deleuil ex André (1883); *Yucca antwerpensis* hort. ex Baker (1880); *Yucca atkinsii* Trelease (1894) (*nom. illeg.*, ICN Art. 53.1); *Yucca barrancasecca* hort. ex Pasquale (1867); *Yucca ×brasiliensis* Sprenger pro sp. (1903); *Yucca ×carrierei* Deleuil ex André (1883); *Yucca conspicua* hort. ex Regel (1871) (*nom. illeg.*, ICN Art. 53.1); *Yucca crinifera* Lemaire (1846); *Yucca ehrenbergii* Baker (1875); *Yucca ×ensifera* Deleuil ex André (1883); *Yucca ensifolia* Baker (1870) (*nom. illeg.*, ICN Art. 53.1); *Yucca fuauxiana* hort. (s.a.); *Yucca gloriosa* fa. *planifolia* Engelm (1873); *Yucca gracilis* Link ex Sweet (1830); *Yucca horrida* Humboldt ex Steudel (1840); *Yucca howard-smithii* Trelease (1937); *Yucca ×juncea* Deleuil ex André (1883); *Yucca ×massiliensis* Deleuil ex André (1883); *Yucca mexicana* Sessé & Moçino (1894) (*nom. illeg.*, ICN Art. 53.1); *Yucca quinnarjenii* Hochstätter (2016) (*nom. inval.*, ICN Art. 29.1, Ex. 2); *Yucca ×rigida* Deleuil ex André (1883); *Yucca rubra* hort. ex Lavallée (1877); *Yucca ×striatula* Deleuil ex André (1883); *Yucca ×sulcata* Deleuil ex André (1883); *Yucca toneliana* Lemaire (1865) (*nom. illeg.*, ICN Art. 53.1); *Yucca ×treleasei* Sprenger (1901); *Yucca ×vomerenis* Sprenger (1901).

**Y. aloifolia** Linné (Spec. Pl. [ed. 1], 1: 319, 1753). **Type:** [lecto—icono]: Dillenius, Hort. Eltham. 2: 435, t. 323: fig. 416, 1732.—**Lit:** Trelease (1902: 88–94, tt. 49–50); Matuda & Piña Luján (1980: 107–109, with ills.); Lott & García-Mendoza (1994: online version with ills.); Hess & Robbins (2002); Diggs & al. (2006: 415, ills. p. 417). **Distr:** USA (Virginia, North Carolina, South Carolina, Georgia, Alabama, Florida, Mississippi, Louisiana, Texas), sand dunes or shell mounds near the coast; Mexico (esp. Veracruz and Yucatán), plains and slopes in tropical deciduous forests, to 1800 m; flowers March to August; neophyte in many (sub-) tropical regions (e.g. RSA, Spain). **I:** Curtis's Bot. Mag. 41: t. 1700 (1814–1815); Piña Luján (1980: 280); Hochstätter (2002a: 103–104); Boeuf (2007a: 52–53); Boeuf & al. (2009: 18–19).

≡ *Sarcocoyucca aloifolia* (Linné) Lindinger (1933); **incl.** *Yucca draconis* Linné (1753) ≡ *Yucca aloifolia* var. *draconis* (Linné) Engelm (1873) ≡ *Yucca aloifolia* fa. *draconis* (Linné) Voss (1895); **incl.** *Yucca haruckermaniana* Crantz (1768); **incl.** *Yucca serrulata* Haworth (1812); **incl.** *Yucca arcuata* Haworth (1819) ≡ *Yucca aloifolia* fa. *arcuata* (Haworth) Voss (1895) ≡ *Yucca aloifolia* var. *arcuata* (Haworth) Trelease (1902); **incl.** *Yucca conspicua* Haworth (1819) ≡ *Yucca aloifolia* var. *conspicua* (Haworth) Engelm (1873) ≡ *Yucca aloifolia* fa. *conspicua* (Haworth) Trelease (1902); **incl.** *Yucca crenulata* Haworth (1819) ≡ *Yucca aloifolia* fa. *crenulata* (Haworth) Voss (1895); **incl.** *Yucca tenuifolia* Haworth (1819) ≡ *Yucca aloifolia* fa. *tenuifolia* (Haworth) Voss (1895) ≡ *Yucca aloifolia* var. *tenuifolia* (Haworth) Trelease (1902); **incl.** *Yucca armata* Steudel (1841); **incl.** *Yucca aloifolia* var. *flexifolia* J. Bommer (1859); **incl.** *Yucca aloifolia* var. *marginata* J. Bommer (1859) ≡ *Yucca aloifolia* fa. *marginata* (J. Bommer) Trelease (1902); **incl.** *Yucca aloifolia* var. *roseomarginata* Regel (1859); **incl.** *Yucca aloifolia* var. *stenophylla* J. Bommer (1859); **incl.** *Yucca aloifolia* var. *tricolor* J. Bommer (1859) ≡ *Yucca aloifolia* fa. *tricolor* (J. Bommer) Trelease (1902); **incl.** *Yucca parmentieri* hort. ex Carrière (1859) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca quadricolor* De Smet ex Regel (1864); **incl.** *Yucca striata*

Anonymus (1865); **incl.** *Yucca aloifolia* var. *variegata* Naudin (1870); **incl.** *Yucca quadricolor* var. *stokesii* B. S. Williams (1870); **incl.** *Yucca serrulata* var. *angustifolia* B. S. Williams (1870); **incl.** *Yucca serrulata* var. *variegata* B. S. Williams (1870); **incl.** *Dracaena lenneana* Regel (1871); **incl.** *Yucca aloifolia* var. *quadricolor-variegata* Carrière (1873); **incl.** *Yucca yucatana* Engelm (1873)  $\equiv$  *Yucca aloifolia* var. *yucatana* (Engelmann) Trelease (1902); **incl.** *Yucca aloifolia* var. *versicolor* Carrière (1878); **incl.** *Yucca aloifolia* var. *purpurea* Baker (1880); **incl.** *Yucca atkinsii* Baker (1880); **incl.** *Yucca purpurea* hort. ex Baker (1880)  $\equiv$  *Yucca aloifolia* fa. *purpurea* (Baker) Trelease (1902); **incl.** *Yucca tricolor* hort. ex Baker (1880); **incl.** *Yucca quadricolor* hort. ex Baker (1880) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca aloifolia* var. *menandii* Trelease (1902); **incl.** *Yucca aloifolia* var. *gigantea* Sprenger (1906); **incl.** *Yucca aloifolia* var. *serratifolia* Sprenger (1906).

[Lc] Arborescent, forming colonies, stems to 8 m, slender, erect or somewhat declining, simple or sparsely branched, sometimes with offsets; **L** rigid, erect, thick, flattened or slightly canaliculate, 12–40 (–60)  $\times$  2.5–6 cm, brilliant light to dark green, tip acute (pungent), margins rather horny, sharply denticulate or entire, rarely filiferous with straight fibres; **Inf** erect, paniculate, peduncle to 30 cm, flowering part 45–61 cm, somewhat conical, lower  $\frac{1}{4}$ – $\frac{1}{2}$  within the the rosette leaves, glabrous or slightly pubescent; **Ped** stout, 25–50 mm; **Fl** pendent, globose, to 70 mm; **Tep** spreading, lanceolate, connate basally for <1 mm, 30–40  $\times$  12–22 mm, whitish with purple or green tinge towards the base; **Fil**  $\pm$  20 mm, slightly papillose; **Ov** oblong, basally constricted, 20–50 mm; **Sty** 5 mm; **Sti** distinct; **Fr** fleshy berries, indehiscent, pendent, ellipsoid, prismatic, 35–50  $\times$  20–26 mm, blackish, pulpa fleshy, purple; **Se** ovoid, thick, 5–6  $\times$  6–7 mm, dull black.—**Cytology**:  $n = 30$  (Watkins 1936),  $2n = 60$  (Sató 1935).

Introduced as garden plant to Europe no later than 1596 and described from European gardens, the plant is seen as having no known geographical origin (Pellmyr 2003: 46). The above-cited lectotype was designated by Wijnands (1983: 140). It

is aberrant in *Yucca* in being self-compatible and erratically forming fruits in the absence of any specific pollinator in the USA and in cultivation in many regions (Pellmyr 2003). In the USA, it is effectively pollinated by European honeybees contributing significantly to its fruit set (Rentsch & Leebens-Mack 2014). The species exhibits further domestication features such as elevated vegetative propagation, core loss in the fruit, and poorly synchronized flowering (Pellmyr 2003). These findings led Pellmyr (2003) to suggest that *Y. aloifolia* could represent an escaped, naturalized cultivar, possibly derived from *Y. guatemalensis* (as *Y. elephantipes*), which might also explain its disjunct distribution. Herbarium specimens from Mexico at MEXU were cultivated specimens or *Y. guatemalensis* (as *Y. elephantipes*) (Pellmyr 2003).

Molecular studies show a close relationship with *Y. gloriosa* (Clary 1997, cited by Hess & Robbins 2002) or with *Y. filifera* and *Y. periculosa* (weak support; *Y. guatemalensis* (as *Y. elephantipes*) groups more distantly, *Y. gloriosa* not sampled; Smith & al. 2008a). For the macrosporogenesis and embryo sac development, see Wolf (1940).

Vegetatively often confused with *Y. gloriosa* or *Y. guatemalensis*, but clearly recognizable by its light to dark green, slightly canaliculate, finely denticulate and more rigid leaves with very sharp tip (Boeuf 2007b: 52). Widely cultivated as foliage plant in (sub-) tropical gardens as well as indoors, esp. in the form of variegated cultivars (Guillot Ortiz & Meer 2008: 23–24, 98, Boeuf & al. 2009: 120–121, 2010: 50–53, Boeuf & Heim 2014: 18–19). Hardy down to  $-15$  °C (Boeuf 2007a: 53) or  $-18$  °C (Irish & Irish 2000: 235). For the in-vitro propagation, see Karpov (2004). Widely naturalized in the Mediterranean and other climatically suitable regions (Spain: Asensi & al. (2016); RSA: Smith & al. (2012); Caribbean: Proctor & Acevedo-Rodríguez (2005: 124); further listings: Hurrell & Delucchi (2009: 18)).

**Y. angustissima** Engelm ex Trelease (Annual Rep. Missouri Bot. Gard. 13: 58–59, t. 23: fig. 1, t. 24: fig. 1, t. 83: fig. 6, 1902). **Type** [lecto]: USA, Arizona (*Bigelow* s.n. [MO 148375]).—**Lit**: Reveal (1977: 533–536, with ill.); Hess &

Robbins (2002); Hawker (2016: 298–310, with ills.). **Distr:** USA (S Utah, N Arizona, NW New Mexico).

The protologue cites specimens of Bigelow, Toumey, Trelease, Palmer, and Jones (= syntypes). The designation of *Bigelow* s.n. in 1854 (MO 148375!) as “type” by Webber (1953: 52) represents a lectotypification. Molecular data (1–2 samples; Pellmyr & al. 2007, Smith & al. 2008a) place the species close to *Y. baileyi* and *Y. utahensis* (as *Y. elata utahensis*).

*Y. quinnarjenii* Hochstätter, invalidly published (ICN Art. 29.1 & Ex. 2), and with a lamentably incomplete protologue, might represent an aberrant population or hybrid of this species or of *Y. baileyi*.

**Y. angustissima** ssp. **angustissima** — **Lit:** Reveal (1977: 533–536, with ills., as var.); Welsh & al. (1987: 649, as *Y. angustissima*); Hess & Robbins (2002: as var.); Hawker (2016: 298–301, with ills., as var.). **Distr:** USA (SE Utah, N Arizona, NW New Mexico); desert flats or mesas, sandy places, sandstone outcrops or rocky hillsides, 900–2200 m; flowers May to June. **I:** Hochstätter (2000: 94–95, as *Y. angustissima*); Boeuf & al. (2009: 20).

[3b] Stems none to short and procumbent, 10–40 cm; **Ros** compact, solitary or in small to large colonies; **L** rigidly spreading, mostly flexible, narrow, long-tapering, primarily flat or distally canaliculate, smooth on both faces, 25–45 × 0.5–0.8 cm, pale blue-green to yellowish-green, margins entire, becoming filiferous with few fine slightly curled fibres, white, becoming brownish, grey or green, **terminal Sp** 3–7 mm; **Inf** erect, racemose, peduncle 0.3–0.5 m, flowering part 0.8–1 m, well above the rosette leaves, with few part-**Inf**, glabrous, or finely pubescent; **Ped** slender, 10–25 (–40) mm; **Fl** pendent, campanulate to globose, 45–55 mm; **OTep** elliptic to ovate, pale green, often tinged rose or rosy purple; **ITep** broader than the **OTep**, lanceolate, white to cream or greenish-white, often tinged with rose or rose-purple; **Tep** basally connate to form a tube 3–7 mm long; **Fil** 7–25 mm, glabrous; **Ov** ± 15 mm; **Sty** 10–13 mm; **Sti** lobed; **Fr** dry capsules, often with a deep constriction near the middle,

oblong-cylindrical, 35–50 (–57) × 20–30 mm; **Se** thin, 5–7 mm, dull black.—**Cytology:** 2n = 60 (McKelvey & Sax 1933).

The treatment of *Y. angustissima* follows Reveal (1977) and Hess & Robbins (2002) who considered four varieties (here treated as subspecies) that are well isolated geographically but overlap morphologically with one another. Reveal’s treatment is supported by molecular data (Clary 1997, cited from Hess & Robbins 2002) in which *Y. angustissima*, *Y. kanabensis* and *Y. toftiae* form distinct clades. However, significant intergradation among these taxa is present (Welsh & al. 1987). See also the note under ssp. *avia*. Webber (1953) regarded the variation in *Y. angustissima* as resulting from hybridisation with *Y. glauca*, *Y. baileyi*, or *Y. elata*, but no evidence for hybridisation was seen by Reveal (1977: 536).

**Y. angustissima** ssp. **avia** (Reveal) Hochstätter (Cactaceae Rev. 1(2): 21, 1999). **Type:** USA, Utah (*Jones* 5639a [US]).—**Lit:** Welsh & al. (1987: 649); Hess & Robbins (2002); Hawker (2016: 301–303, 305, with ills.); all as var. **Distr:** USA (S-C Utah); moist mountain hillsides, on loamy-rocky soils, 2100–2700 m; flowers May to July. **I:** Hochstätter (2000: 98–99); Boeuf & al. (2009: 21).

≡ *Yucca angustissima* var. *avia* Reveal (1977).

[3b] Differs from ssp. *angustissima*: Stems none or to 2 m and erect; **L** lanceolate, longer, 40–60 cm; **Inf** flowering part longer, 0.8–1.8 m; **Fl** shorter, 35–45 (–52) mm; **Sty** shorter, 7–10 mm.

This and ssp. *angustissima* share deeply constricted smaller capsules and smaller inflorescences, while ssp. *kanabensis* and ssp. *toftiae* have larger, moderately constricted capsules and larger inflorescences (Hess & Robbins 2002: as vars.). Welsh & al. (1987) consider this taxon as a N variant from high elevations at the end of a continuous cline within the species.

**Y. angustissima** ssp. **kanabensis** (McKelvey) Hochstätter (Cactaceae Rev. 1(2): 21, 1999). **Type:** USA, Utah (*McKelvey* 4347A [A]).—**Lit:** Welsh & al. (1987: 650, as *Y. kanabensis*); Hess &



Robbins (2002: as var.); Hawker (2016: 303–307, with *ills.*, as var.). **Distr:** USA (SW Utah, N Arizona); sandy places in juniper-pinyon or pine-oak woodlands, desert canyon hillsides, 1400–1900 m; flowers May to June. **I:** Hochstätter (2000: 97); Boeuf & al. (2009: 20).

≡ *Yucca kanabensis* McKelvey (1947) ≡ *Yucca angustissima* var. *kanabensis* (McKelvey) Reveal (1977).

[3b] Differs from var. *angustissima*: Forming small to extremely large colonies; **L** plano-convex or flat and keeled, stiff but somewhat flexible, slightly roughened on the lower face, longer, 45–80 (–150) × 1.2–2 cm; **Inf** peduncle longer, 1–1.5 m, flowering part longer, 1–2 m; **Fl** longer, 55–65 mm; **Tep** elliptic to orbiculate, often tinged pink or brown; **Fil** longer, 25–28 mm; **Ov** longer, 25–27 mm; **Sty** shorter, 5–8 mm; **Fr** moderately constricted, larger, 65–75 mm.

Differs from ssp. *toftiae* in longer flowers, mostly longer leaves, longer ovaries and a mostly lower height at flowering time (Hess & Robbins 2002). See ssp. *avia* for differences from that and ssp. *angustissima*. Most, but not all of the molecular trees in Pellmyr & al. (2007) and Smith & al. (2008a) place this taxon separate from ssp. *angustissima*.

The study by Humphries & Addicott (2000) showed that the taxon is able to regulate the flower pollination mutualism with yucca moths by selectively abscising flowers with low pollen load or without oviposition.

**Y. angustissima** ssp. *toftiae* (S. L. Welsh) Hochstätter (Cactaceae Rev. 1(2): 21, 1999). **Type:** USA, Utah (*Welsh* 11935a [BRY, NY, US]).—**Lit:** Welsh (1975: with *ills.*, as *Y. toftiae*); Welsh & al. (1987: 650, as *Y. toftiae*); Hess & Robbins (2002: as var.); Hawker (2016: 306–310, with *ills.*, as var.). **Distr:** USA (SE Utah); sandy alluvium and sandstone outcrops and mesas, 2000 m; flowers May to June. **I:** Hochstätter (2000: 96).

≡ *Yucca toftiae* S. L. Welsh (1975) ≡ *Yucca angustissima* var. *toftiae* (S. L. Welsh) Reveal (1977).

[3b] Differs from ssp. *angustissima*: Stems none or erect, to 1 m; **L** linear, rigid, longer, 25–75 × 0.4–1.7 cm; **Inf** mostly racemose,

sometimes paniculate proximally, peduncle longer, 1.2–2.5 m, flowering part longer, 0.4–2 m; **Fl** mostly smaller, 30–52 mm; **Tep** creamy-white; **Ov** mostly longer, 12–22 mm; **Sty** shorter, 3–10 mm; **Fr** moderately constricted, mostly larger, 45–60 mm.

See notes for ssp. *angustissima* and ssp. *kanabensis*.

**Y. arkansana** Trelease (Annual Rep. Missouri Bot. Gard. 13: 63–64, tt. 30, 31, 83: fig. 7, 92: fig. 2, 1902). **Type** [lecto]: USA, Arkansas (*Engelmann* 182 [MO]).—**Lit:** Hess & Robbins (2002); Diggs & al. (2006: 415, 421, *ills.* p. 417). **Distr:** USA (SE Kansas, SW Missouri, NE, C and SE Oklahoma, NW, W & SW Arkansas, NE, C, E & S Texas); limestone outcrops, rocky hillsides, pine-woods, and prairies, in gravelly or sandy soils, 100–1060 m; flowers March to mid-May. **I:** Hochstätter (1999: 3); Boeuf (2007a: 54); Boeuf & al. (2009: 24–25).

**Incl.** *Yucca angustifolia* var. *mollis* Engelmann (1873) ≡ *Yucca glauca* var. *mollis* (Engelmann) Branner & Coville (1888); **incl.** *Yucca arkansana* var. *paniculata* McKelvey (1947) ≡ *Yucca louisianensis* var. *paniculata* (McKelvey) Shinnors (1956).

[3c] Forming small colonies; stems none to short and decumbent, to 0.2 m; **Ros** 1 or several in small and lax colonies; **L** ascending, or sometimes somewhat recurved, base ± stiff, major part flexible and weak, widest near the middle, straight, lower face convex, upper face flat, somewhat canaliculate at the tip, 20–60 (–70) × 0.7–2 (–2.5) cm (at the base 0.3–0.7 cm), mostly yellowish-green, margins entire, whitish at first, papery, with short curled fibres, with age almost naked, **terminal Sp** acute, straw-coloured, 1.6–3.2 mm; **Inf** erect, racemose, occasionally paniculate proximally, peduncle 0.2–0.5 (–0.6) m, flowering part 0.3–0.6 (–0.8) m, within or just above the rosette leaves, lower part little-branched and with few flowers, glabrous (pubescent in “var. *paniculata*”); **Fl** pendent, globose, 30–60 mm; **Tep** elliptic to orbicular or oblong, 32–65 × 20–50 mm, tomentose, greenish-white, margins irregular, sometimes roughly dentate; **Fil** 13–25 mm; **Ov** oblong to cylindrical, thick

and robust, 15–19 mm; **Sty** dark green, 7–13 mm; **Sti** lobed; **Fr** dry capsules, erect, oblong-cylindrical to obovoid-cylindrical, constricted near the middle, 40–65 (–70) × 20–30 mm, walls thick; **Se** black, shiny, 10 × 5 mm.—**Cytology**: 2n = 60 (Watkins 1936).

Rather variable, esp. in the E part of its range (Hess & Robbins 2002). The “var. *paniculata*” may be an E extension of the species with a taller, paniculate and pubescent inflorescence (McKelvey 1947). *Y. arkansana* approaches “*Y. louisianensis*”, which is here synonymized with *Y. flaccida* (Hess & Robbins 2002). Molecular data of Clary (1997, cited by Hess & Robbins 2002) place *Y. arkansana* and “*Y. louisianensis*” closest to one another, whereas those of Pellmyr & al. (2007) place 2 samples of *Y. arkansana* (as *Y. “glaucata arkansana”*) separate from each other — one groups with *Y. glauca*, and the other with *Y. constricta* near to “*Y. louisianensis*”. — The lectotype cited above was designated (as “type”) by McKelvey (1947: 152).

**Y. baccata** Torrey (in Emory, Rep. US Mex. Bound. 2(1): 221, 1859). **Type**: USA, New Mexico (Bigelow 823 [NY 320132]).—**Lit**: Trelease (1902: 109–110, tt. 68–69); Reveal (1977: 528–529, with ills.); Hess & Robbins (2002). **Distr**: S USA, NW Mexico.

≡ *Sarcocoyucca baccata* (Torrey) Lindinger (1933).

For details of the typification see Reveal (1977). One of the most variable indehiscent-fruited yuccas (Webber 1953: 28). Samples of *Y. baccata* group with *Y. schidigera* and *Y. arizonica* (here treated as *Y. baccata* ssp. *thornberi*) in the molecular phylogenies of Pellmyr & al. (2007) and Smith & al. (2008a). An ethnobotanical study of the species was presented by Potter-Bassano (1991). Vernacular name: “Banana Yucca” (for further vernacular names, see Lenz & Hanson 2001: 167).

**Y. baccata** ssp. **baccata** — **Lit**: Reveal (1977: 528–529, with ills.); Matuda & Piña Luján (1980: 65–68, with ills.); Benson & Darrow (1981: 54–55, with ills.); Turner & al. (1995: 409–410, ecology); Hess & Robbins (2002: with ills.); Hawker (2016: 310–315, with ills.). **Distr**: SW & S USA (S California, S Nevada, SE Utah, S-C & SW Colorado, Arizona, New Mexico, SW Texas), NW Mexico (N Chihuahua, Coahuila); rocky slopes in pinyon, oak, and juniper woodlands or grasslands, 400–2500 m; flowers (March to) April to June (to October). **I**: Hochstätter (2002a: 108–120); Boeuf (2007a: 55); Boeuf & al. (2009: 26–27). – Fig. 1.

**Incl.** *Yucca filamentosa* Wood (1868) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca fragilifolia* Baker (1870) ≡ *Yucca baccata* fa. *fragilifolia* (Baker) Voss (1895); **incl.** *Yucca scabrifolia* Baker (1870) ≡ *Yucca baccata* var. *scabrifolia* (Baker)

**Fig. 1** *Yucca baccata* ssp. **baccata** (“var. *vespertina*”). (Copyright: U. Eggli)



Baker (1880); **incl.** *Yucca baccata* fa. *genuina* Engelm. (1873) (*nom. inval.*, ICN Art. 22.1); **incl.** *Yucca filifera* hort. ex Engelm. (1873) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca baccata* var. *hystrix* Baker (1880); **incl.** *Yucca hanburyi* Baker (1892); **incl.** *Yucca baccata* fa. *parviflora* McKelvey (1938); **incl.** *Yucca baccata* var. *vespertina* McKelvey (1938)  $\equiv$  *Yucca vespertina* (McKelvey) S. L. Welsh (1993)  $\equiv$  *Yucca baccata* ssp. *vespertina* (McKelvey) Hochstätter (2001).

[1b] Stems none or rarely up to 6, to 0.3 m, aerial or subterranean; **Ros** asymmetrical and rather open, mostly simple and (50–) 60–75  $\times$  130–150 cm, or forming colonies 1–5 m  $\varnothing$ ; **L** at the base spreading, inner leaves more erect, straight, deeply canaliculate, rigid, falcate and rather narrow (esp. in “var. *vespertina*”), (30–) 50–70 (–75)  $\times$  2.5–4 (flattened 3–6) cm, bluish-green, margins of the upper  $\frac{1}{2}$  forming broad coarse recurved to curly fibres, **terminal Sp** stout, stiff, 1.5–7 mm; **Inf** erect, paniculate, glabrous, mostly green (reddish-purple in “var. *vespertina*”), peduncle 0.6–0.8 m, flowering part short, 0.6–0.8 m, arising completely within or mostly extending  $\frac{1}{4}$  beyond the rosette leaves, with  $\pm 15$  part-**Inf**; **Ped** terete to slightly flattened, 7–40 mm; **Fl** pendent, campanulate; **Tep** lanceolate,  $\pm 50$ –150  $\times$  14–30 mm, dorsally red-brown, ventrally creamy-white, basally connate to form a tube 7–12 mm long; **Fil** 3.2–12 mm, connate proximally into a collar-like structure; **Ov** (30–) 50–70 (–75) mm; **Sty** 5–7 mm; **Sti** distinct; **Fr** fleshy berries, pendent, elongate, upper  $\frac{1}{3}$  constricted, (50–) 150–170 (–230)  $\times$  (30–) 40–75 mm, green, or tinged orange or tan; **Se** rugose, 7–11  $\times$  3 mm, dull black.

This is the common broad-leaved *Yucca* in much of Arizona and New Mexico. The large fleshy fruits are eaten raw, roasted or dried by the Navajos (Benson & Darrow 1981). Differs from ssp. *thornberi* in being acaulescent or short-caulescent with up to 6 aerial or subterranean stems to 0.3 m, and leaf margins with coarse and curling fibres (Hess & Robbins 2002). Variegated cultivars are mentioned by Boeuf & al. (2010: 77–79). Hardy down to  $-29$  °C (Irish & Irish 2000: 238).

**Y. baccata** ssp. **thornberi** (McKelvey) Hochstätter (Succulenta 80(4): 172, 2001). **Type:** USA, Arizona (McKelvey 1627 [A 441073]).—**Lit:** Gentry (1972: 166–169, with ills., as *Y. arizonica*); Matuda & Piña Luján (1980: 72–75, with ills., as *Y. arizonica*); Turner & al. (1995: 407–409, ecology, as *Y. arizonica*); Hess & Robbins (2002); Hawker (2016: 310–315, with ills.). **Distr:** S USA (SE Arizona, SW New Mexico), N Mexico (N Sonora); hills, mesas and flats in the Sonoran Desert, desert grasslands and oak woodlands, 350–2000 m; flowers March to May. **I:** Hochstätter (2002a: 121–131, as *Y. baccata* ssp. *thornberi* & ssp. *confinis*, *Y. arizonica*)).

$\equiv$  *Yucca thornberi* McKelvey (1935); **incl.** *Yucca brevifolia* A. Schott ex Torrey (1859) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca treleasei* J. F. Macbride (1918) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca arizonica* McKelvey (1935); **incl.** *Yucca confinis* McKelvey (1938)  $\equiv$  *Yucca baccata* ssp. *confinis* (McKelvey) Hochstätter (2002) (*nom. inval.*, ICN Art. 41.5); **incl.** *Yucca baccata* var. *brevifolia* L. D. Benson & Darrow (1943).

[1b] Differs from ssp. *baccata*: Caulescent, stems up to 24, aerial, often branched, to 2–3 m; **L** margins finely filiferous; **Inf** arising almost completely within to mostly extending beyond the rosette leaves; peduncle shorter, to 0.3 m.

Widely recognized as *Y. baccata* var. *brevifolia*, but treated here at subspecific rank due to its geographical and morphological distinctness. Lenz & Hanson (2001) include this taxon in the synonymy of *Y.  $\times$ schottii* (see there). Plants in Sonora are generally taller (to 3 m) and form smaller clumps than those in Arizona (to 2 m tall) (Gentry 1972).

**Y. baileyi** Wooton & Standley (Contr. US Nation. Herb. 16: 114–115, 1913). **Type:** USA, New Mexico (Standley 7638 [US 686602, US [iso]]).—**Lit:** Webber (1953: 49–52, tt. 44–45); Reveal (1977: 532–533, with ills.); Welsh & al. (1987: 649); Hess & Robbins (2002); Hawker (2016: 316–323, with ills.). **Distr:** SW USA (SE Utah, S Colorado, NE Arizona, E New Mexico); mountains, adjacent woodlands and grasslands, 1300–2500 m; flowers April to June. **I:**

Hochstätter (2000: 100); Boeuf (2007a: 56); Boeuf & al. (2009: 28–29).

**Incl.** *Yucca navajoa* J. M. Webber (1945) ≡ *Yucca baileyi* var. *navajoa* (J. M. Webber) J. M. Webber (1953); **incl.** *Yucca standleyi* McKelvey (1947).

[3b] Stems none to rarely short and (semi-) erect, to 0.2 (–1.2) m; **Ros** symmetrical, solitary or caespitose and forming colonies 1.3–2 m Ø; **L** somewhat crowded, divergently spreading, rigid, linear, occasionally falcate, lower face convex or keeled, upper face flat, smooth on both faces, 25–45 (–50) × 0.6–0.9 cm, pale or yellowish-green, margins entire, recurved, whitish, becoming separate and forming conspicuous fine curly fibres, tip gradually tapering towards a short **terminal Sp** to 3.2 mm; **Inf** erect, racemose, simple, peduncle 10–20 cm, flowering part 25–45 (–85) cm, arising within or just beyond the rosette leaves, glabrous; **Ped** 10–20 mm; **Fl** pendent, campanulate, 50–65 mm; **Tep** ovate to obovate or elliptic, 50–65 × 15–32 mm, greenish-white, usually tinged with deep purple esp. on the outer face, basally connate to form a tube 3–7 mm long; **Fil** to 20 mm; **Ov** 18–25 × 8 mm; **Sty** white, 7 mm; **Sti** lobed; **Fr** dry capsules, erect, oblong-cylindrical, not or only slightly constricted, 40–70 × 25–50 mm; **Se** thin, with broad marginal wing, 6–10 mm, dull black.

Populations comprising compact colonies with short, branched stems 0.4–1.2 m tall instead of

scattered, caespitose individuals were separated as var. *navajoa* by Webber (1953: 51). According to Webber (1953), *Y. baileyi* appears to hybridize with *Y. glauca* and *Y. angustissima*. Hochstätter (2000: 46) assumed that *Y. baileyi* is related to *Y. elata* and *Y. angustissima* based on its relatively small rosettes with narrow green strongly filiferous leaves, as well as on the distribution area. Molecular data of Pellmyr & al. (2007) and Smith & al. (2008a) group *Y. baileyi* close to *Y. angustissima* and to *Y. utahensis* (as *Y. elata utahensis*), whereas *Y. elata* is more distant. Following Hess & Robbins (2002), *Y. baileyi* var. *intermedia* is accepted here at species rank as *Y. intermedia*.

**Y. brevifolia** Engelmann (in S. Watson, Bot. US Geol. Expl. 40. Parallel 5: 496, 1871). **Type** [lecto]: USA, California (*Bigelow* s.n. [NY, US]).—**Lit**: Reveal (1977: 530–531, with ills.); Matuda & Piña Luján (1980: 111–114, with ills.); Benson & Darrow (1981: 51–53, ills. & t. H1, as var. *brevifolia*); Turner & al. (1995: 409–410, ecology); Hess & Robbins (2002: with ills.); Lenz (2007: with ills.); Hawker (2016: 310–315, with ills.). **Dist**: SW USA (SE California, S Nevada, SW Utah, NW Arizona); dry desert slopes and mesas, 400–2200 m; flowers April to May. **I**: Hochstätter (2002a: 139–153, 156–158); Boeuf & al. (2009: 30–31). – Figs. 2 and 3.

**Fig. 2** *Yucca brevifolia*.  
(Copyright: U. Eggli)







**Fig. 3** *Yucca brevifolia*. (Copyright: U. Eggli)

≡ *Clistoyucca brevifolia* (Engelmann) Rydberg (1918) ≡ *Sarcoyucca brevifolia* (Engelmann) Lindinger (1933); ≡ *Yucca draconis* var. *arborescens* Torrey (1857) ≡ *Yucca arborescens* (Torrey) Trelease ex Merriam (1893) (*nom. illeg.*, ICN Art. 52.1) ≡ *Clistoyucca arborescens* (Torrey) Trelease (1902) (*nom. illeg.*, Art. 52.1); **incl.** *Yucca brevifolia* var. *wolfei* M. E. Jones (1935) (*nom. inval.*, ICN Art. 39.1); **incl.** *Yucca brevifolia* fa. *herbertii* J. M. Webber (1953) ≡ *Yucca brevifolia* var. *herbertii* (J. M. Webber) Munz (1958) ≡ *Yucca brevifolia* ssp. *herbertii* (Munz) Hochstätter (2001); **incl.** *Yucca brevifolia* fa. *kernensis* Hochstätter (2000) (*nom. inval.*, ICN Art. 38.1a).

[2] Usually solitary, arborescent, to (3–) 5–12 (–16) m, main stem usually 1, occasionally several to many, simple or usually monopodially branched distally; **Br** usually from 1–3 m above the ground, stout, 1–3 m long; **Ros** broad, flat- or round-topped, 0.3–1 (–1.5) × 0.3–0.5 m; **L** straight, rigid, smooth, lower face convex or triquetrous, upper face plane, glabrous, (10–) 15–28 (–35) × 0.7–1.5 cm, green, base whitish, margins nearly entire, thin, horny, minutely denticulate, yellow, **terminal Sp** 7–12 mm; **Inf** erect, paniculate, flowering part (25–) 30–55 × 30–38 cm, ellipsoid-ovoid, for ± ¼–½ enclosed within the rosette leaves, with numerous part-**Inf** with crowded flowers, glabrous; **Ped** 7–12 (–25) mm; **Fl** erect, globose to depressed-globose, never opening fully, (30–) 40–70 mm; **Tep** broadly ovate, strongly incurved, fleshy, 25–70 × 11–22 mm, cream, barely connate at the base;

**Fil** 10–12 mm; **Ov** conical, tapering from the base, 25–30 mm; **Sty** 5.5–11 mm; **Sti** distinct; **Fr** pendent, dry, indehiscent, ovoid to broadly ovoid, rounded at the apex, deeply furrowed, rather spongy, 60–85 (–100) × 30–50 (–65) mm; **Se** flat, thin, smooth, 8–12 mm, dull black.

For details of the typification see Reveal (1977: 530). This taxon (vernacular name: “Western Joshua Tree”) and *Y. jaegeriana* (the “Eastern Joshua Tree”, only recently recognized as a separate species) are both characteristic elements of the Mojave Desert of the SW USA, often dominating the landscape.

A variant from the W edge of the Mojave Desert that reproduces asexually by short rhizomes producing large clusters of seemingly different individuals was described as fa. *herbertii* (variously also treated as var. or ssp.; illustrations: Webber 1953: t. 18, Hochstätter 2002a: 151–153, Hawker 2016: 330). Other forms reproduce similarly, but the rhizomes run underground for a longer distance so that the resulting plants are widely spaced (Benson & Darrow 1981).

The inflorescences grow primarily on branches oriented towards the S, or if not S-oriented, bend towards the S, thus maximizing exposure to solar radiation (Warren & al. 2016). Dispersed seeds show substantial loss by granivore removal or loss of germinability (reduced to 50–68% after 1 year; Reynolds & al. 2012). The seeds are distributed by various seed-caching rodents (Vander Wall & al. 2006). During the mast fruiting year 2013, seed production was 100× higher than in the following year, and much less infection by larvae and lower seed predation by rodents took place (Borchert & DeFalco 2016). Esque & al. (2015) studied the seedling establishment after an exceptionally high rainfall event 1983–1984 for 22 years up to 2014: 19% of a study cohort of 53 seedlings survived for 22 years, the highest mortality is in the first 2 years caused by rodents, and the annual growth rates (average of 3.12 cm) are strongly correlated with the amounts of rainfall.

**Y. campestris** McKelvey (Yuccas Southwest US, 2: 173, tt. 62–63, 1947). **Type:** USA, Texas (McKelvey 2849 [A]).—**Lit:** Hess & Robbins (2002); Hawker (2016: 332–334, with ills.).



**Distr:** USA (W Texas); in sand dunes and loose, sandy soils, 220–900 m; flowers May to June. **I:** Hochstätter (1999: 6, 9); Hochstätter (2000: 106); Boeuf & al. (2009: 32–33).

[3b/c] Stems none or short, 0.6–1 m; **Ros** lax, in dense groups, forming small to large colonies; **L** spreading, linear, rigid, widest near the middle, lower face convex, upper face flat, smooth on both faces, 40–65 × 0.3–0.7 (–1.5) (in the middle) cm, bluish-green, margins entire, white to grey, finely fibrous, later glabrous, **terminal Sp** acicular, 7 mm; **Inf** erect, paniculate, peduncle 0.5–1 m, flowering part 0.6–1 m, narrowly ellipsoid, starting between (rarely above) the rosette leaves, part-**Inf** many, thin, fragile, ascending, to 13 cm, glabrous; **Fl** pendent, globose; **Tep** 41–65 × 15–25 mm, **ITep** broader than the **OTep**, often concave, dull green, sometimes tinged pink, basally connate to form a tube ±13 mm long, upper margin irregular, toothed, slightly tomentose; **Fil** ± 13–21 mm; **Ov** oblong-ovoid, 13–20 mm; **Sty** ± 8–12 mm, bright green; **Sti** lobed; **Fr** erect dry capsules, rarely constricted, 45–55 (–63) × 30–50 mm, reddish-brown, aged grey; **Se** large, 11–14 × 8–11 mm, shiny black.

Webber (1953: 62–64) considered this species as the hybrid *Y. constricta* × *Y. elata*, but the occurrence in dense stands in a relatively small area in the plains region of W Texas (Hochstätter 1999: 126, 2000: 56) dismisses its status as a hybrid. The morphological-cladistic study of Clary & Simpson (1995) groups the species with *Y. arkansana*, *Y. glauca*, and *Y. intermedia*, and molecular chloroplast DNA sequence data (Smith & al. 2008a: fig. 2a) with *Y. pallida* and *Y. rupicola*.

Martin & Hutchins (1980: 409) include plants from sandy areas in extreme SE New Mexico (Lea County) here, and Sivinski (2008: 3) suggests that all the millions of stemless *Yuccas* with short peduncles, paniculate inflorescences and green styles widespread in E-C and SE New Mexico may belong here. Hawker (2016) reports an isolated occurrence on sand dunes SE of El Paso in W-most Texas.

**Y. capensis** L. W. Lenz (Cact. Succ. J. (US) 70 (6): 289–293, ills., 1998). **Type:** Mexico, Baja

California Sur (Lenz 4501 [RSA]).—**Distr:** Mexico (Baja California Sur: Cape region); thorn scrub, tropical deciduous forests, and oak woodlands, 100–1000 m; flowers March to July. **I:** Hochstätter (2002a: 96–99; 2003d: 212, 214); Boeuf & al. (2009: 34–35).

[1b] Stems 1–5.5 m, solitary, or plants becoming rhizomatous and group-forming with several un- or few-branched stems from the base, in age often decumbent; **L** spreading, upper leaves ± upcurved, narrowed above the expanded base, canaliculate in the middle, flat distally, rather thin, rough, 50–100 × 3–6 cm, yellowish-green, margins dark grey, smooth to somewhat scabrous, without fibres, tip sharp, brownish, but without a distinct **terminal Sp**; **Inf** erect or somewhat inclined, paniculate, peduncle shorter than the rosette leaves, fertile part 0.4–0.8 m, beginning within the rosette leaves, broadly ellipsoid, many-flowered, dense, with broad leathery **Bra** clasping the young inflorescence, densely tomentose to glabrous; **Fl** spreading to ± pendent, flat or saucer-shaped to more subglobose, to 100 mm Ø; **Tep** elliptic, abruptly attenuate to the narrow tips, to 50 × 25 mm, cream-coloured; **Fil** to 12 mm; **Ov** ± 15 mm; **Sty** short; **Sti** lobed; **Fr** fleshy berries, pendent, oblong-cylindrical, 80–120 × 50 mm, green, black when ripe; **Se** finely sculptured, 3–8 × 3–8 mm, black.

According to the protologue, plants placed here were formerly included in the widespread *Y. valida*, but differ clearly in their long, wide, flexible leaves without fibrous margins, long slender stems eventually falling down, and broad, clasping bracts, as first noted by Lenz (1992: 6). It is regarded as being related with a group of mountain-dwelling mainland *Yuccas* (*Y. ×schottii* [as *Y. schottii*], *Y. madrensis* and *Y. jaliscensis*). Molecular AFLP data (Pellmyr & al. 2007, Smith & al. 2008a) place the species closest to *Y. valida* (and separate from *Y. ×schottii* and *Y. jaliscensis*), while chloroplast DNA sequence data place one sample within *Y. ×schottii* and the other sample (in a second analysis both samples) separate from both *Y. madrensis* and *Y. jaliscensis* (Smith & al. 2008a). However, it is uncertain whether the “*Y. schottii*” samples are *Y. ×schottii* or *Y. schottii* auct. = *Y. madrensis*.

The species rarely forms fruits, esp. in more arid habitats. Birds feed on the fleshy fruits, but do not disperse the seeds (Lenz 1998: 293). Arteaga & al. (2015) studied morphological characters and flowering in 12 populations and found significant differences between sites, and a positive correlation of inflorescence production with average annual rainfall. Population genetic studies (Luna Ortiz 2018) largely separate the populations from the W slopes of the Sierra de La Laguna from those of the N and E slopes.

**Y. carnerosana** (Trelease) McKelvey (Yuccas Southwest US, 1: 24, tt. 6–7, 1938). **Type** [lecto]: Mexico, Coahuila (*Pringle* 3912 [MO, A, F, HBG, JE, K, NY, PH, PUL, S, UC, US]).—**Lit**: Matuda & Piña Luján (1980: 60–61, with ill.); Robbins (1983: 14–19, 31–32, 37–38). **Distr**: C Mexico (S Coahuila, S Nuevo León, E Durango, NE Zacatecas, N & C San Luis Potosí, SW Tamaulipas); dry calcareous hills and slopes in desert scrub or pine-oak forests, 850–2200 m; flowers March to April. **I**: Piña Luján (1980: 277); Hochstätter (2002a: 81); Boeuf & al. (2009: 36–37 & front cover).

≡ *Samuela carnerosana* Trelase (1902).

[1a] Stems generally simple (very rarely with 1 or 2 **Br** in the upper part), sometimes forming groups of stems united at the base, stems 0.6–7.5 m or more, 11–39 cm Ø below the rosette, with a long skirt of dried deflected leaves often reaching down to the ground; **L** spreading, rigid, constricted near the base, smooth on both faces, 23–130 × 2.1–9.8 cm in the middle (10–15 cm at the base), apple-green, margins with coarse recurving detaching filaments, **terminal Sp** 10–18 mm; **Inf** erect, paniculate, peduncle 23–40 cm, strong, flowering part 27–100 cm, ovoid to ellipsoid, above the rosette leaves or lowest part within the rosette leaves, with 14–40 densely branching part—**Inf**, with large persistent white **Bra**, glabrous, rarely tomentose; **Fl** pendent, campanulate, 40–84 mm; **Tep** broadly lanceolate, **OTep** 39–95 × 7–21 mm, **ITep** 39–92 × 11–26 mm, tube 6–25 mm, white to greenish-white; **Fil** 13–29 mm; **Ov** ± 15–55 × 5–11 mm; **Sty** 6–10 mm; **Sti** lobed; **Fr** fleshy berries, pendent, oblong, 31–99 × 20–33 mm, beak

5–36 mm, red-brown to nearly black; **Se** flat, rugose, 1–3 mm thick, 6–10 × 6–10 mm, dull black.

The protologue cites *Pringle* 2841 and *Pringle* 3912 as syntypes. McKelvey (1938: 25?) cites 3 specimens of *Pringle* 3912 at MO as “type”, which represents a lectotypification.

Trelase (1902: 116–122) originally separated plants from W Texas and possibly adjacent Mexico with a conical perianth tube <10 mm long as *Y. faxoniana* from plants from Carneros Pass (Coahuila, Mexico) and further S with a tube 12–25 mm long as *Y. carnerosana*. Robbins (1983) studied many leaf, inflorescence, flower and fruit characters and found a ± broad overlap in all studied characters, including tube length, distinguishing both species not consistently, but by tendency only, or not at all. Robbins considered both species as conspecific, but upheld them in the concept of Trelase pending further biochemical and genetic studies; this is followed here.

Wild populations of *Y. carnerosana* (vernacular name: “palma samandoca”) were and are intensively used especially for fibre (Sheldon 1980; see also under ethnobotany).

**Y. cernua** E. Keith (Sida 20(3): 892–893, ill., 2003). **Type**: USA, Texas (*Keith* 183 [TEX, BRIT, SHST]).—**Lit**: Diggs & al. (2006: 416, ill. p. 307, 417). **Distr**: USA (E-most Texas: Jasper and Newton Counties); open or slightly shaded areas, apparently restricted to brownish acidic clay soils. **I**: Boeuf & al. (2009: 38–39); Behan (2012).

[3a] Acaulescent; **Ros** forming large colonies, spreading from thick rhizomes 1–2 cm Ø; **L** divergently spreading, rigid, acute or slightly acuminate, becoming canaliculate and inrolled 0.7–2.5 cm below the tip, lowermost **L** usually undulate and twisting, (30–) 40–70 (–80) × (3–) 3.5–6.5 cm at the widest point, narrowed to 0.7–1.2 cm just above the base, young leaves glaucous, older leaves becoming yellowish-green to olive-green, margins corneous, yellowish and minutely denticulate, **terminal Sp** 3–10 mm, pungent, yellowish at the base and reddish-brown at the tip; **Inf** erect, paniculate, peduncle (1.2–) 1.5–3.2 m, flowering part (0.3–) 0.5– ± 1.2 m,

narrowly ellipsoid, high above the rosette leaves, part-**Inf** characteristically recurved and drooping as they lengthen, to 35 cm, moderately to densely floccose; **Ped** 10–20 mm; **Fl** pendent, campanulate; **Tep** (narrowly) elliptic or lanceolate, 34–50 (–58) × 7.5–18 mm, mostly white or slightly greenish-white, free, glabrous; **Fil** ± 15 mm; **Ov** oblong-cylindrical, slender, ± 17 × 4–8 mm Ø; **Sty** ± 10 mm; **Sti** lobed; **Fr** dry capsules, pendent, oblong-cylindrical, 32–45 × 20–25 mm, beak 0.5–1 cm; **Se** variable, obovate to D-shaped, 5–7 × 4–6 mm.

A very distinctive species due to the drooping part-inflorescences. It is known from only 7 populations, and despite usually occurring on a unique soil type, it appears tolerant of soil disturbance and also grows along roadsides, and rapidly colonizes bare ground (Keith 2003). *Y. cernua* is similar to *Y. pallida* and *Y. rupicola* in its acaulescent habit, denticulate leaves and beaked capsules, and a closer relationship is also corroborated by molecular data (Pellmyr & al. 2007). For the cultivation in the USA, see Behan (2012).

**Y. constricta** Buckley (Proc. Acad. Nat. Sci. Philadelphia 14: 8, 1863). **Type:** USA, Texas (Buckley s.n. [PH]).—**Lit:** Webber (1953: 53–55, t. 47); Diggs & al. (2006: 416, ill. pp. 307 & 419); Hess & Robbins (2002); Hawker (2016: 334–337, with ill.). **Distr:** USA (C, W-C & S Texas), NE Mexico (N Coahuila); limestone outcrops, scrub, woodland and grassland areas, 300–700 m; flowers April to June. **I:** Hochstätter (1999: 127–128); Boeuf & al. (2009: 42–43).

**Incl.** *Yucca glauca* var. *constricta* Hort. Mesa Garden (s.a.) (*nom. inval.*, ICN Art. 30.6); **incl.** *Yucca angustifolia* Carrière (1860) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca albo-spica* hort. ex van Houtte (1867) (*nom. inval.*, ICN Art. 23.6c?); **incl.** *Yucca polyphylla* Baker (1870).

[3c] Acaulescent or occasionally caulescent with procumbent or erect stems to 40 cm; **Ros** asymmetrical, with 100–200 leaves, forming small to large open colonies; **L** divergent, spreading, linear or somewhat wider near the middle, straight, grass-like, flexible, weak, sometimes appearing somewhat stiff, narrow at the base, straight, flattened or plano-convex, mostly 25–65

× (0.3–) 0.7–1.5 cm, light to dark green, margins entire, white, grey to green when old, becoming filiferous, fibres curly but soon eroding away, **terminal Sp** sharp; **Inf** erect, paniculate, racemose distally, peduncle 1–2 m, flowering part ovoid, 0.45–1.2 m, arising 20–46 cm beyond the rosette leaves, with few to many ascending-spreading part-**Inf** to 15–25 cm, glabrous; **Fl** pendent, semiglobose; **Tep** thin, acute, 25–48 × 11–26 mm, pale greenish-white; **Fil** 17–22 mm, pubescent; **Ov** oblong-cylindrical, 20 × 5–6 mm; **Sty** 8–11 mm, whitish or pale green; **Sti** lobed; **Fr** erect dry capsules, oblong-cylindrical, not, slightly or commonly deeply constricted near the middle, (35–) 46–63 × (15–) 25–43 mm; **Se** thin, 8–15 mm Ø, shiny black.—**Cytology:** 2n = 60 (McKelvey & Sax 1933).

McKelvey (1938, 1947) placed *Y. louisianensis* (here treated as synonym of *Y. flaccida*) and *Y. tenuistyla* here as synonyms, but later authors (e.g. Hess & Robbins 2002) accept both as separate species with pubescent inflorescences. The morphological-cladistic study of Clary & Simpson (1995) groups *Y. constricta* with *Y. standleyi* (here included in *Y. baileyi*) and *Y. elata*. The molecular phylogenies of Pellmyr & al. (2007) and Smith & al. (2008a) are inconclusive but suggest a relationship with *Y. glauca* and/or *Y. elata*.—Widespread in Texas (USA), but in Mexico apparently recorded only by the specimen Gentry & Engard 23696 (US). The plant with a distinct stem depicted by Hochstätter (1999: 128, 2002a: 106) might be *Y. elata*.

**Y. decipiens** Trelease (Annual Rep. Missouri Bot. Gard. 18: 228, 1907). **Type:** Mexico, San Luis Potosí (Trelease 154 [MO 3346084]).—**Lit:** Matuda & Piña Luján (1980: 93–96, with ill.); Robbins (1983: 19–22, 45–46). **Distr:** Mexico (S Coahuila, S Nuevo León, E & SE Durango, C & E Zacatecas, W & C San Luis Potosí, N Aguascalientes, NE Jalisco, NW Guanajuato); well-drained plains with deep sandy soil or rock slopes, in desert or oak scrub, 1750–2650 m; flowers January to April. **I:** Trelease (1902: tt. 62–66, as *Y. valida*); Piña Luján (1980: 280); Hochstätter (2004a: 110–115); Boeuf & al. (2009: 44–45).

≡ *Sarcoyucca decipiens* (Trelease) Lindinger (1933).

[1c] Arborescent, to 15 m, with a trunk 1–2 m Ø, or trunk branching at ground level, richly branched, **Br** to 90 or more, usually with a long skirt of deflected dried leaves below the rosettes; **Ros** often asymmetrical, 40–80 cm Ø; **L** linear-ensiform, straight, nearly flat, not very rigid, slightly scabrous on both faces, 28–66 × 1.3–3.9 cm, dark green, margins with numerous fine to coarse curled greyish to whitish fibres, easily detaching, sometimes soon naked, **terminal Sp** sharp, ± 15 mm, grey or brown; **Inf** erect, paniculate, mostly with the peduncle above the rosette leaves, flowering part 49–137 cm, broadly ovoid, mostly compact, upright in the direction of the subtending bract, hence either erect, oblique, or horizontal, glabrous; **Ped** to 25 mm, glabrous or minutely puberulous; **Fl** pendent, globose to campanulate, 25–56 mm; **Tep** 30–55 mm, **OTep** 7–18 mm wide, **ITep** 10–25 mm wide, creamy-white, sometimes tinged purple; **Fil** 9–22 mm; **Ov** 15–30 mm; **Sty** rather short; **Fr** fleshy berries, pendent, oblong, 46–91 × 16–32 mm, rostrate for 3–15 mm; **Se** rough, 6–7 × 7–8 mm.

The protologue does not cite a type, but the specimen *Trelease* 154 (MO 3346084 digital image!), labelled by Trelase as “*Yucca decipiens*, n. sp.”, is regarded as type (= holotype) at MO, thus rendering the neotypification by Hochstätter (2003b: 112) superfluous. New state records are collections from S Coahuila placed here by Robbins (1983), and several specimens from Municipio Galeana, Nuevo León, collected by Hinton & al. The similar *Y. filifera*, which occurs E-wards of the range of *Y. decipiens*, differs in its pendent inflorescences. Molecular data place *Y. decipiens* mostly near *Y. jaliscensis* (Pellmyr & al. 2007, Smith & al. 2008a: fig. 2a, 2b) or closest to *Y. carnerosana* (Smith & al. 2008a: fig. 2c). Vernacular name: “palma chino”.

**Y. declinata** Laferrière (Cact. Succ. J. (US) 67 (6): 347–348, ill., 1995). **Type:** Mexico, Sonora (*Gentry* 16615 [ARIZ 267477, ARIZ, US]).—**Lit:** Hochstätter (2004a: 21, with ill.). **Distr:** Mexico (E Sonora, W Chihuahua); rocky mountain slopes and open woodland, volcanic and

limestone soils, 700–1230 m. **I:** Gentry (1972: figs. 63 & 64, as *Y. grandiflora*); Matuda & Piña Luján (1980: 73: at least upper fig., as *Y. grandiflora*); Piña Luján (1980: fig. 4, as *Y. grandiflora*); Hochstätter (2003c: 154–155); Bechtold & Metorn (2005: 32); Boeuf & al. (2009: 46–47).

[1b] Arborescent, stems thick, robust, 3–6 m, branching above and forming a crown of few rosettes, suckering at the base when fully grown, with a long skirt of dried deflected leaves below the rosette; **L** erect or spreading, straight, stiff, strong, canaliculate, broadest in the middle, narrowed towards base and apex, glabrous on both faces, 40–140 × 3–6 (in the middle) cm, yellowish-green, margins smooth, pale (white), with age fraying into few fine threads, **terminal Sp** 10–20 mm, greyish to brownish; **Inf** usually inclined, paniculate, peduncle 5–30 cm, flowering part 0.55–1 m, lower part within the rosette leaves, part-**Inf** (slightly) ascending, ± 20–25, to 40 cm, glabrous; **Fl** small; **Tep** lanceolate, 30–50 × 8–12 mm, white; **Fil** 11–18 mm, pubescent; **Ov** elongate, 30–50 mm; **Sty** ± 4–7 mm; **Fr** fleshy indehiscent berries, oblong, tapering at the base, 100–200 × 40 mm, distinctly beaked, brownish when ripe; **Se** flat, slightly ovoid, finely sculptured, 6–15 mm Ø, black.

The type collection was previously tentatively identified as *Y. grandiflora* by Gentry (1972: 162). Since Gentry’s fieldnotes indicated that he considered the plant significantly different from its close relatives *Y. grandiflora* and *Y. arizonica*, Laferrière formally described the plant based on Gentry’s specimens and notes. According to the protologue, *Y. declinata* is most distinctive in its ± horizontally oriented inflorescences. In addition, it differs from *Y. grandiflora* in its smaller flowers and glabrous rachis, from *Y. arizonica* (here treated as synonym of *Y. baccata* ssp. *thornberi*) in its taller habit, larger leaves, and more open inflorescences with flowers with shorter tepals and shorter stamens, and from *Y. ×schottii* by its elongate ovary and glabrous inflorescence. Bechtold & Metorn (2005) provide a new photographic record from W-most Chihuahua. Vernacular name: “datil”. See also under *Y. grandiflora*.

**Y. ×desmetiana** Baker *pro sp.* (Gard. Chron. 27: 1217, 1870). **Type:** not typified.—**Lit:** Ullrich (1991). **Distr:** Cultivated only. **I:** Trelease (1902: t. 48); Guillot Ortiz & Meer (2008: 102); Boeuf & al. (2009: 118; 2010: 83, as *Y. 'De Smetiana'*).

**Incl.** *Yucca atkinis* hort. ex K. Koch (1873); **incl.** *Yucca smetiana* hort. ex K. Koch (1873); **incl.** *Yucca helkinsi* hort. ex Trelease (1902) (*nom. inval.*, ICN Art. 36.1c).

[1c × 3c?] Unique by its symmetrically arranged, flexible, elegantly down-curved leaves with conspicuous purplish- to reddish-brown colour “quite unlike any other *Yucca*” (Trelease 1902: 87). Of unknown origin and distributed by the Belgian nurseryman de Smet (Koch 1873: 212), cultivated in many gardens in 1873 (Engelmann 1873: 41). Koch (1873: 212) considered it as a form, and Sprenger (1920a: 103) as a mutation (“Sport”) of *Y. aloifolia*. Later authors added further possible parental species for its hybrid origin: *Y. gloriosa*, *Y. gloriosa* var. *tristis* (as *Y. recurvifolia*), *Y. filamentosa*, *Y. glauca*, and *Y. treculiana* (Ullrich 1991; Boeuf & al. 2009: 118). No inflorescences have ever been observed except for a published photograph of doubtful identity cited by Ullrich (1991). The specimen Baker s.n. from 1873 (K001096522) was prepared later than the protologue and thus does not represent original (type) material. Hardy down to  $-12\text{ }^{\circ}\text{C}$  (Boeuf & al. 2009).

**Y. elata** Engelmann (Bot. Gaz. 7: 17, 1882). **Type** [lecto]: USA, Arizona (Palmer 201 [MO]).—**Lit:** Webber (1953); Reveal (1977); Matuda & Piña Luján (1980); all with ills.; Hess & Robbins (2002). **Distr:** S USA, N Mexico. **I:** Piña Luján (1980: 281).

This name is treated as new name (*nom. nov.*, ICN Art. 58.1) for *Y. angustifolia* var. *elata* Engelmann 1873 (*nom. illeg.*, ICN Art. 52.1), because it is a superfluous renaming of *Y. angustifolia* var. *radiosa* Engelmann 1871). All names have thus the same type, i.e. the lectotype designated by Reveal (1977: 533).

Easily recognizable in its native range by its elegant crown of narrow flexible finely filiferous leaves with thin white margins on well-developed

trunks (Gentry 1972). Webber (1953) assumes hybridisation with *Y. glauca*, *Y. constricta* and *Y. baileyi* wherever they grow together, but Reveal (1977) believed that Webber did not provide evidence for his hybrid hypothesis. Reveal’s concept of *Y. elata* embraces all those plants from the SW USA with paniculate inflorescences with only the uppermost flowers arranged in racemes. Consequently, he reduced *Y. utahensis* and *Y. verdiensis* to varieties of *Y. elata* (Reveal 1977). This is only partly accepted here, since *Y. utahensis* is clearly separated from *Y. elata* in the molecular phylogenies of Pellmyr & al. (2007) and Smith & al. (2008a).

*Y. elata* is almost always caulescent, in contrast to *Y. angustissima* (plants generally acaulescent, inflorescences almost always strictly racemose) (Reveal 1977). The two infraspecific taxa of *Y. elata* recognized here are difficult to distinguish consistently (Hess & Robbins 2002).

**Y. elata** ssp. **elata** — **Lit:** Gentry (1972: 155–157); Reveal (1977: 533–534); Matuda & Piña Luján (1980: 130–132); Benson & Darrow (1981: 48–49); Lenz & Hanson (2001: 168–169); Hess & Robbins (2002); Hawker (2016: 336–341); all with ills. except Lenz & Hanson. **Distr:** USA (C, S & SE Arizona, C & S New Mexico, W Texas), N Mexico (NE Sonora, N & C Chihuahua, N Coahuila); desert hillsides, grassland (USA), small-leaved desert scrub and open forests (Mexico), on sandy and gravelly soils, 320–1900 m; flowers April to July. **I:** Curtis’s Bot. Mag. 125: t. 7650 (1899); Piña Luján (1980: 281); Hochstätter (2000: 101–103); Boeuf (2007a: 61–62, 113); Boeuf & al. (2009: 48–49).

**Incl.** *Yucca elata* var. *magdalenae* Hort. Mattern (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Yucca angustifolia* var. *radiosa* Engelmann (1871) ≡ *Yucca radiosa* (Engelmann) Trelease (1902); **incl.** *Yucca angustifolia* var. *elata* Engelmann (1873) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Yucca constricta* Baker (1880) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca coahuilensis* Matuda & Piña Luján (1980).

[3b] In the USA arborescent, with 1–7 stems 1–1.5 (–5) m tall, often few-branched above, stems with a skirt of dried deflected leaves



below the rosettes, in Mexico (Coahuila) stems mostly none or very short and rosettes forming lax colonies; **Ros** solitary or in small colonies, symmetrical or asymmetrical; **L** numerous, divergent, narrowly linear, flexible, widest near the middle, lower face convex, upper face flat or canaliculate, striate, 30–95 × 0.2–1.3 cm, pale to yellow- or bluish-green, margins white, greenish-white or greyish, copiously finely filiferous, fibres ± curly, tip long-acuminate, **terminal Sp** short, ± 5 mm, very pungent; **Inf** erect, paniculate, sometimes distally racemose, green to reddish or yellowish, peduncle 1–2 m, flowering part 0.7–1.5 m, narrowly ovoid to ovoid, relatively slender, high above the rosette leaves, part-**Inf** 7–35 cm, glabrous; **Ped** (7–) 10–25 mm; **Fl** pendent, campanulate to somewhat globose; **Tep** narrowly to broadly elliptic or ovate, 32–57 × 13–32 mm (**ITep** broader), creamy-white, often tinged with green or pink, basally connate to form a tube 2–7 mm long; **Fil** 12–25 (–32) mm, pubescent; **Ov** oblong-cylindrical, with deep sutures, 15–20 × 6–10 mm; **Sty** 6–11 mm, white or pale green, pubescent; **Sti** lobed; **Fr** dry capsules, oblong-cylindrical, rarely constricted, rather thin-walled, 50–82 × 20–40 mm, smooth, whitish; **Se** thin, 7–11 (–14) mm Ø, dull black.—**Cytology**:  $n = 30$  (Pinkava & Baker 1985);  $2n = 60$  (McKelvey & Sax 1933, Watkins 1936, as *Y. radiosa*).

Successful pollination is effected by *Yucca* moths only and by outbreeding; the many diurnal insects visiting the flowers do not effect fruit set (James & al. 1993).

*Y. coahuilensis*, only known from ±3 collections in N Coahuila (Mexico), is acaulescent according to the protologue, but Boeuf & al. (2009: 40) depict plants with a short stem from Múzquiz, Coahuila. Hochstätter (2003a: 67–69) and Hochstätter (2004a: 52–53, 152) includes very similar plants from just across the border in Maverick and Zavala counties, Texas (USA), in *Y. coahuilensis*, and places it with *Y. elata* in his Ser. *Glaucæ*. According to Boeuf & al. (2009: 40–41) *Y. coahuilensis* is easily confused with *Y. elata* when young, but distinguished by the lack of a distinct stem and somewhat shorter inflorescences. K. H. Clary (label, 2003) identified the

type collection of *Y. coahuilensis* (Matuda & Piña Luján 38790 [MEXU, MO]) as *Y. elata*. Thus, *Y. coahuilensis* merely represents a redundant name for stemless or short-stemmed *Y. elata* populations from Coahuila (Mexico) and is here accordingly treated as synonym.

**Y. elata** ssp. **verdiensis** (McKelvey) Hochstätter (*Yucca* I, 50, ills. (p. 104), 2000). **Type** [syn]: USA, Arizona (McKelvey 2752 [A]).—**Lit**: Reveal (1977: 533–534); Hess & Robbins (2002); Hawker (2016: 342–348, with ills.). **Distr**: SW USA (C Arizona); rocky hillsides and canyons, 300–1900 m; flowers April to mid-June.

≡ *Yucca verdiensis* McKelvey (1947) ≡ *Yucca elata* var. *verdiensis* (McKelvey) Reveal (1977).

[3b] Differs from ssp. *elata*: Plants predominantly caulescent, 1.5–3.5 m tall, stems distinct but short, 1–1.5 m, rarely none; **L** shorter, 25–45 × 0.2–0.6 (–1.3) cm; **Inf** paniculate, distally racemose, peduncle 1–1.5 m; **Tep** smaller, 32–45 × 13–20 mm; **Ov** 20–25 mm; **Fr** smaller, 40–45 × 20–40 mm.

The type consists of three sheets, which are not cross-labelled, and therefore represent syntypes. McKelvey (1938, 1947) suggested that this could be a mountain variant of *Y. angustissima* but stated that the features bear “no resemblance to those of *Y. angustissima*”. Webber (1953: 63) suggested that ssp. *verdiensis* (as *Y. verdiensis*) is a hybrid between *Y. elata* and *Y. angustissima*. Lenz & Hanson (2001: 169) refer the taxon to the synonymy of *Y. elata*.

**Y. endlichiana** Trelease (Annual Rep. Missouri Bot. Gard. 18: 229–230, tt. 15–17, 1907). **Type** [syn]: Mexico, Coahuila (*Endlich* 6 [MO]).—**Lit**: Matuda & Piña Luján (1980: 68–71); Robbins (1983: 10–13, 41); Hochstätter (2008a); García-Mendoza (2003); Greulich (2015); all with ills. **Distr**: Mexico (S Coahuila); arid Chihuahuan Desert scrub in very hot and dry places, in calcareous soil, 1000–1200 (–1600) m, flowers in May. **I**: Hart (1977); Piña Luján (1980: 278); Glass & Foster (1986: 61); Hochstätter (2004a: 81–83, 2009); Mays (2005: front cover); Boeuf & al. (2009: 52–53); Ríha (2013). – Fig. 4.



**Fig. 4** *Yucca endlichiana*. (Copyright: J. Trager)

≡ *Sarcoyucca endlichiana* (Trelease) Lindinger (1933).

[1b] Acaulescent; **Ros** with strong, thick-fleshy rhizomes, surculose, forming dense colonies 30–60 (–80) cm Ø; **L** few, erect or recurving, rigid, thick, semicircular to triangular in cross-section at the base, conduplicate further up, 19.5–50 × 1.5 cm, bluish-green, brown-red-dish at the base, covered with narrow dark brown to black bands, margins chestnut-brown to black, with coarse, short, curled, recurved grey fibres, **terminal Sp** conical, strong, short, sometimes blunt at age, dark brown; **Inf** diffuse, without main axis, much shorter than the rosette leaves, to 10 cm, part-**Inf** with 3–6 flowers, glabrous; **Ped** filiform, >25 mm; **Fl** to 18 mm Ø; **Tep** ovate, tips acute, thick-fleshy, 15 × 8 mm, cream to pale yellowish inside, wine-red to brownish-red outside, **ITep** with paler margins; **Fil** short, 3–10 mm, finely papillose, pale yellowish; **Ov** oblong, wine-red; **Sty** short, slender; **Sti** white; **Fr** fleshy berries, pendent, subglobose to narrowly ellipsoid, thin-walled, 20–40 × 17–25 mm, ripe brownish; **Se** 6–8 × 5–6 mm, 1–2 mm thick.

This is possibly the most succulent species of *Yucca*. It certainly is very desirable and suitable for collections due to its small size. The highest

density with up to 200 plants/ha is found near the type locality Estación Marte (Matuda & Piña Luján 1980). In the protologue placed closest to *Y. baccata*, which shares the acaulescent habit, thick rhizome and leaves, and very small flowers. Hochstätter (2008a) argues that the species is without close relatives and sufficiently distinct to merit its own section, Sect. *Endlichiana*, but this is not followed here. In the molecular phylogeny of Pellmyr & al. (2007), *Y. endlichiana* is placed with weak support near the dry-fruited *Y. treculiana*.—Greulich (2015: 12) shows an artificial hybrid with *Y. filamentosa*. Hardy down to ± –10 to –12 °C (Boeuf 2007a; Boeuf & al. 2009).

**Y. faxoniana** (Trelease) Sargent (Man. Trees [ed. 1], 121, fig. 106, 1905). **Type:** USA, Texas (*Anonymus* s.n. [A [status?]]).—**Lit:** Matuda & Piña Luján (1980: 61–64, with ill.); Robbins (1983: 14–19, 31–32, 38–39); Hess & Robbins (2002); Hawker (2016: 348–354, with ill.). **Distr:** S USA (SW Texas), NE Mexico (E Chihuahua, N Coahuila); dry rocky slopes and flats in desert scrub, 500–2100 m; flowers March to April. **I:** Piña Luján (1980: 277); Hochstätter (2002a: 76, 78–81); Boeuf (2007a: 63); Boeuf & al. (2009: 54–55). – Fig. 5.

≡ *Samuela faxoniana* Trelease (1902); **incl.** *Yucca baccata* var. *macrocarpa* Torrey (1859) ≡ *Yucca macrocarpa* (Torrey) Coville (1893) (*nom. illeg.*, ICN Art. 53.1) ≡ *Sarcoyucca macrocarpa* (Torrey) Lindinger (1933); **incl.** *Yucca australis* Trelease (1894) (*nom. illeg.*, ICN Art. 53.1) ≡ *Sarcoyucca australis* (Trelease) Lindinger (1933); **incl.** *Yucca macrocarpa* Sargent (1895) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca australis* var. *valida* M. E. Jones (1929) (*nom. inval.*, ICN Art. 35.1).

[1a] Arborescent, stems erect, 0.6–5.9 m, simple or often with 2–4 **Br** in the upper part, 14–60 cm Ø below the rosettes, with a long skirt of dried deflected leaves often reaching down to the ground; **L** spreading, rigid, constricted near the base, smooth on both faces, 43–114 × 3.1–8.4 cm in the middle (12–18 cm at the base), apple-green, margins often with conspicuous coarse curling filaments, **terminal Sp** 15–25 mm, grey; **Inf** erect, paniculate, peduncle

**Fig. 5** *Yucca faxoniana*.  
(Copyright: U. Eggli)



15–83 cm, strong, flowering part 40–172 cm, usually broadly ovoid, above the rosette leaves or lowest part within the rosette leaves, with 30–40 densely branching part—**Inf**, with large persistent white **Bra**, glabrous; **Ped** 20 mm or more; **Fl** pendent, campanulate, 44–124 mm; **Tep** obovate, **OTep** 39–108 × 10–30 mm, **ITep** 28–98 × 13–38 mm, whitish to greenish-white, often tinged rose or purple, tube 1–32 mm; **Fil** 14–38 mm; **Ov** 23–74 × 6–12 mm; **Sty** 2–10 mm; **Sti** distinct; **Fr** fleshy berries, pendent, elongate, 36–136 × 18–36 mm, beak 9–36 mm, brownish to black; **Se** flat, 2–4 mm thick, finely sculptured, 7–9 mm Ø, dull black.—**Cytology**: 2n = 60 (McKelvey & Sax 1933: as *Samuela*).

Trelease (1902) published the segregate genus *Samuela* to accommodate *Y. faxoniana* and *Y. carnerosana*, characterized by a clearly developed perianth tube (tepals free or only basally slightly fused in all other species). Molecular data by Clary (1997) (cited by Hess & Robbins 2002) and Smith & al. (2008a: fig. 2b) confirm the close relationship, but other data place both species separate (Smith & al. 2008a: fig. 2a, c). In any case, both species are embedded within *Yucca*, and *Samuela* cannot be recognized. Both species are doubtfully distinct (see under *Y. carnerosana*). Plants from Brewster County, Texas, formerly placed in *Y. carnerosana* (McKelvey 1938, 1947, Webber 1953: 18), are placed here by

Robbins (1983) and Hess & Robbins (2002).—*Y. faxoniana* is often used for landscaping in (semi-) arid regions of the S USA (Starr 2000, Irish & Irish 2000: 244–246).

**Y. feeanoukiae** Hochstätter (Cactus & Co. 17 (1): 75, ills. (pp. 72–76), 2013). **Type** [syn]: USA, Utah (Hochstätter 1186.70 + 1190.56 [SRP]).—**Distr**: USA (N Utah); limestone hills, 2000 m; flowers in June.

[3b] Caespitose; **Ros** solitary or offsetting and forming small colonies; **L** variable, pointing upwards, curved and contorted, plano-convex, rigid, glaucous, smooth to finely rough, to 10–30 × 1.2–1.5 cm (in the middle, 0.3–0.5 cm at the base), margins finely fibrous, fibres curved and contorted, tip sharp; **Inf** erect, racemose, 30–60 cm, lowest parts of the flowering part within the rosette leaves; **Fl** pendent, 20–40 × 20–30 mm; **Tep** white, **OTep** sometimes purple; **Fr** dry capsules, flattened, 30 × 30 mm, brownish; **Se** crescent-shaped, 6 × 5 mm, dull black.

The published description is short and lamentably incomplete. The species is compared with *Y. harrimaniae* ssp. *sterilis* which is said to differ in forming colonies of many small compact rosettes with downward-pointing, barely fibrous leaves, and in propagating vegetatively only. The published description and photographs conform to *Y. harrimaniae* ssp. *sterilis* except for the

production of fruits and seeds; *Y. feeanoukiae* may represent the fertile taxon from which the former evolved.

**Y. filamentosa** Linné (Spec. Pl. [ed. 1], 1: 319, 1753). **Type** [lecto]: USA, Virginia (*Clayton* 720 [BM]).—**Lit**: Hess & Robbins (2002); Hochstätter (2002a: 274–278, ills. pp. 281–290); Ward (2011: with ills.). **Distr**: E USA (S Maryland, S West Virginia, Virginia, E Tennessee, North Carolina, C & S Mississippi, Alabama, Georgia, South Carolina, C & S Louisiana, N & C Florida); sandy soils; flowers June to July; naturalized in France, Italy, Turkey and New Zealand. **I**: Curtis's Bot. Mag. 23: t. 900 (1806); Curtis's Bot. Mag. 53: t. 2662 (1826, as *Y. glauca* Noisette ex Sims); Refug. Bot. 5: t. 315 (1872, as *Y. glauca* Noisette ex Sims); Hochstätter (2001a: 8–9); Hochstätter (2002a: 36–39); Boeuf (2007a: 64); Boeuf & al. (2009: 56–57).

**Incl.** *Yucca glauca* Noisette ex Sims (1826) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca filamentosa* var. *mexicana* S. Schauer (1847); **incl.** *Yucca filamentosa* var. *maxima* Carrière (1860); **incl.** *Yucca filamentosa* var. *media* Carrière (1860); **incl.** *Yucca filamentosa* var. *patens* Carrière (1860); **incl.** *Yucca filamentosa* var. *ramosa* Carrière (1860); **incl.** *Yucca filamentosa* var. *variegata* Carrière (1860)  $\equiv$  *Yucca filamentosa* fa. *variegata* (Carrière) Trelease (1902); **incl.** *Yucca filamentosa* var. *recurvifolia* Alph. Wood (1861); **incl.** *Yucca filamentosa* var. *bracteata* Engelm. (1873); **incl.** *Yucca filamentosa* var. *laevigata* Engelm. (1873); **incl.** *Yucca filamentosa* var. *latifolia* Engelm. (1873); **incl.** *Yucca filamentosa* fa. *genuina* Engelm. (1873) (*nom. inval.*, ICN Art. 24.3); **incl.** *Yucca filamentosa* [?] *foliis-aureovariegatis* Pynaert (1886) (*nom. inval.*, ICN Art. 23.1); **incl.** *Yucca filamentosa* var. *bicolor* hort. ex Trelease (1902); **incl.** *Yucca filamentosa* var. *elmensis* Sprenger (1906); **incl.** *Yucca filamentosa* var. *nobilis* Sprenger (1906).

[3c] Acaulescent and stems mostly (almost) none, hidden by the leaves when present, or rarely caulescent and stems to 0.5 m, stems always simple; **Ros** stoloniferous and clump-forming; **L** erect to spreading, lower ones often becoming

reflexed near the middle, lanceolate, flexible, thin, usually soft and limp, distinctly narrowed towards the base, widest near the middle, rather abruptly tapering and furrowed towards the tip, scabrous, 50–75  $\times$  2–4 cm, green or slightly glaucous, margins entire, otherwise splitting into stout, long and curled fibres, inrolled at the tip, tip occasionally somewhat pungent; **Inf** erect, paniculate, peduncle 1–3 m, <2.5 cm  $\varnothing$ , flowering part 0.75–1.5 cm, ovoid, well above the rosette leaves, glabrous; **Fl** pendent, globose, 50–70 mm; **Tep** ovate, abruptly short-mucronate, 50–70  $\times$  20–30 mm, white, sometimes tinged with cream, green or rarely brown, glabrous; **Fil** 20–22 mm; **Ov** 15–30 mm; **Sty** elongated, white; **Sti** lobed; **Fr** erect dry capsules, oblong, 38–50  $\times$  20 mm; **Se** thin, flat, winged, 6 mm  $\varnothing$ , dull black.—**Cytology**:  $n = 30$  (Watkins 1936),  $2n = 60$  (Satô 1935, McKelvey & Sax 1933).

The lectotype cited above was designated by Fernald (1944: 8, t. 808: fig. 1). Many slightly different variants have been described but are rarely recognized in recent literature. Very close to and possibly not distinct from *Y. flaccida* (see there for differences, and also Ward 2011).—Hardy outdoors in C Europe and many cultivars are widely cultivated, including variegated forms (Irish & Irish 2000: 247, Guillot Ortiz & Meer 2008: 49–55, Boeuf & al. 2009: 122–125, Boeuf & al. 2010: 58–62, Boeuf & Heim 2014: 22–24). It has become naturalized in France, Italy, Turkey (Euro+Med 2006+: accessed Dec. 2018), and New Zealand (Zimer 2014).

In 18 sampled populations, considerable genetic variation was found, and on average 83% of the total genetic variation was found within populations (Massey & Hamrick 1998). The peak flowering time is later than the peak pollinator activity, larger inflorescences attract more pollinators, and the fruit set may be impacted by the intensity of herbivory damage to the flowers (Althoff & al. 2005). The Bogus Yucca Moth larvae (*Prodoxus decipiens*) feed in the peduncle tissue, but its presence does not appear to affect the reproductive fitness negatively (Althoff & al. 2004). The floral volatiles show low variations between populations, indicating highly



selective attraction by the obligate pollinating moths (Svensson & al. 2005).

**Y. filifera** Chabaud (Rev. Hort. (Paris) 48: 432–434, fig. 97, 1876). **Type**: [lecto—icono]: l.c. fig. 97.—**Lit**: Matuda & Piña Luján (1980: 100, 102–104, with ills.); McVaugh (1989: 281–282, with ills., as *Y. australis*); Robbins (1983: 19–22, 46–48); Fontaine (2013: with ills.). **Distr**: C Mexico (S Coahuila, W & S Nuevo León, SW Tamaulipas, NE Zacatecas, Aguascalientes, N, C & SW San Luis Potosí, NE Jalisco, N & NE Guanajuato, C & S Querétaro, W Hidalgo, NE Michoacán, N México, Distrito Federal); plains with arid desert scrub, 450–2400 m; flowers April to May. **I**: Curtis's Bot. Mag. 117: t. 7197 (1891); Piña Luján (1980: 280); Boeuf & al. (2009: 58–59).

≡ *Yucca canaliculata* var. *filifera* (Chabaud) Fenzi (1889) ≡ *Yucca baccata* var. *filifera* (Chabaud) Schelle (1903); **incl.** *Yucca baccata* var. *australis* Engelm (1873) ≡ *Yucca australis* (Engelm) Trelease (1892).

[1c] Arborescent, stems to 6–10 (–13) m tall, much-branched, old plants with up to 40 **Br**, crown relatively open, trunk short, to 1.5 m Ø, first branch often at ground level, stems 7.4–25.8 cm Ø below the rosettes; **L** linear-oblancoolate, constricted near the base, rigid, generally asperous on both faces, 18–60 × 1.3–3.9 cm, margins often with numerous fine, spiralled, white detaching fibres, esp. on young leaves, **terminal Sp** stout, 10–30 mm, dark; **Inf** pendent, paniculate, peduncle 19–39 cm, flowering part 27–148 cm, ± cylindrical, nearly always beyond the rosette leaves, obscurely puberulent to glabrous; **Ped** to 27 mm; **Fl** 30–57 mm; **Per** white to cream, **OTep** 30–55 × 7–25 mm, **ITep** 30–57 × 14–28 mm; **Fil** 10–26 mm, puberulent; **Ov** 13–28 × 4–10 mm; **Sty** 1–4 mm; **Fr** fleshy berries, pendent, oblong, 27–88 × 12–33 mm, beak 2–16 mm, with the flavour and consistency of dates; **Se** somewhat rugose, 1–4 mm thick, 5–9 mm Ø.

The neotypification by Hochstätter (2003b: 110) is superfluous, since the illustration accompanying the protologue (Chabaud 1876: fig. 97) is available; it is **here formally designated as**

**lectotype**.—This is the most widely distributed Mexican species, first reported by Josiah Gregg in 1844 (Fontaine 2013: 37), and it forms an important element of the tree stratum of the Chihuahuan Desert scrub of C Mexico (Matuda & Piña Luján 1980). The characteristic pendent inflorescences distinguish it from other arborescent species in the area (except *Y. potosina*, see there). The extremely sweet fruits (Hoxey 2011) are eaten fresh, cooked or dried (Fontaine 2013: 39) and are usually curved in the middle, but may also have a distal constriction (Villavicencio & Pérez-Escandón 1995; see also introduction). In molecular phylogenies (Pellmyr & al. 2007, Smith & al. 2008a), the species groups as sister of *Y. jaliscensis* in most analyses. See also under *Y. potosina*.

The seeds remain viable for at least 4 years after harvesting with somewhat reduced germination rates, but seeds 14 years old showed no germination (Cambrón-Sandoval & al. 2013). Seeds in habitat show high germination rates independent of warming treatment and season (Aragón-Gastélum & al. 2018).

**Y. flaccida** Haworth (Suppl. Pl. Succ., 34–35, 1819). **Type** [neo]: USA, Florida (Ward 10736 [FLAS, FSU, FTG, GA, MO, NCU, NY, TEX, USF]).—**Lit**: Hess & Robbins (2002); Diggs & al. (2006: 416–417, ills. p. 419, as *Y. louisianensis*). **Distr**: Canada (S Ontario), NE, E and SE USA (Wisconsin, Michigan, Illinois, Kansas, Missouri, Indiana, Ohio, Pennsylvania, Maryland, Oklahoma, Arkansas, Tennessee, North Carolina, E Texas, Louisiana, Mississippi, Alabama, Georgia, South Carolina, Florida); (semi-) open sites in pine scrub or pine-hardwood woodland, old fields and coastal sands; flowers May to July. **I**: Curtis's Bot. Mag. 103: t. 6316 (1871); Refug. Bot. 5: t. 323 (1872); Hochstätter (2002a: 291–296); Hochstätter (2002c: 41–43); Boeuf (2007a: 65); Boeuf & al. (2009: 60–61, 74–75 as *Y. louisianensis*).

≡ *Yucca filamentosa* var. *flaccida* (Haworth) Engelm (1873) ≡ *Yucca filamentosa* fa. *flaccida* (Haworth) Voss (1895); **incl.** *Yucca concava* Haworth (1819) ≡ *Yucca filamentosa* var. *concava* (Haworth) Robinson (1871) ≡



*Yucca filamentosa* fa. *concava* (Haworth) Voss (1895)  $\equiv$  *Yucca filamentosa* ssp. *concava* (Haworth) Hochstätter (2001); **incl.** *Yucca glaucescens* Haworth (1819)  $\equiv$  *Yucca filamentosa* var. *glaucescens* (Haworth) Baker (1880)  $\equiv$  *Yucca filamentosa* fa. *glaucescens* (Haworth) Voss (1895)  $\equiv$  *Yucca flaccida* var. *glaucescens* (Haworth) Trelease (1902); **incl.** *Yucca puberula* Haworth (1828)  $\equiv$  *Yucca filamentosa* var. *puberula* (Haworth) Baker (1880)  $\equiv$  *Yucca filamentosa* fa. *puberula* (Haworth) Voss (1895); **incl.** *Yucca orchioides* Carrière (1861)  $\equiv$  *Yucca filamentosa* var. *orchioides* (Carrière) Baker (1880)  $\equiv$  *Yucca filamentosa* fa. *orchioides* (Carrière) Voss (1895)  $\equiv$  *Yucca flaccida* fa. *orchioides* (Carrière) Trelease (1902); **incl.** *Yucca filamentosa* [?] *meldensis* Lescuyer (1862)  $\equiv$  *Yucca meldensis* (Lescuyer) Ellacombe (1875); **incl.** *Yucca concava* var. *longifolia* B. S. Williams (1870); **incl.** *Yucca exigua* Baker (1872)  $\equiv$  *Yucca flaccida* var. *exigua* (Baker) Trelease (1902); **incl.** *Yucca filamentosa* var. *grandiflora* Baker (1872)  $\equiv$  *Yucca flaccida* var. *grandiflora* (Baker) Trelease (1902); **incl.** *Yucca filamentosa* var. *angustifolia* Engelmann (1873); **incl.** *Yucca orchioides* var. *major* Baker (1877)  $\equiv$  *Yucca flaccida* var. *major* (Baker) M. L. Rehder (1920); **incl.** *Yucca filamentosa* var. *maxima* Baker (1880) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca filamentosa* var. *antwerpensis* hort. ex Baker (1881) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Yucca flaccida* fa. *integra* Trelease (1902); **incl.** *Yucca flaccida* fa. *lineata* Trelease (1902); **incl.** *Yucca louisianensis* Trelease (1902)  $\equiv$  *Yucca arkansana* ssp. *louisianensis* (Trelease) Hochstätter (1999); **incl.** *Yucca smalliana* Fernald (1944)  $\equiv$  *Yucca filamentosa* var. *smalliana* (Fernald) Ahles (1964)  $\equiv$  *Yucca filamentosa* ssp. *smalliana* (Fernald) Hochstätter (2001)  $\equiv$  *Yucca flaccida* var. *smalliana* (Fernald) D. B. Ward (2004); **incl.** *Yucca freemanii* Shinnery (1951)  $\equiv$  *Yucca arkansana* ssp. *freemanii* (Shinnery) Hochstätter (2000).

[3c] Caespitose, forming small colonies, erect, acaulescent or rarely stems to 0.3 m, simple; **Ros** stoloniferous, usually small, dying slowly after flowering; **L** lanceolate, erect, thin, rigid or soft and limp, gradually tapering towards the tip, flattened, arching or curved in the middle with age,

glabrous on both faces, 40–80  $\times$  1–4 (–5) cm, widest near the middle, margins entire, filiferous, terminal **Sp** pungent; **Inf** erect, paniculate, peduncle 0.5–2.75 m, mostly pubescent, flowering part 0.4–1.5 m, narrowly ovoid, arising beyond the rosette leaves, part-**Inf** ascending, to 25 cm, mostly pubescent; **Ped** 15–30 mm; **Fl** pendent, 40–50 mm; **Tep** lanceolate to elliptic, 30–50  $\times$  10–30 mm, white, creamy-white or light greenish-white, mostly pubescent, tips obtuse; **Fil**  $\pm$  20 mm; **Ov** 15 mm, pale green; **Sty**  $\pm$  8 mm, greenish-white to white, papillate; **Sti** diverging; **Fr** erect dehiscent capsules, oblong, inversely pear-shaped or conical, to 35–40  $\times$  15–20 mm; **Se** thin, 6–8  $\times$  5–6 mm, dull black.—**Cytology**: 2n = 60 (McKelvey & Sax 1933, Watkins 1936: as *Y. louisianensis*).

The neotypification by Hochstätter (2001a: 12) was ineffectively published under ICN Art. 7.11. Ward (2006) validly designated a neotype as given above, and treats *Y. recurva* Haworth as synonym of *Y. gloriosa*, and *Y. concava* Haworth as synonym of *Y. filamentosa*.

Very close to and probably better regarded as a variety of *Y. filamentosa* from which it differs mainly in its thinner, narrower leaves, mostly pubescent inflorescences with tepals 30–50 mm (vs. thicker, rigid leaves and glabrous inflorescences with tepals 50–70 mm in the latter) (Hess & Robbins 2002). Ward (2011: 224–225) applies additional characters to distinguish both species.

The synonymous *Y. freemanii* was described for glabrous plants from NE Texas and SW Arkansas, but some plants otherwise attributable to *Y. freemanii* are mostly pubescent throughout the inflorescence and fall within the variation of *Y. flaccida* (Hess & Robbins 2002). *Y. louisianensis*, synonymized here following Hess & Robbins (2002), was considered as a possible synonym of *Y. constricta* by McKelvey (1947), whereas Hochstätter (1998) treats it as a subspecies of *Y. arkansana*. Molecular data (Clary 1997, cited by Hess & Robbins 2002) indicate that *Y. louisianensis* is genetically distinct and more closely related to *Y. filamentosa* than to *Y. flaccida*. In recent molecular studies (Pellmyr & al. 2007, Smith & al. 2008a), two samples of *Y. louisianensis* place separate from

each other and group mostly with *Y. glauca*, or with *Y. filamentosa* (*Y. flaccida* s.s. not sampled).

Variegated forms are reported from cultivation in Europe (Boeuf & al. 2010: 62–64, Guillot Ortiz & Meer 2008: 59–60, ill. p. 105, Boeuf & Heim 2014: 22–24) and the USA (Irish & Irish 2000: 251).

**Y. gigantea** Lemaire (Ill. Hort. 6 (Misc.): 91, 1859). **Type:** not typified.—**Lit:** Trelease (1898: 141–144, tt. 40–42); Trelease (1902: 71–72); Smith & Figueiredo (2016: with ills.). **Distr:** Probably cultivated only.

≡ *Yucca elephantipes* var. *gigantea* (Lemaire) Molon (1914) (*nom. inval.*, ICN Art. 35.1).

[1c] Arborescent, with massive trunk or stems 3–10 m or more, base of trunk often straight and hardly swollen, angled because of buttress-like projections, richly branched in the upper parts, branches brittle, with large, broad, arcuate-cordiform leaf scars; **L** numerous, horizontal, lower ones pendent, oblong-lanceolate, flat or slightly canaliculate, > 100–140 × 8–10 cm, brilliant green, tip acute, margins finely membranous, slightly roughened, not filiferous; **Inf** erect, paniculate, flowering part ±65 cm, 50 cm Ø, candle flame-shaped, dense, surpassing the rosette leaves with the upper ½ or more, with 12–15 part-**Inf** with 7–10 flowers each, to 25 cm; **Fl** pendent, campanulate to open-spreading, ± 90 mm, ± 180 mm Ø; **Tep** oblong, narrow, long acuminate, tip apiculate, hood-like, incurved, papillose on the outer face, ± 90 × 25 mm, white; **Fil** 8–10 mm; **Ov** oblong, ± 22 × 10 mm; **Sti** recurved, papillose; **Fr** fleshy berries, resembling those of *Y. gloriosa* but not further described; **Se** not described.

In modern treatments mostly included in *Y. guatemalensis* (as *Y. elephantipes*), but recently re-established as a species of its own right by Smith & Figueiredo (2016). It differs from the latter in its massive size, a trunk straight and hardly swollen at the base, brittle branches, leaves longer than 1 m, and a candle flame-shaped inflorescence with larger flowers (vs. medium to large size, an enlarged, fat-footed trunk, sturdy branches, leaves usually less than 1 m, and a

more open, egg-shaped inflorescence with smaller flowers (Smith & Figueiredo 2016).

Apparently known from cultivation only and possibly a hybrid of *Y. guatemalensis* (Trelease 1902: 71, as *Y. elephantipes*); fruits, flowers, and seeds resemble *Y. gloriosa* (Trelease 1898: 142). No complete description exists, and the above data were mainly taken from the protologue and Trelease (1898). The species forms ripe fruits in cultivation in the absence of yucca moths (Trelease 1898: 142) (also found in *Y. aloifolia*). Most records and photographs of wild, cultivated, and naturalized plants labelled *Y. gigantea* apparently belong to *Y. guatemalensis*.

**Y. glauca** Nuttall (Cat. Pl. Upper Louisiana no. 89, 1813). **Type** [neo]: USA, Montana (*Hochstätter* 1178.69 [SRP]).—**Lit:** Benson & Darrow (1981: 49, with ill.); Hess & Robbins (2002); Hawker (2016: 353–357, 359, with ills.). **Distr:** S Canada (SE Alberta), USA (Montana, North Dakota, South Dakota, Wyoming, Nebraska, Iowa, Colorado, Kansas, Missouri, New Mexico, Oklahoma, Texas); common in Great Plains grasslands, badlands and mountains, 500–2600 (–2800) m; flowers May to July. **I:** Curtis's Bot. Mag. 48: t. 2222 (1821, as *Y. stricta*); *Hochstätter* (1998: 76–78); *Hochstätter* (2000: 104–105); Boeuf (2007a: 66); Boeuf & al. (2009: 62–63).

**Incl.** *Yucca glauca* var. *arkansana* Hort. Mesa Garden (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Yucca glauca* var. *elata* Hort. Mesa Garden (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Yucca glauca* var. *radiosa* Hort. Mesa Garden (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Yucca angustifolia* Pursh (1814); **incl.** *Yucca stricta* Sims (1821) ≡ *Yucca angustifolia* var. *stricta* (Sims) Baker (1880) ≡ *Yucca angustifolia* fa. *stricta* (Sims) Voss (1895) ≡ *Yucca glauca* var. *stricta* (Sims) Trelease (1902) ≡ *Yucca glauca* ssp. *stricta* (Sims) *Hochstätter* (1999); **incl.** *Yucca stenophylla* Steudel (1841); **incl.** *Yucca stricta* var. *elatior* Carrière (1859); **incl.** *Yucca stricta* var. *intermedia* Carrière (1859); **incl.** *Yucca angustifolia* fa. *genuina* Engelmann (1873) (*nom. inval.*, ICN Art. 24.3); **incl.** *Yucca glauca* var. *rosea* D. M. Andrews (1937); **incl.** *Yucca glauca* var. *gurneyi* McKelvey (1947) ≡ *Yucca glauca* ssp. *gurneyi*

(McKelvey) Hochstätter (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Yucca glauca* fa. *montana* Hochstätter (1998) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Yucca glauca* ssp. *albertana* Hochstätter (2000).

[3c] Stems none or short and to 40 cm, erect, occasionally branched; **Ros** first single but soon clump-forming, 1–15 per colony, colonies dense, 0.8–2.5 m Ø; **L** divergently spreading, linear to linear-lanceolate, rigid, plano-convex, widest near the middle, occasionally triquetrous or nearly flat, striate, 40–60 × 0.8–1.2 cm, pale green, margins entire, white or greenish-white, soon finely filiferous, apex blunt, or with a short acute brownish **terminal Sp**; **Inf** erect, racemose, occasionally paniculate proximally, peduncle 0.2–0.5 m, flowering part 0.5–1 m, from between or just beyond the rosette leaves, branches usually none or rarely few, abortive at the base; **Fl** pendent, globose or campanulate; **Tep** elliptic, acute, 50–53 × 26–35 mm, greenish-white to white, commonly tinged with purple and shiny; **Fil** 17–19 mm, white; **Ov** obovoid, 20 × 9–13 mm, white or rarely greenish-white, abruptly terminating into the style; **Sty** dark green, 10 mm; **Sti** lobed; **Fr** erect dry capsules, cylindrical to obovoid, rarely constricted, 50–80 (–90) × 30–45 (–50) mm, beaked; **Se** thin, with broad marginal wing, 7–9 × 8–10 mm, black, slightly glossy.—**Cytology**: 2n = 60 (Watkins 1936).

Hochstätter (1998: 74) provided a somewhat cryptic neotypification for this name. His measurements partly differ considerably from those of Webber (1953) and Hess & Robbins (2002) reproduced here. Webber (1953) suggested hybridisation of *Y. glauca* with *Y. baileyi*, *Y. elata*, *Y. constricta* and *Y. angustissima*. *Y. glauca* and *Y. arkansana* are very similar. The leaves of *Y. glauca* are uniform in size, rigid, linear or linear-lanceolate, and up to 1.2 cm wide, while mature leaves of *Y. arkansana* are generally somewhat flexible, lanceolate, and to 2.5 cm wide, and the young leaves immediately surrounding the peduncle are distinctly shorter than the outer leaves (Hess & Robbins 2002). The molecular data of Clary (1997, cited by Hess & Robbins 2002) do not confirm the close relationship between *Y. glauca* and *Y. arkansana* suggested by the morphological characters. Three accessions of *Y. glauca* variously

group together with *Y. constricta*, *Y. louisianensis* and *Y. arkansana* in the molecular AFLP phylogenies of Pellmyr & al. (2007) and Smith & al. (2008a). *Y. glauca* ssp. *albertana* from Canada differs in minor quantitative features only that fall well within the variability of the species given by Webber (1953). The inflorescences of *Y. glauca* are primarily racemose, but may occasionally be paniculate proximally, and such plants were given varietal names. *Y. glauca* is the most widely distributed North American *Yucca* and represents a characteristic element of the prairie grassland plains in the mid-western USA. It is the most cold-hardy form of any *Yucca* (Irish & Irish 2000: 253).

**Y. gloriosa** Linné (Spec. Pl. [ed. 1], 1: 319, 1753). **Type**: L 0052810: Herb. Adriaan van Royen No. 913.62–412.—**Distr**: SE USA (North Carolina, Mississippi, Alabama, Georgia, South Carolina, Louisiana, Florida).

**Incl.** *Yucca gloriosa* fa. *genuina* Engelmänn (1873) (*nom. inval.*, ICN Art. 24.3).

The lectotype cited above was designated by Ferrer-Gallego & al. (2015). The earlier designation of a type (lectotype) by Hochstätter (2002d: 90) is ineffectively published under ICN Art. 7.11. *Y. gloriosa*, usually placed in Sect. *Yucca*, differs from all other species in that section in its indehiscent fruits which are corky-leathery rather than fleshy. Based on morphology, Trelease (1902: 87) suggested that the species may be a hybrid between *Y. aloifolia* and *Y. filamentosa*. Recent molecular data of Rentsch & Leebens-Mack (2012) indeed provide strong support that *Y. gloriosa* originated as homoploid intersectional hybrid *Y. aloifolia* × *Y. filamentosa* (also explaining its intermediate fruit type), but leave it unclear whether it is of single or multiple origins.—Vernacular name: “Mound Lily Yucca” (Ward 2004).

Probably the most widely grown *Yucca* species with many cultivars, hybrids and selections, including variegated forms. For the cultivation in Europe, see Heim & Lorek (2008), and in the USA, see Irish & Irish (2000: 254–257).

**Y. gloriosa** var. **gloriosa** — **Lit**: Trelease (1902: 72–76, tt. 43–46); Hess & Robbins

(2002: with ills.); Hochstätter (2002a: 35–38, ills. pp. 134, 136). **Distr:** SE USA (North Carolina, South Carolina, Georgia); coastal dunes near sea-level, uncommon; flowers July to September; locally naturalized in Spain, Portugal, France, Italy, Turkey and India. **I:** Curtis's Bot. Mag. 31–32: t. 1260 (1810); Refug. Bot. 5: t. 320 (1872); Hochstätter (2002d: 90).

**Incl.** *Yucca integerrima* Stokes (1812); **incl.** *Yucca obliqua* Haworth (1812) ≡ *Yucca gloriosa* var. *obliqua* (Haworth) Baker (1880) ≡ *Yucca gloriosa* fa. *obliqua* (Haworth) Voss (1895); **incl.** *Yucca superba* Haworth (1819) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca acuminata* Sweet (1827) ≡ *Yucca gloriosa* var. *acuminata* (Sweet) Carrière (1868) ≡ *Yucca gloriosa* fa. *acuminata* (Sweet) Voss (1895); **incl.** *Yucca ensifolia* Groenland (1859) ≡ *Yucca flexilis* var. *ensifolia* (Groenland) Baker (1880) ≡ *Yucca flexilis* fa. *ensifolia* (Groenland) Voss (1895); **incl.** *Yucca gloriosa* var. *maculata* Carrière (1859) ≡ *Yucca gloriosa* fa. *maculata* (Carrière) Trelease (1902); **incl.** *Yucca gloriosa* subvar. *parviflora* Carrière (1860); **incl.** *Yucca gloriosa* var. *glaucescens* Carrière (1860); **incl.** *Yucca gloriosa* var. *minor* Carrière (1860) ≡ *Yucca gloriosa* fa. *minor* (Carrière) Trelease (1902); **incl.** *Yucca gloriosa* var. *nobilis* Carrière (1860) ≡ *Yucca gloriosa* fa. *nobilis* (Carrière) Trelease (1902); **incl.** *Yucca gloriosa* var. *plicata* Carrière (1860) ≡ *Yucca plicata* (Carrière) K. Koch (1873); **incl.** *Yucca gloriosa* var. *robusta* Carrière (1860); **incl.** *Yucca gloriosa* var. *longifolia* Carrière (1862) ≡ *Yucca gloriosa* fa. *longifolia* (Carrière) Trelease (1902); **incl.** *Yucca acutifolia* Truffaut (1869); **incl.** *Yucca ellacombei* hort. ex Baker (1870) ≡ *Yucca gloriosa* var. *ellacombei* (Baker) Baker (1880); **incl.** *Yucca gloriosa* var. *recurvata* Baker (1870); **incl.** *Yucca patens* André (1870) ≡ *Yucca flexilis* fa. *patens* (André) Trelease (1902); **incl.** *Yucca pruinosa* Baker (1870) ≡ *Yucca gloriosa* var. *pruinosa* (Baker) Baker (1880) ≡ *Yucca gloriosa* fa. *pruinosa* (Baker) Voss (1895); **incl.** *Yucca tortulata* Baker (1870) ≡ *Yucca gloriosa* var. *tortulata* (Baker) Baker (1880) ≡ *Yucca gloriosa* fa. *tortulata* (Baker) Voss (1895) ≡ *Yucca flexilis* var. *tortulata* (Baker) Trelease (1902); **incl.** *Yucca plicatilis* hort. ex

K. Koch (1873); **incl.** *Yucca gloriosa* var. *plicata* Engelmann (1873) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca gloriosa* var. *mediopicta* Carrière (1880); **incl.** *Yucca gloriosa* var. *mediostriata* Planchon (1880) ≡ *Yucca gloriosa* fa. *mediostriata* (Planchon) Trelease (1902); **incl.** *Yucca gloriosa* var. *superba* Baker (1880) ≡ *Yucca gloriosa* fa. *superba* (Baker) Trelease (1902).

[1c × 3e] Caulescent to arborescent, simple or more often branching near the stem tips and forming colonies, stems erect, to 5 m; **L** mostly erect, ascending, straight, rigid, becoming more flexible with age, thin, lanceolate, somewhat narrowed towards the base, plano-convex, smooth on both faces, 40–70 × 4–6 cm, glaucous, margins entire or roughly and minutely denticulate, often becoming filiferous, fibres straight, brown, opaque; **Inf** erect, paniculate, peduncle 0.9–1.5 m, flowering part ovoid to ellipsoid, 0.75–1.2 m, to 45 cm broad, extending 0.4–0.5 m beyond the rosette leaves, glabrous or occasionally pubescent; **Ped** to 20 mm; **Fl** pendent, globose to campanulate; **Tep** oblong-lanceolate, 40–50 × 20–25 mm, white to creamy-white; **Fil** ± 26 mm, granular or powdery, pubescent; **Ov** ± 28 mm, light green; **Sty** ± 9 mm; **Sti** separate; **Fr** berry-like, indhiscent-leathery and not fleshy, pendent, elongate, 6-winged or 6-ribbed, 55–80 mm; **Se** ovate, thin, 5–8 mm Ø, shiny black.—**Cytology:** 2n = 60 (Bhattacharya & Dutta 1978).

Many forms now sunk in synonymy have been named based on slight differences in habit and leaf morphology. Var. *gloriosa* differs from var. *tristis* in its mostly erect, rigid leaves (vs. mostly recurving, flexible), its inflorescences extending well beyond the rosettes (vs. inflorescences barely extending), and its pendent larger fruits 55–80 mm (vs. mostly erect fruits 25–45 mm) (Hess & Robbins 2002). Ward (2004) records the taxon from Virginia (as *Y. gloriosa*), but later (Ward 2011: 223) gives the plants as cultivated only. Variegated cultivars are shown by Boeuf & al. (2010: 65–70) and Boeuf & Heim (2014: 24–27). *Y. ellacombei* hort. ex Baker (1870) represents another name for the horticultural selection *Y. gloriosa* ‘Nobilis’.



Locally established as neophyte in Spain (López-Pujol & Guillot Ortiz 2014a, Aymerich 2015), Portugal (Verloove & Alves 2016, Almeida 2018: 272), France, Italy, Turkey (Euro+Med 2006+: accessed Dec. 2018), and India (Howes 1946), where it is used as hedge plant.

**Y. gloriosa** var. **tristis** Carrière (Rev. Hort. (Paris) 1859: 363–364, 1859). **Type:** not typified.—**Lit:** Trelease (1902: 76–78, tt. 46–47, as *Y. recurvifolia*; 78–81, t. 47, as *Y. flexilis*); Hess & Robbins (2002); Hochstätter (2002a: 38–40, ill. pp. 132, 135, 137, as *Y. recurvifolia*); **Distr:** SE USA (SE Louisiana, S Mississippi, S Alabama, S Georgia, NW & N Florida); coastal dunes of Gulf coast plains, in sandy soils, 0–100 m; flowers April to May; locally naturalized in Texas (USA), Spain and Italy. **I:** Hochstätter (2002d: 92, as *Y. recurvifolia*).

≡ *Yucca recurvifolia* var. *tristis* (Carrière) Trelease (1902); **incl.** *Yucca recurvifolia* Salisbury (1806) ≡ *Yucca gloriosa* var. *recurvifolia* (Salisbury) Engelmann (1873); **incl.** *Yucca recurva* Haworth (1812); **incl.** *Dracaena ensifolia* Haworth (1812) (*nom. illeg.*, Art. 52.1?); **incl.** *Yucca rufocincta* Haworth (1819) ≡ *Yucca recurvifolia* var. *rufocincta* (Haworth) Baker (1870) ≡ *Yucca gloriosa* var. *rufocincta* (Haworth) Baker (1880) ≡ *Yucca gloriosa* fa. *rufocincta* (Haworth) Voss (1895) ≡ *Yucca recurvifolia* fa. *rufocincta* (Haworth) Trelease (1902); **incl.** *Yucca angustifolia* Karwinsky ex G. Don (1839) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca pendula* Groenland (1858) ≡ *Yucca gloriosa* fa. *pendula* (Groenland) Schelle (1903); **incl.** *Yucca flexilis* Carrière (1859) ≡ *Yucca gloriosa* var. *flexilis* (Carrière) Trelease (1902); **incl.** *Yucca japonica* hort. ex Carrière (1859); **incl.** *Yucca acuminata* hort. ex Carrière (1859) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca angustifolia* hort. ex Carrière (1859) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca longifolia* hort. ex Carrière (1859) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca pendula* Sieber ex Carrière (1859) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca stenophylla* hort. ex Carrière (1859) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca gloriosa* var. *mollis* Carrière (1860); **incl.** *Yucca boerhaavii* Baker

(1870) ≡ *Yucca flexilis* fa. *boerhaavii* (Baker) Trelease (1902); **incl.** *Yucca semicylindrica* Baker (1870) ≡ *Yucca falcata* var. *semicylindrica* (Baker) Baker (1880) ≡ *Yucca flexilis* var. *semicylindrica* (Baker) Baker (1880) ≡ *Yucca flexilis* fa. *semicylindrica* (Baker) Trelease (1902); **incl.** *Yucca gloriosa* var. *planifolia* Engelmann (1873); **incl.** *Yucca pendula* var. *variegata* Carrière (1875) (*incorrect name*, ICN Art. 11.4) ≡ *Yucca gloriosa* var. *variegata* (Carrière) Carrière (1880) ≡ *Yucca recurvifolia* fa. *variegata* (Carrière) Trelease (1902); **incl.** *Yucca falcata* Anonymus (1876) ≡ *Yucca flexilis* var. *falcata* (Anonymus) Baker (1880); **incl.** *Yucca pendula* var. *aurea* Carrière (1877) (*incorrect name*, ICN Art. 11.4); **incl.** *Yucca flexilis* var. *nobilis* Hort. Peacock ex Baker (1880); **incl.** *Yucca gloriosa* var. *elegans* Carrière (1880) ≡ *Yucca recurvifolia* fa. *elegans* (Carrière) Trelease (1902); **incl.** *Yucca gloriosa* var. *marginata* Carrière (1880) ≡ *Yucca recurvifolia* var. *marginata* (Carrière) Trelease (1902); **incl.** *Yucca gloriosa* var. *marginata-aurea* Carrière (1880); **incl.** *Yucca peacockii* Baker (1880) ≡ *Yucca flexilis* fa. *peacockii* (Baker) Trelease (1902); **incl.** *Yucca eylesii* Hort. Peacock ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca mexicana* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca nobilis* Hort. Peacock ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca laevigata* hort. ex Nicholson (1887); **incl.** *Yucca flexilis* var. *hildrethii* Trelease (1902); **incl.** *Yucca grandis* Sprenger (1904).

[1c × 3c] Differs from var. *gloriosa*: **L** mostly recurved, flexible; **Inf** barely extending beyond the rosettes; **Fr** mostly erect, 25–45 mm.—**Cytology:** 2n = 60 (Satô 1935: as *Y. recurvifolia*).

Insufficiently known and probably not distinct from var. *gloriosa* (Hess & Robbins 2002). The taxon has also been treated at the rank of species or forma based on the name *Y. recurvifolia*. The record of “*Yucca gloriosa*” from Pinellas County (Sorrie & LeBlond 2008: 1354), the third county record from Florida and the only one from the W coast of the peninsula, may belong here. Variegated cultivars are presented by Sprenger (1920b), Irish & Irish (2000: 261–262), Boeuf & al. (2010: 70–77), and Boeuf & Heim (2014: 24–27) (all as *Y. recurvifolia*). See also under *Y. thompsoniana*.



The taxon is locally naturalized in Texas (Diggs & al. 2006: 416, as *Y. gloriosa* var. *recurvifolia*), Spain (López-Pujol & Guillot Ortiz 2014a: as *Y. recurvifolia*), and Italy (Afferni 2003: as *Y. recurvifolia*).

**Y. grandiflora** Gentry (Madroño 14: 51–53, 1957). **Type:** Mexico, Sonora (Gentry 11601 [US, ARIZ, MEXU]).—**Lit:** Gentry (1972: 162–165); Matuda & Piña Luján (1980: 71–73); Hochstätter (2004a: 20, 86); all with ills. **Distr:** N Mexico (E & SE Sonora, W-most Chihuahua); grassy slopes in open woodland, on volcanic or limestone rocks, 600–1350 m; flowers February to May. **I:** Hochstätter (2003c: 153); Boeuf & al. (2009: 66–67).

[1b] Arborescent, stems branched at the base and above into few rosettes, 4–6 m, with a long skirt of dried deflected leaves often reaching down to the ground; **L** ascending to descending, rather flexible, slightly narrowed above the base, smooth on both faces, 70–100 (–140) × 4–5 (in the middle) cm, dark green, margins narrow, brown, filiferous with long fine brittle fibres, **terminal Sp** stout, broadly grooved, (chestnut-) brown; **Inf** erect, peduncle 10–30 cm, glabrous below, flowering part 0.5–1 m, open, part-**Inf** horizontal or slightly ascending, densely white-tomentose, with dull white scarious **Bra**; **Ped** short to nearly none; **Fl** erect or divergent; **Tep** spreading, ovate, thin, bluntly mucronate, connate at the base, 60–100 × 18–27 mm, **OTep** slightly smaller and thicker than the **ITep**, creamy-white; **Fil** 45–48 mm, hyaline-pubescent; **Ov** elongate, slender, deeply sutured, 45–60 mm; **Sty** ± 5 mm, forming a short beak below the stigma; **Sti** deeply lobed; **Fr** fleshy berries, cylindrical, large, 100–200 × 30–50 mm, with a short beak, brown when ripe; **Se** variable, 3–8 mm.

The holotype consists of two sheets which are not cross-labelled. According to the protologue the species differs from all other species in its large, nearly sessile flowers on tomentose part-inflorescences. It resembles *Y. madrensis* (as *Y. schottii*) in its arborescent habit, long, flexible, broad leaves and its pubescent inflorescences, but has otherwise little similarity with the latter (Gentry 1972: 162). The species shows a close

relationship with *Y. arizonica* (here treated as *Y. baccata* ssp. *thornberi*) in its arborescent habit and large flowers and fruits (Gentry 1972: 162). Martin & al. (1998: 471) provide a new record from W-most Chihuahua and report that the fruits are eaten raw or roasted. Plants from Bacanora previously assigned here (Gentry 1972: figs. 63 & 64, Matuda & Piña Luján 1980: 73, at least upper fig., Piña Luján 1980: fig. 4) are *Y. declinata*.

**Y. guatemalensis** Baker (Refug. Bot. 6: t. 313 + text, 1872). **Type:** sine loco (*Ehrenberg* s.n. [HAL [ex cult. England]]).—**Lit:** Trelease (1902: 94–96, tt. 51, 82, as *Y. elephantipes*); Matuda & Piña Luján (1980: 104–107, with ills., as *Y. elephantipes*); Lott & García-Mendoza (1994: online version with ills.); Robbins (2001: online version with ills.); Hammel & al. (2003: 34); Smith & Figueiredo (2016: with ills.). **Distr:** Native: Mexico (Chiapas) and possibly Guatemala; probably cultivated only: Mexico (Veracruz, Yucatán), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama; in tropical deciduous forests, 0–2700 m; flowering February to July; locally naturalized in Portugal, Spain, the Balears, and New Zealand. **I:** Curtis's Bot. Mag. 131: t. 7997 (1905); Piña Luján (1980: 280, as *Y. elephantipes*); Hochstätter (2003e: 267–268, as *Y. elephantipes*); Boeuf & al. (2009: 50–51, as *Y. elephantipes*); Ondrovic (2018: as *Y. elephantipes*).

**Incl.** *Yucca elephantipes* hort. ex Regel (1859) (*nom. inval.*, ICN Art. 36.1b) ≡ *Sarcococca elephantipes* (hort. ex Regel) Lindinger (1933) (*nom. inval.*, ICN Art. 36.1b); **incl.** *Dracaena ehrenbergii* hort. ex Baker (1875) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Dracaena lenneana* hort. ex Baker (1875) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca mooreana* Hort. Peacock ex Baker (1880); **incl.** *Dracaena ensifolia* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Dracaena fintelmannii* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Dracaena lennei* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Dracaena yuccoides* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca ghiesbreghtii* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c) ≡ *Yucca elephantipes* var.

*ghiesbreghtii* (Baker) Molon (1914) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca roezlii* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca mazellii* Hort. Dognin ex André (1883); **incl.** *Yucca eleana* Hort. Dognin ex W. Watson (1889) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca elephantipes* Regel ex Trelease (1902) (*nom. illeg.*, ICN Art. 52.1).

[1c] Arborescent, stems 3–10 m, usually numerous from a thickened-inflated trunk-like base, slender and densely branched in the upper parts, bark rough; **L** patent, narrowed to 1.5–2 cm above the base, flat or slightly canaliculate, lower face sometimes rough, upper face smooth, (35–) 50–100 × 5–7 cm, brilliant dark green, margins finely denticulate, with a yellow border, not filiferous, tip acute, soft, green; **Inf** erect, paniculate, peduncle short, flowering part dense, surpassing the rosette leaves with ± the upper  $\frac{3}{4}$ , glabrous; **Fl** pendent, globose; **Tep** narrowly ovate, **ITep** somewhat broader than the **OTep**, 30–50 × (10–) 15–20 mm, white to whitish; **Fil** 8–10 mm; **Ov** oblong, not constricted at the base, 10–15 mm; **Sty** short, oblong; **Fr** fleshy berries, ellipsoid, 70–80 × 45 mm, pulp greenish to whitish; **Se** nearly circular, 8–10 mm Ø.

Unfortunately, the widely used name *Y. elephantipes* was not validly published (Smith & Figueiredo 2016). Lott & García-Mendoza (1994) instead use the homotypic replacement name *Y. guatemalensis* Baker.—Widely cultivated as an ornamental in (sub-) tropical gardens, esp. also as variegated cultivars (Boeuf & al. 2010: 53–58, Guillot Ortiz & Meer 2008: 42–45, Boeuf & Heim 2014: 20–22, all as *Y. elephantipes*). The flowers are reportedly edible. *Y. gigantea*, in modern treatments mostly included in *Y. guatemalensis*, was recently re-established as a species of its own right (for differences see there). Most records and photographs of wild, cultivated, and naturalized plants apparently belong here and not to *Y. gigantea*. It has become locally naturalized in Portugal (Almeida 2018: 272, as *Y. gigantea* (*Y. elephantipes*)), Spain (López-Pujol & Guillot Ortiz 2014b: as *Y. gigantea* (*Y. elephantipes*)), the Balears (Sáez & al. 2016: 126), and New Zealand (Zimer 2014: as *Y. gigantea* (*Y. elephantipes*)).

**Y. harrimaniae** Trelease (Annual Rep. Missouri Bot. Gard. 13: 59, tt. 28–29, 83: fig. 10, 93: fig. 1, 1902). **Type** [lecto]: USA, Utah (*Trelease* s.n. [MO]).—**Lit**: Reveal (1977: 530–532, with ills.); Hochstätter (2000: 31–38, ills. pp. 84–92, p.p. as *Y. nana*); Schönherr (2017: p.p. as *Y. nana*); all with ills. **Distr**: SW USA.

The protologue cites specimens collected by Parry, Jones, Trelease and Baker. McKelvey (1947: 141) designated a range of specimens at MO (“148567–148572”) of an unnumbered collection by Trelease from 1901 as “type”.

**Y. harrimaniae** ssp. **harrimaniae** — **Lit**: Reveal (1977: 530–532, with ills.); Welsh & al. (1987: 649–650); Hochstätter (2000: 32–33, 36, ills. pp. 84, 86–88, 91, p.p. as ssp. *gilbertiana*); Hess & Robbins (2002: as *Y. harrimaniae*); Hawker (2016: 357–365, with ills., as *Y. harrimaniae*). **Distr**: W USA (E-C Nevada, N & C Utah, W & SW Colorado, N Arizona, NW New Mexico); desert slopes, foothills and plateaus, limestone and volcanic outcrops, usually 1000–2500 m; flowers April to July. **I**: Hochstätter (1998: 223, as *Y. harrimaniae*); Boeuf (2007a: 68, as *Y. harrimaniae*); Boeuf & al. (2009: 68); Schönherr (2017: 38, 39, 41, 45, as *Y. harrimaniae*).

**Incl.** *Yucca harrimaniae* var. *gilbertiana* Trelease (1907) ≡ *Yucca gilbertiana* (Trelease) Rydberg (1918) ≡ *Yucca harrimaniae* ssp. *gilbertiana* (Trelease) Hochstätter (2000); **incl.** *Yucca coloma* Andrews (1926); **incl.** *Yucca nana* Hochstätter (1998).

[3b] Stems none or short, to 0.3 m; **Ros** asymmetrical or symmetrical, 30–80 cm Ø, caespitose, forming dense to open colonies of 3–20 rosettes and 0.25–1.5 m Ø, rhizomes short; **L** linear or spatulate-lanceolate, straight, canaliculate, rigid, widest near the middle, (7.5–) 30–50 × (0.6–) 1.8–4.3 cm, pale green, margins entire, soon separating into long fine to coarse curly fibres, white or brown, tip tapering gradually to a short pungent ivory-coloured **terminal Sp**; **Inf** erect, racemose or rarely paniculate and proximally with few short part-**Inf**, peduncle 10–20 cm, flowering part 35–70 cm, arising within or just beyond the rosette leaves, glabrous; **Ped** 10–20 mm; **Fl** pendent, broadly campanulate; **Tep** broadly lanceolate,

40–50 (–53) × 16–34 mm, **ITep** broader than the **OTep**, yellow or greenish-yellow, usually tinged purple, basally connate to form a tube 2–4 mm long; **Fil** 16–28 mm; **Ov** 15–20 mm, pale green; **Sty** pale to bright green, 9–13 mm; **Sti** lobed; **Fr** erect dry capsules, cylindrical, usually deeply constricted towards the middle, 30–50 (–55) × 20–30 mm; **Se** thin, 5–8 × (3.5–) 4–8 mm, dull black.

No *Yucca* in the SW USA is more diverse in form (Hawker 2016: 357). *Y. neomexicana* was included in *Y. harrimaniae* by McKelvey (1947: 139) and Reveal (1977: 530), who gave it varietal status. According to the early molecular data of Clary (1997; cited by Hess & Robbins 2002), *Y. harrimaniae* and *Y. neomexicana* are not related at all, and *Y. neomexicana* was re-established as a species of its own (Hess & Robbins 2002). *Y. nana*, popular in horticulture as the smallest of all yuccas (Hochstätter 1998, Mattern 1999, Boeuf & al. 2009: 80–81, Schönherr 2017, all as *Y. nana*), is dismissed by most botanists as a small-growing local variant from the upper altitudinal and lower size range within this variable taxon (Hawker 2016: 364–365).

**Y. harrimaniae** ssp. **sterilis** (Neese & S. L. Welsh) Hochstätter (Cactaceae Rev. 1(2): 21, 1999). **Type:** USA, Utah (*Welsh* 18461 [BRY, ASU, NY]).—**Lit:** Neese & Welsh (1986); Hochstätter (1998: 225–226, as var.); Hochstätter (2000: 35, ill. pp. 86, 90); the latter two with ill. **Distr:** SW USA (NE Utah: Uintah Basin); salt desert shrub communities, 1470 m. **I:** Boeuf & al. (2009: 69); Utah Native Plant Society (2003–2016: accessed Dec. 2018).

≡ *Yucca harrimaniae* var. *sterilis* Neese & S. L. Welsh (1986) ≡ *Yucca sterilis* (Neese & S. L. Welsh) S. L. Welsh & L. C. Higgins (2008).

[3b] Differs from ssp. *harrimaniae*: Rhizomes long and **Ros** often widely spaced; **L** flaccid, often reclining on the ground, typically curved, margins sparingly or not filiferous; **Fr** not known to be formed.

A geographically isolated subspecies not known to produce fruits and reproducing exclusively vegetatively by rhizomes. Its status is much disputed: Hess & Robbins (2002) do not

recognize it as separate entity, Welsh & al. (1987: 650), Hochstätter (1998: 225–226, 2000: 35) and the first edition of this handbook recognize it at infraspecific rank (variety or subspecies), while Welsh & al. (2008: 779) and Govaerts (2014+: accessed Dec. 2018) treat it at species rank. See also under *Y. feeanoukia*.

**Y. intermedia** McKelvey (*Yuccas* Southwest US, 2: 116, tt. 44–46, 1947). **Type:** USA, New Mexico (*McKelvey* 4902 [A [2 syn]]).—**Lit:** Webber (1953: 56–59, sub *Y. glauca*); Reveal (1977: 532–533, as *Y. baileyi* var.); Hess & Robbins (2002); Sivinski (2008: 2, as *Y. baileyi* var.); Hawker (2016: 371–373). **Distr:** USA (C & NE New Mexico); juniper-pinyon pine woodlands and adjacent grasslands, 1100–2100 m; flowers May to June. **I:** Earle (1968); Hochstätter (1998: 81, as *Y. baileyi* var.); Hochstätter (2000: 45, as *Y. baileyi* ssp.).

≡ *Yucca baileyi* var. *intermedia* (McKelvey) Reveal (1977) ≡ *Yucca baileyi* ssp. *intermedia* (McKelvey) Hochstätter (1999); **incl.** *Yucca intermedia* var. *ramosa* McKelvey (1947).

[3b] Stems none or occasionally with erect simple stems <1 m; **Ros** caespitose, forming widely separated colonies of 1–5 rosettes; **L** linear, somewhat flexible, plano-convex or lower face keeled, widest near the middle, 33–65 × 0.5–0.8 cm, margins entire, white to greyish; **Inf** erect, racemose, sometimes paniculate proximally, occasionally paniculate and long-racemose distally, peduncle 10–50 cm, flowering part (50–) 70–130 cm, arising within the rosette leaves, glabrous; **Fl** pendent, campanulate or rarely globose; **Tep** narrowly to broadly elliptic, 55–70 × 20–32 mm, cream or greenish, often tinged rose or rosy-brown; **Fil** to 25 mm; **Ov** oblong-cylindrical, to 25 mm; **Sty** 7 mm, white or pale yellowish-green; **Sti** lobed; **Fr** erect dry capsules, oblong-cylindrical, often constricted near the middle, 50–57 × 20–25 mm; **Se** thin, 6–10 mm, glossy or dull black.

The type consists of two sheets which are not cross-labelled. According to the protologue intermediate between *Y. glauca*, *Y. angustissima* and *Y. baileyi* (as *Y. standleyi*), and considered as a hybrid between *Y. glauca* and the 2. or 3. species

listed (Webber 1953). This is rejected by Reveal (1977) because of the high pollen viability and regular fruit production, and because the putative parents are not present in the range of *Y. intermedia*. Species rank (vs. varietal rank under *Y. baileyi*) is strongly supported by the molecular data of Pellmyr & al. (2007), where *Y. intermedia* is shown as sister of *Y. harrimaniae* and separate from *Y. baileyi*. McKelvey (1947) based var. *ramosa* on populations in the SE area of the total range with paniculate inflorescences, but populations only with paniculate inflorescences as well as populations with racemose and paniculate inflorescences exist (Hess & Robbins 2002).

**Y. jaegeriana** (McKelvey) L. W. Lenz (Aliso 24(1): 99, 2007). **Type:** USA, California (McKelvey 2732 [A]).—**Lit:** Webber (1953: 31–32, t. 16); Benson & Darrow (1981: 52–53, with ill.); Hawker (2016: 328–331, with ill.), all as *Y. brevifolia* var. **Distr:** SW USA (S California, S Nevada, SW Utah, NW & W Arizona); hills and alluvial fans of the Upper Mojave Desert, 760–1500 m; flowers April to May. **I:** Hochstätter (2002a: 148–150, as *Y. brevifolia* ssp.).

≡ *Yucca brevifolia* var. *jaegeriana* McKelvey (1935) ≡ *Yucca brevifolia* ssp. *jaegeriana* (McKelvey) Hochstätter (2001).

[2] Plants ±3–6 (–9) m, stemless or with short main stem, branching dichotomously until flowering, irregularly thereafter; lowest **Br** 0.25–2.3 m, usually <1 m above the ground, relatively numerous, somewhat slender, short, nearly erect, forming an extremely dense compact crown; **Ros** symmetrical, crowded, 0.3–0.6 × ± 0.2–0.4 m; **L** straight, rigid, smooth, 9.5–22 (–27) × 0.6–1.2 (–1.5) cm, green to yellowish-green, margins nearly entire, thin, horny, minutely denticulate, **terminal Sp** ± 5–8 mm; **Inf** erect, paniculate, peduncle 2.5–5 cm, flowering part 22.5–40 cm, ovoid, for ¼–½ enclosed within the rosette leaves, with short stout part **Inf** 2.5–6.25 cm long with densely crowded flowers, glabrous; **Ped** 4–22 mm; **Fl** erect, narrowly campanulate, conspicuously expanded at the base, narrowed above, ± 45–60 mm; **Tep** narrowly oblong, apex recurving, ± 26–53 × 7–12 mm, greenish to cream, barely connate at the base; **Fil** ± 10 mm;

**Ov** lanceolate-ovoid, ± 10–16 × 4–10 mm; **Sti** 4–9 (–12) mm; **Sti** distinct; **Fr** pendent, dry, indehiscent capsules, ellipsoid, tapering at the apex, deeply furrowed, rather spongy, ± 67–86 × 30–38 mm; **Se** not described.

Occurring to the E of *Y. brevifolia*, and first separated at the rank of variety (McKelvey 1935: 269–270, t. 139). Reveal (1977: 530) did not recognize it as separate taxon as he considered it not clearly separable; this view was shared by Webber (1953: 31–32), McKinney & Hickman (1993), Hess & Robbins (2002), and Govaerts (2014+: accessed Dec. 2018), but not by Benson & Darrow (1981), Kartesz (1996), USDA (2001) and Hochstätter (2002a). Lenz (2007) treated it at species rank, arguing that differences in branching patterns, leaves, flowers and fruits, the allopatric distribution, and different pollinating moths provide a sufficiently clear and important base for such a decision. The detailed population genetic studies by Yoder & al. (2013) found that the two taxa are only weakly isolated despite the significant correlation between floral morphology and pollinator ovipositor length, indicating that substantial gene flow exists between the two taxa. Gene flow is largely asymmetric and unidirectional from *Y. jaegeriana* to *Y. brevifolia* due to different degrees of host specificity of the pollinating moths (Starr & al. 2013). However, population genomic studies by Royer & al. (2016) showed that both species are genetically highly differentiated and strongly diverged and rarely form hybrids in the hybrid zone at Tikaboo Valley (S Nevada), with selection maintaining the differences and separation between both species. The annual growth rate of young plants is 8–16 cm (Webber 1953: 92). Vernacular name: “Eastern Joshua Tree”.

**Y. jaliscensis** Trelease (Contr. US Nation. Herb. 23(1): 92–93, 1920). **Type** [lecto]: Mexico, Jalisco (*Pringle* 4392 [US [lecto, 2 sheets], BR, HBG, JE, KFTA, MO, NDG, S, VT]).—**Lit:** Matuda & Piña Luján (1980: 88–90, with ill.); McVaugh (1989: 282–283, with ill.); Hochstätter (2004a: 26–27, ill. pp. 100–103). **Distr:** Mexico (S Nayarit, W & C Jalisco, W Guanajuato, N Colima); plains with deeper soils or moderate



slopes, wooded ravines, barrancas near streams, pine or tropical deciduous forests, 1000–2200 m; flowers June to September (McVaugh 1989: September to May or almost throughout the year). **I:** Trelease (1902: t. 56, as *Y. schottii* var.); Piña Luján (1980: 279); Hochstätter (2003c: 152); Boeuf & al. (2009: 70–71).

**Incl.** *Yucca* × *schottii* var. *jaliscensis* Trelease (1902).

[1c] Arborescent, stems to 2–10 m, in cultivation to 12–15 m, trunk short, 20–60 (–150) cm Ø, often with 5–8 long upright and often much branched **Br**; **L** diverging, flexible, concave, glabrous, (30–) 50–100 × (3–) 6–7.5 (–8) cm, glaucous-green, persistent, margins hardly fibrous, pale grey to brown, occasionally with few fine fibres, tip sharp-pointed but scarcely differentiated as spine, brownish; **Inf** erect, or drooping at fruiting time, paniculate, peduncle short, flowering part 0.4–1 m, narrowly ellipsoid, dense, largely enclosed within the rosette leaves, densely tomentose to canescent with thick blunt hairs; **Ped** pubescent; **Fl** pendent, subglobose, 30–40 mm; **Te**p narrowly lanceolate, 22–40 × 8–16 mm; **Fil** 12–15 mm, pilose; **Ov** 15–22 × 5–7 mm Ø; **Sty** 3 mm; **Fr** fleshy berries, ellipsoid, narrowed at the base, asymmetrical, conical at the apex, 60–120 × 25–50 mm, brownish when ripe; **Se** flat, rugose, 5–7 × 7–10 mm.

The designation “type from Zapotlán” in the protologue refers to *Pringle* 4392 (see Gentry 1972: 161). Espejo Serna & López Ferrari (1993: 40) designated “US” as lectotype where 2 specimens are present. According to McVaugh (1989), it is often cultivated and spreading around settlements, but seldom found in the wild. In the molecular phylogenies of Pellmyr & al. (2007), the taxon groups in most analyses as sister to *Y. filifera*.

The rather short protologue of *Y. barrancasecca* hort. (1867) is based on a plant cultivated at BG Naples, Italy (esp. “foliis ... 1 meter long ad basim. 3–4 cent. lat, ad apicem fibrilloso-sphacelatis”), and the species was even thought to probably represent a species of *Dasylyrion* due to the “fibrillate” leaves, but they are much too broad for that genus (Trelease 1902: 114). According to Sprenger (1920b: 145–146), he

sold the original plant to BG Naples, where it was published as *Y. barrancasecca*; earlier it was listed by him as *Y. brasiliensis*, and it is neither “*Y. australis*” nor “*Y. schotti jaliscensis*” nor *Y. decipiens*. Govaerts (2014+: accessed Dec. 2018) lists *Y. barrancasecca* in the synonymy of *Y. jaliscensis* (which it would have to replace due to priority), but Sprenger’s comments cited above contradicts this placement, and the name should be treated as of uncertain application.

**Y. × karlsruhensis** Graebener (Gartenwelt 8(1): 7–9, ills., 1903). **Type:** not typified.—**Lit:** Weissbeck (2012b: with ills.). **Distr:** Cultivated only. **I:** Hochstätter (2000: 122); Smith (2004: 60); Boeuf & al. (2010: 33, 42).

[3c] This hybrid *Y. glauca* × *Y. filamentosa* is the earliest *Yucca* hybrid in Germany, raised by Leopold Graebener at Karlsruhe in 1899 (the earliest *Yucca* hybrids were raised by Deleuil (1880) and the earliest nothospecies were named by André (1883), see introduction). Propagations of the original plant are still cultivated at BG Karlsruhe and elsewhere (Weissbeck 2012a), so that it represents the oldest extant hybrid.

**Y. lacandonica** Gómez-Pompa & Valdés (Bol. Soc. Bot. México 27: 43–44, ills., 1962). **Type:** Mexico, Chiapas (*Gómez Pompa* 353 [MEXU, GH]).—**Lit:** Matuda & Piña Luján (1980: 109–111, with ills.); Lott & García-Mendoza (1994: online version with ills.); García-Mendoza (2003); Hochstätter (2004a: 39–40, ills. pp. 135–136); Véliz Pérez & Archila Morales (2015: with ills.). **Distr:** Mexico (Veracruz, Tabasco, Campeche, Yucatán, Oaxaca, Chiapas), Belize (Toledo), Guatemala (Alto Verapaz, El Petén); humid tropical evergreen forests, mostly epiphytic, also epilithic, 150–1030 m; flowers April to June. **I:** Gómez-Pompa & al. (1971: 220); Piña Luján (1980: 281); Hochstätter (2004b: 39–40); Roosbroeck (2017).

[1c] Terrestrial or epiphytic, stems 2.5–4 m, to 25 cm Ø at the base, 12 cm at mid-stem, 8 cm in the upper part, branching at the base, stems variably curving or twisting, partly horizontal, upcurving apically; **L** long lanceolate, narrowed towards the base (1–1.5 cm broad) and towards



the tip, weak, thin, fleshy, rigid, smooth on both faces, 30–85 × 3–7 cm, green, margins denticulate, 0.5 cm broad, with a yellowish band 0.5 mm broad, tip short, very acute, pungent, flexible, brownish; **Inf** paniculate, erect, peduncle short, ± 40 cm, flowering part 40–100 cm, arising within the rosette leaves, part-**Inf** flexible, ascending, to 20 cm, glabrous; **Fl** pendent, campanulate; **Tep** oblong-linear, very narrow, membranous-fleshy, 30–45 × 8–10 mm, white or whitish; **Fil** 7 mm; **Ov** oblong, 10–15 × 4–6 mm; **Fr** fleshy berries, indehiscent, cylindrical, subtrigonal, 40–100 × 20–45 mm, immature fruits conical, 40 × 20 mm; **Se** flattened to globose, unwinged, 5–7 × 4–6 mm.—**Cytology**: 2n = 60 (Gómez-Pompa & al. 1971).

This species was for long considered as the only strictly epiphytic taxon in the *Agavaceae* (a few species of *Agave* may rarely occur as facultative epiphytes under humid conditions), but was recently also found to occur terrestrially (Hochstätter 2004a, Roosbroeck 2017). It was first collected in Belize in 1935 (*Schipp* 1324, MO; Tropicos accessed 2015) and recently also found in N-C Guatemala (Véliz Pérez & Archila Morales 2015). The inflated stem-base, the leaves with narrowed base and yellow margins, and the short inflorescence emerging from within the leaves indicate a relationship with *Y. guatemalensis*. Such a placement is corroborated by the AFLP data (Pellmyr & al. 2007, Smith & al. 2008a: fig. 2c), but chloroplast sequence data (Smith & al. 2008a: fig. 2a, 2b) show a weakly supported grouping with *Y. periculosa* and thus distant from *Y. guatemalensis* (as *Y. elephantipes*).

**Y. linearifolia** Clary (Brittonia 47(4): 394–396, ills., 1995). **Type**: Mexico, Nuevo León (*Clary* 364 [MEXU, ANSM, CAS, GH, MO, TEX, US]).—**Lit**: Ferguson (1996: as *Y. linearis*); Hochstätter (2004a: 37–38, ills. pp. 126, 131–133); Boeuf (2007b); Heim (2011); all with ills. **Distr**: Mexico (S Coahuila, W Nuevo León); desert scrub on shale in shaded canyons, 1100–1300 m; flowers April to June. **I**: Hochstätter (2003e: 266); Boeuf (2007a: 69); Guillot Ortiz & Meer (2008: 108); Boeuf & al. (2009: 72–73).

**Incl.** *Yucca rostrata* var. *linearis* Trelease (1907) ≡ *Yucca linearis* (Trelease) D. J. Ferguson (1996).

[1c] Stems 2–3.5 m, mostly unbranched, 30–50 cm Ø at breast height, forming isolated colonies of 3–15 stems from rhizomes or fallen plants; **Ros** radially symmetrical, with somewhat flattened top; **L** numerous, linear, distally twisting slightly outwards, rounded to quadrangulate towards the base, persistent when old and then reflexing and completely covering the trunk, lower face very scabrous, upper face smooth, 34–38 (–50) × 0.4–0.5 (in the middle) cm, greyish-green to glaucous (esp. in new growth), later also green, margins thin, horny, pale yellow, with many minute denticles, **terminal Sp** 3–8 mm, dark reddish-brown to black; **Inf** erect, paniculate, peduncle short, flowering part 60–80 cm, pyramidal, basally enclosed within the rosette leaves, moderately to richly branched, lower (= largest) part-**Inf** 11 – ±17 cm, with 4–6 or more flowers, glabrous; **Fl** pendent, campanulate; **OTep** elliptic, 30–33 × 15 mm; **ITep** obovate, 30 × 20 mm, creamy-white, tube none; **Fil** 16–17 mm; **Ov** oblong-cylindrical, 17–20 × 9–10 mm; **Sty** white, 6–7 mm; **Sti** lobed, papillose; **Fr** fleshy berries, indehiscent, asymmetrical, narrowly ovoid, tip constricted, 40–70 × 23–25 mm, green; **Se** polymorphic, to 5–7 × 4–6 mm, dull, black.

*Y. linearifolia* is, besides *Y. queretaroensis*, the only fleshy-fruited *Yucca* with narrow denticulate leaves, resembling *Dasylyrion* in habit. The protologue places it with the dry-fruited *Y. rostrata*, and with *Y. queretaroensis*, which was first published with unknown fruits. Molecular data place *Y. linearifolia* within Sect. *Yucca* (as *Sarcocarpa*) and separate from *Y. queretaroensis* (Pellmyr & al. 2007, Smith & al. 2008a). In habitat, no remains of flowers, fruits or seeds can be found, since all young flowers are harvested for food so that the generative reproduction fails (Heim 2011: 99).

*Y. rostrata* var. *linearis*, wrongly synonymized under *Y. rostrata* by Hess & Robbins (2002) and Govaerts (2014+), and later elevated to species rank as *Y. linearis* (Ferguson 1996), belongs here according to its narrow leaves (label of K. H. Clary 2002/2003 on the holotype *Purpus* s.n.,

MO 148706!). An original plant collected by C. A. Purpus at about 1905 is still cultivated at BG Darmstadt, Germany (Schneckenburger 2001: 67–69). Heim (2011) reports a putative natural hybrid with *Y. torreyi* (here treated as synonym of *Y. treculiana*) needing further study. Apart from the typical form with green leaves, plants with glaucous leaves also occur (Boeuf 2007b, Heim 2011) which need additional study as to possible further differences. For the cultivation, see Boeuf (2007b) and Heim (2011). ‘Line Dance’ is a rare variegated cultivar with white margins (Boeuf & Heim 2014: 25–26).

**Y. madrensis** Gentry (US Dept. Agric. Handb. 399: 159–161, ills., 1972). **Type:** Mexico, Sonora (Gentry 21209 [US 2557499, ARIZ, DES, MEXU, MICH]).—**Lit:** Matuda & Piña Luján (1980: 85–87, with ills.); Lenz & Hanson (2001: 168); Hess & Robbins (2002); Hawker (2016: 372–376, with ills.). **Distr:** S USA (SE Arizona, NW New Mexico), N Mexico (N & E Sonora, W Chihuahua); on rocky volcanic and limestone slopes in oak woodlands and pine-oak forests, 1200–2200 m; flowers June to July. **I:** Piña Luján (1980: 279); Hochstätter (2000: 128–130; 2003d: 214); Hochstätter (2003e: 264–265); Boeuf & al. (2009: 76–77).

[1c] Caulescent, stems short or up to 3.5 m, simple or eventually few-branched from the base, usually with a long skirt of dried deflected leaves; **L** numerous, spreading to ascending, rarely recurving, linear-lanceolate, thin, flexible, nearly flat to slightly conduplicate, smooth and striate on both faces, mostly 50–80 (–100) × (2–) 3.5–6.5 cm, bluish-glaucous or green (to yellowish-green), margins thin, brown, friable, serrulate, detaching with age, rarely sparingly filiferous, brown to greyish, **terminal Sp** weak, 5–15 mm, reddish-brown to grey; **Inf** erect, paniculate, peduncle short, flowering part 30–80 cm, elongate-ovoid, somewhat open, arising  $\frac{1}{4}$ – $\frac{1}{2}$  within the rosette leaves, part-**Inf** ascending, short, 6 – ±12 cm or more, densely to sparsely tomentose; **Fl** pendent, globose, ±35 mm, broader than long, basally truncate; **Tep** ovate-lanceolate to lanceolate, 20–40 × 10–20 mm, cream or tinged with purple, free or barely connate

basally; **OTep** brownish, mucronate; **ITep** broader than the outer tepals; **Fil** 15 mm; **Ov** thick, ±20 mm; **Sty** abruptly tapering into the stigma; **Sti** lobed, papillate; **Fr** fleshy berries, becoming pendent, rounded at the base, tapering at the tip, frequently irregularly constricted, with irregular warts to 20 mm Ø, 60–130 × 25–50 mm, green; **Se** unwinged, 7–10 mm Ø, 5–9 mm thick, rough, grey.

*Y. madrensis* is characterized by its pliable, light bluish-green leaves, short inflorescences with small flowers, and a summer-flowering habit (Gentry 1972). The fruits, unknown at the time of the protologue, were later found to be fleshy and the species was placed in Ser. *Treculianae* (= Ser. *Yucca*) of Sect. *Yucca* (as *Sarcocarpa*) (Matuda & Piña Luján 1980, Laferrière 1990).

According to Lenz & Hanson (2000: 98), the plants with long, broad, flexible, bluish leaves in S Arizona commonly misnamed as *Y. schottii* sensu Trelease (1902: 98) *non* Engelmann actually belong here (e.g., Benson & Darrow 1981: 54, Irish & Irish 2000: 207–271, Hochstätter 2001b: 131–132, Hochstätter 2002a: 25–26, ills. pp. 100–102, Guillot Ortiz & Meer 2008: 88–89, 111, Faber 2015, all as *Y. schottii* auct., all with ills.).

The notion of Lenz & Hanson (2001: 168) that *Y. madrensis* may have hybridized with *Y. treculiana* in Chihuahua is unlikely, since both species occur clearly separated. The plants are intensively used by the Warihio (Guarijío) and Pima for soap (roots), cordage (leaves) and food (fruits) (Laferrière 1990).

**Y. mixtecana** García-Mendoza (Acta Bot. Mex. 42: 1–4, ills., 1998). **Type:** Mexico, Oaxaca (García-Mendoza & al. 6198 [MEXU, BM, ENCB, MO, NY, OAX, TEX]).—**Lit:** Hochstätter (2004a: 29, ills. pp. 106–109); García-Mendoza (2011: 87–89, with ills.). **Distr:** Mexico (S Puebla, NW Oaxaca); xerophytic scrub and transition to tropical deciduous forests, 1370–2200 m; flowers March to July. **I:** Hochstätter (2003b: 115–116); Boeuf & al. (2009: 78–79).

[1c] Arborescent, stems 2.5–5 m, ± conical, simple or with 2–4 branches in the upper 1–3 m, at the base forming rhizomatous colonies of 10–25 stems; **L** erect, linear-lanceolate or linear, flexible,

narrowed at the base to 1–2 cm, broadest in the middle, rough on the lower face, glabrous on the upper face, 40–65 (–80) × 1–3 cm, glaucous to greenish-yellowish, deciduous when dry, margins entire, with a brown or grey border, filiferous with fine and soft, white or grey threads, **terminal Sp** 5–10 mm, dark brown, canaliculate; **Inf** erect, paniculate, peduncle 20–30 cm, flowering part 50–80 cm, moderately branched, lower part within the rosette leaves, pilose; part-**Inf** 10–20 cm, with 15–20 flowers each; **Ped** (10–) 15–20 mm, pilose; **Fl** pendent, campanulate, (15–) 20–25 (–30) mm; **Tep** elliptic, glabrous, 20–25 (–30) mm; **OTep** 4–7 (–10) mm broad; **ITep** 6–10 (–13) mm broad, whitish to yellowish; **Fil** 10–15 (–20) mm; **Ov** cylindrical, ± 13–17 (–27) × 6–8 mm; **Sty** short; **Sti** lobed; **Fr** fleshy berries, pendent, sometimes constricted, cylindrical, (30–) 50–80 × 20–25 mm, brownish when ripe; **Se** flat, drop-shaped, 5 mm Ø, black.

According to the protologue closest to *Y. periculosa* and *Y. jaliscensis*, from both of which it differs by its shorter, conical, slender, sparsely branched stems, narrower caducous leaves and much smaller flowers and fruits. The molecular data of Pellmyr & al. (2007) shows 2 samples of *Y. mixtecana* nested within 3 accessions of *Y. periculosa*, and both well separate from *Y. jaliscensis*. The fruits, not currently used as food, have great dietary potential (Barriada-Bernal & al. 2018).

**Y. necopina** Shimmers (Spring Fl. Dallas-Fort Worth Area, 408, 1958). **Type:** USA, Texas (*Shimmers* 20102 [BRIT, BRIT]).—**Lit:** Diggs & al. (1999: 1083–1084, ills. pp. 108, 1085); Hess & Robbins (2002); Diggs & al. (2006: 418, ills. pp. 308, 419); Boeuf (2016: with ills.). **Distr:** USA (N Texas); river terraces in deep sandy soils, 200–300 m; flowers May to June.

[3c] Stems none or short and erect, to 0.4 m; **Ros** with ±50–85 leaves, caespitose, forming small colonies; **L** erect, slightly twisted, flexible but firm, plano-convex, widest near the middle, 50–80 × (1.5–) 2–4 cm, margins entire, filiferous with curly fibres, white, tip acicular; **Inf** erect, paniculate and racemose distally or entirely racemose, peduncle 0.8–1.6 m, flowering part

0.5–1.2 m, ovoid, beginning mostly beyond the rosette leaves, part-**Inf** ascending, to 15 cm, glabrous; **Fl** pendent, globose; **Tep** 40–45 × 15–30 mm, greenish-white; **Fil** 12–20 mm; **Ov** 15–38 mm, 2× as long as style and stigma; **Sti** lobed; **Fr** erect dry capsules, not conspicuously constricted, 40–70 × ± 20–35 mm; **Se** not described.

Originally known from a single locality only, but several new locations were reported by Diggs & al. (1999). It was compared with *Y. arkansana* in the protologue, and suggested to represent a hybrid between that species and *Y. pallida*. However, *Y. necopina* occurs in many rather uniform individuals in widely separated localities where neither *Y. arkansana* nor *Y. pallida* typically occur. Recognition of the taxon as separate species is also supported by molecular data which relate it to *Y. elata* and its ssp. *verdiensis* (as *Y. verdiensis*) (Clary 1997, cited by Boeuf 2016: 58). Morphologically, it appears to be closest to *Y. flaccida*, which is distinguished by its usually narrower leaves and pubescent inflorescences (Diggs & al. 1999: as *Y. louisianensis*).

**Y. neomexicana** Wooton & Standley (Contr. US Nation. Herb. 16: 115, 1913). **Type:** USA, New Mexico (*Standley* 6208 [US 685238, GH, K, MO, NY, UC, US]).—**Lit:** Webber (1953: 43–44, tt. 24, 25); Reveal (1977: 530, 532, as *Y. harrimaniae* var.); Hochstätter (2000: 34, ills. pp. 89–90, as *Y. harrimaniae* ssp.); Hess & Robbins (2002); Hawker (2016: 376–379, with ills.). **Distr:** SW USA (S Colorado, N & NE New Mexico, W Oklahoma), exposed rocky ledges in open woodlands and grasslands, 1300–2700 m; flowers May to July. **I:** Hochstätter (1998: 224, as *Y. harrimaniae* var.).

≡ *Yucca harrimaniae* var. *neomexicana* (Wooton & Standley) Reveal (1977) ≡ *Yucca harrimaniae* ssp. *neomexicana* (Wooton & Standley) Hochstätter (1999).

[3b] Stems none or rarely short, < 1 m, and primarily rhizomatous; **Ros** mostly asymmetrical, solitary or usually caespitose, in open colonies and separated by 35–60 cm; **L** spreading, spatulate-lanceolate, thin, flexible, canaliculate, widest near the middle, 15–46 × 0.7–2 cm, rather glaucous, margins entire, filiferous, brown or

straw-coloured, tapering to the pungent apex; **Inf** erect, racemose, rarely paniculate proximally, peduncle 10–40 cm, flowering part 40–70 cm, arising within or more often to 20 cm beyond the rosette leaves, part-**Inf** few, short, glabrous, with purplish **Bra** to 10 cm; **Ped** 12–20 mm, stout; **Fl** pendent, campanulate; **Tep** broadly lanceolate, 30–47 × 15–30 mm, white to somewhat greenish-white, usually tinged pink or purple; **Fil** 13–17 mm; **Ov** ± 15–20 mm; **Sty** pale green or rarely white, 9–13 mm; **Sti** lobed; **Fr** erect dry capsules, cylindrical, deeply constricted near the middle, 30–42 × 20–27 mm; **Se** thin, 6–8 × 5–8 mm, dull black.

Included in *Y. harrimaniae* by McKelvey (1947), Reveal (1977), and Hochstätter (2002a, 2004a), but morphologically distinct and allopatric, separated by the San Juan Mountains of Colorado. Hess & Robbins (2002) reinstated the taxon at species rank, supported by earlier molecular data (Clary 1997, cited in Hess & Robbins 2002). Main differences from *Y. harrimaniae* are its usually white flowers held mainly above the leaves (vs. yellow or greenish-yellow flowers, the lowest usually arising within the leaves) (Hochstätter 2004a).

**Y. pallida** McKelvey (Yuccas Southwest US, 2: 57, tt. 13–14, 1947). **Type:** USA, Texas (McKelvey 2862 [A]).—**Lit:** Diggs & al. (1999: 1084–1085, with ills.); Hochstätter (2000: 25–26, ills. pp. 24, 80); Hess & Robbins (2002); Diggs & al. (2006: 418–420, with ills.); Hawker (2016: 378–383, with ills.). **Distr:** USA (N-C Texas); rocky blackland prairies and uplands, rarely limestone outcrops, 100–400 m; flowers April to June. **I:** Hochstätter (1999: 209); Boeuf (2007a: 70); Boeuf & al. (2009: 84–85).

≡ *Yucca rupicola* fa. *pallida* (McKelvey) hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Yucca rupicola* Trelease (1902) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca rupicola* var. *edentata* Trelease (1912) (*incorrect name*, ICN Art. 11.4) ≡ *Yucca pallida* var. *edentata* (Trelease) Cory (1952).

[3a] Acaulescent; **Ros** with <100 leaves, usually distinctly separate from one another, forming loose rhizomatous colonies of usually 10–30 rosettes; **L** lanceolate, thin, flexible, straight when mature, acuminate, flat but concave for

1.3–2.5 cm below the tip, widest at or usually above the middle, 20–60 × 1–4.5 cm, blue- to grey-green, margins flat, bright yellow, finely denticulate or sometimes wavy, apex acute or less often acuminate; **Inf** erect, paniculate, often distally racemose, peduncle 0.6–1.3 m, flowering part 0.7–1.2 m, arising beyond the rosette leaves, part-**Inf** widely spreading, 15–23 cm, glabrous; **Fl** pendent, campanulate, 50–65 mm; **Tep** narrowly to broadly elliptic to ovate, 50–65 × 20–32 mm, greenish-white, margins white, somewhat serrate; **Fil** 18–32 mm; **Ov** oblong-cylindrical, 30–40 mm, pale blue or yellow-green; **Sty** 13–20 mm, white; **Sti** lobed; **Fr** erect dry capsules, oblong-cylindrical, 45–55 × 13–20 mm, yellowish-brown, later dark brown to black; **Se** small, rough, surface sculptured, 4–7 × 2–3 mm, dull black.

Webber (1953) reports difficulties to distinguish *Y. pallida* from *Y. rupicola* and indirectly includes the former as synonym of the latter, but most authors (Kartesz 1996, USDA 2001, Diggs & al. 1999, Hochstätter 2000, Hess & Robbins 2002, Diggs & al. 2006, Hawker 2016) keep the species separate from its close relative *Y. rupicola*. *Y. pallida* differs from *Y. rupicola* in its leaves straight or nearly so, flat, pale bluish to green and conspicuously glaucous, ± smooth on both faces, and with yellow margins (vs. leaves twisted and with margins inrolled most of their length, dark green and not glaucous, ± scabrous on both faces, and margins dark orangish or yellowish-brown or occasionally yellowish) (Diggs & al. 2006: 414–415).

Plants with leaves with entire margins are occasionally found, and were named var. *edentata*, but the protologue suggested that they are hybrids of *Y. pallida* with *Y. arkansana*. According to Keith (2003), *Y. pallida*, *Y. rupicola* and *Y. cernua* are closely related to each other within Sect. *Rupicolae*, and share an acaulescent habit, denticulate leaves, and beaked capsules. This assumed close relationship is strongly supported by molecular data (Pellmyr & al. 2007), which place the three species in a well-supported clade. *Y. cernua* differs by solitary growth, glaucous young leaves becoming olive or yellowish-green with age, and by its puberulent inflorescence with recurved and drooping branches.

**Y. periculosa** Baker (Gard. Chron. 1870: 1088, 1870). **Type:** not typified.—**Lit:** Trelease (1907: 228–229, tt. 13–14); Matuda & Piña Luján (1980: 89–93, with ills.); Hochstätter (2004a: 27–28, ills. pp. 104–105); García-Mendoza (2011: 89–93, with ills.). **Distr:** Mexico (W-C Veracruz, Tlaxcala, E Puebla, N Oaxaca); desert scrub, tropical deciduous forests, on plains with deeper soil or on moderate slopes, 1300–2200 m; flowers March to July. **I:** Piña Luján (1980: 280); Hochstätter (2003b: 114–115); Boeuf & al. (2009: 86–87).

≡ *Yucca baccata* var. *periculosa* (Baker) Baker (1880) ≡ *Yucca baccata* fa. *periculosa* (Baker) Voss (1895) ≡ *Sarcocoyucca periculosa* (Baker) Lindinger (1933); **incl.** *Yucca circinata* Baker (1870) ≡ *Yucca baccata* var. *circinata* (Baker) Baker (1880) ≡ *Yucca baccata* fa. *circinata* (Baker) Voss (1895).

[1c] Arborescent, stems to 10 m (in cultivation to 15 m), cylindrical, much-branched in age, **Br** ascending, 1–2 m, ± cylindrical, leaves persisting as dry skirt below the rosette; **L** erect, lanceolate or linear-lanceolate, rigid, (35–) 50–70 × (2–) 3–3.5 cm, green, margins with a fine dark brown band, finely fibrous, **terminal Sp** (5–) 10–15 mm, dark brown; **Inf** erect to somewhat inclined, paniculate, peduncle 30–40 cm, flowering part 0.7–0.9 (–1.2) m, ovoid, compact, peduncle enclosed within the rosette leaves, with 60–70 part-**Inf** to 15–30 cm, glabrous to pilose; **Ped** 10–20 mm, glabrous or pilose; **Fl** pendent, campanulate, expanded, (25–) 35–40 mm; **Tep** lanceolate, (20–) 25–35 mm, **OTep** 7–10 mm broad, **ITep** 10–15 mm broad, whitish, occasionally with purple tinge, glabrous to pubescent; **Fil** 10–15 (–20) mm; **Ov** cylindrical, 15–20 mm; **Sty** short; **Sti** lobed; **Fr** fleshy berries, pendent, cylindrical, (65–) 80–100 (–120) × 25–30 (–50) mm, green; **Se** 8–10 × 7–9 mm, dull black.

Two specimens apparently from the original plant cultivated by Saunders were both prepared later than the protologue and thus do not represent original material (K 001096505, 4/[18]73; MO 3346126, 1871). The neotypification by Hochstätter (2003b: 114) is ineffective under ICN Art. 7.11. *Y. mixtecana* is imbedded within *Y. periculosa* in the molecular phylogeny of Pellmyr & al. (2007)

(see also there); García-Mendoza (2011) mentions possible hybrids between both species. *Y. mixtecana* differs in its smaller and less branched stems, its narrower, glaucous leaves not persisting on the stems and with a shorter terminal spine, and its shorter inflorescences with smaller flowers and fruits (García-Mendoza 2011).

**Y. potosina** Rzedowski (Ciencia (Mexico) 55 (4–5): 90–91, ill., 1955). **Type:** Mexico, San Luis Potosí (*Rzedowski* 5924 [MEXU, ENCB]).—**Lit:** Matuda & Piña Luján (1980: 99–102, with ills.); Hochstätter (2004a: 32–33, ills. pp. 119–121). **Distr:** Mexico (San Luis Potosí: mainly Mun. Guadalcázar); slopes with shallow soil, desert scrub, submontane scrub or oak scrub, 1500–1800 m; flowers May to July. **I:** Hochstätter (2003c: 151); Boeuf & al. (2009: 88–89).

[1c] Arborescent, stems 2–7 m, to 25 cm Ø, mostly single or rarely poorly branched; **L** stiff, scabrous, flat or somewhat canaliculate, somewhat rough on both faces, 30–100 × 2–6 cm, margins with thin band, dark brown in the lower and grey in the upper part, with thin and curled grey fibres, **terminal Sp** acute, 20–30 mm, grey; **Inf** pendent, paniculate, flowering part 0.8–1.2 m, much extending beyond the rosette leaves, with very dense part-**Inf**, glabrous to pubescent; **Ped** 15–25 mm; **Fl** subglobose; **Tep** white; **OTep** elliptic-oblong, truncate at the base, acute, 25–45 × 8–13 mm; **ITep** obovate, rounded at the base, acute to acuminate, 25–50 × 10–20 mm, pubescent on the margins near the tip; **Fil** 8–15 mm, pubescent; **Ov** 15–20 mm; **Sty** very short; **Sti** finely pubescent; **Fr** fleshy berries, oblong, 40–80 × 20–35 mm, brownish when ripe; **Se** obovate, unwinged, 6–8 × 5–6 mm, 3–5 mm thick, black.

In the protologue compared with the co-occurring, rather different *Y. treculiana*, with typical unbranched plants growing in sparse soil on slopes, whereas plants on alluvial soils show tendencies towards branching and resemble *Y. filifera*. All features of *Y. potosina*, including the pendent inflorescences, fall within the range of character expressions of the widespread *Y. filifera*, and *Y. potosina* may represent nothing more than a habitat modification of *Y. filifera* with smaller growth and less branching induced by the arid



calcareous soil, as already hinted upon in the protologue. Sparsely branched plants of *Y. potosina* (Hochstätter 2004a: 119) are indistinguishable from finally sparsely branched plants identified as *Y. filifera* (Hochstätter 2004a: 122–123). Magallán Hernández & al. (2013b: 17) mention a hybrid with *Y. queretaroensis*.

**Y. queretaroensis** Piña Luján (Cact. Suc. Mex. 34(3): 51–56, ills., 1989). **Type:** Mexico, Querétaro (*Piña Luján* s.n. [MEXU 472851, ASU, ENCB, IEB, IZTA, MEXU]).—**Lit:** García-Mendoza (2003); Hochstätter (2008b: with ills.); Weissbeck (2010: with ills.); Weissbeck (2011: with ills.); Magallán Hernández & al. (2013a: with ills.); Magallán Hernández & al. (2013b: with ills.); Magallán Hernández & al. (2014); Spracklin (2015: with ills.). **Dist:** Mexico (NE Guanajuato, C Querétaro, W Hidalgo); broad valleys enclosed by high mountains, steep mountain slopes, in stony soil, in desert scrub and pine-oak forests, 800–1500 m; flowers April to June. **I:** Hochstätter (2003a: 19, 66); Boeuf & al. (2009: 90–91).

[1c] Caulescent, stems nearly always unbranched, (2–) 3–6 m, 20–40 (–60) cm Ø, often forming small rhizomatous colonies of up to 30 stems of different lengths; **L** very numerous, ±1500, linear, straight, flexible, broadened at the base to 1.5–2.5 cm, both faces convex and with a slight keel and 2 furrows between keel and margins, papillose on the keels but smooth to the touch, 40–75 (–115) × 0.2–0.5 cm, light to dull green, persistent, with age reflexed and covering the stems, margins horny, yellowish, finely denticulate, **terminal Sp** angled, 2–5 (–8) mm, coffee-brown; **Inf** erect, paniculate, peduncle short, ±6–10 cm, flowering part 0.6–0.9 m, ellipsoid, much-branched, densely flowered, above the rosette leaves; part-**Inf** 120–140, to 14–16 cm, finely tomentose; **Ped** 13–20 mm, tomentose; **Fl** pendent, campanulate to globose, 22–36 mm; **Tep** glabrous; **OTep** lanceolate, apex obtuse to truncate, 28–36 × 10–12 mm; **ITep** elliptic, apex acute, 23–30 × 12–14 mm, white to whitish-cream, tube none; **Fil** 13–15 mm, papillose; **Ov** narrowly ellipsoid to conical, 14–20 × 6–8 mm, pale green; **Sty** cylindrical, 3 mm; **Sti** lobed; **Fr**

fleshy berries, pendent, 70–98 (–115) × 25–39 (–45) mm, green; **Se** of various shapes, flat, 6–9 (–11) × 5–10 mm, 2–3 (–6) mm thick, black.

The fruits were unknown in the protologue, and *Y. queretaroensis* was at that time considered to be closest to the capsular-fruited *Y. thompsoniana* and to *Y. rostrata*, from which it differs in its taller and unbranched stems, biconvex and more slender leaves and smaller flowers. Piña Luján (1990) added a description of the baccate fruits and details of the typification. Hochstätter (2008b) placed *Y. queretaroensis* together with the similar *Y. linearifolia* in a separate, baccate-fruited section *Gracilifoliae*, but this was not accepted by others. *Y. queretaroensis* differs from the similar *Y. linearifolia* by leaves that are more rhomboid in transverse section, and its leaves break when bent into a knot, whereas those of *Y. linearifolia* neatly bend (Weissbeck 2010, 2011). Magallán Hernández & al. (2013a, b) describe habitats and distribution, and the threat by the horticultural trade of wild-collected plants. Magallán Hernández & al. (2014) provide a full description incl. leaf anatomy, and place the species in Ser. *Treculianae* (= Ser. *Yucca*). In the molecular phylogeny of Smith & al. (2008a), *Y. queretaroensis* appears to be closest to *Y. filifera*, but its position remains enigmatic, as some DNA data available from GenBank places it as basal sister to all other species of the genus. Zamudio & Galván Villanueva (2011: 10, 87) provide a new record from N Guanajuato, and Spracklin (2015) reports suspected natural hybrids with *Y. filifera*. Vernacular name: “estoquillo”. For winter-hardiness in cultivation, see Weissbeck (2010, 2011).

**Y. reverchonii** Trelease (Annual Rep. Missouri Bot. Gard. 22: 102, t. 108, 1912). **Type** [lecto]: USA, Texas (*Reverchon* 4030 [MO 148679, BRIT-SMU, MO]).—**Lit:** Webber (1953: 41–43, t. 23); Matuda & Piña Luján (1980: 118–120); Hess & Robbins (2002); Hawker (2016: 383–385); all with ills. **Dist:** USA (Texas), Mexico (Coahuila); usually on rocky limestone ledges and gravelly plains in dense bush, 300–900 m; flowers May to mid-June. **I:** Boeuf & al. (2009: 94–95).

[3a] Acaulescent, solitary or forming dense colonies, with branching subterranean rhizomes;

**Ros** single but in age forming small dense clumps with 2–10 **Ros** 0.3–1 m Ø; **L** < 100, lanceolate, straight, slightly concave, nearly flattened, quite rigid, straight, 25–60 × 1–2 (–2.5) cm, widest in the middle, light glaucous-green, margins hyaline, yellow or reddish-brown, minutely denticulate; **Inf** erect, paniculate, peduncle 46–110 cm, glabrous to heavily floccose, flowering part 35–100 cm, narrowly ovoid to narrowly pyramidal, arising 25–42 cm beyond the rosette, part-**Inf** few-flowered, densely pubescent; **Fl** pendent, campanulate to somewhat globose, hardly opening at anthesis; **Tep** ovate, sharply acuminate, 38–60 × 15–29 mm, white or greenish-white; **Fil** 18–32 mm; **Ov** ± 20–25 × 4–6 mm, tapering or rarely abruptly narrowed into the style; **Sty** 10–20 mm, white or greenish; **Fr** erect dry capsules, ellipsoid, rarely constricted, with an attenuate beak, 38–59 × 18–32 mm; **Se** flat, thin, unwinged, 5–6 × 6–7 mm, dull black.

Webber (1953: 42) designated the lectotype (as “Type”) cited above. This species is similar to *Y. rupicola* in its tall upright inflorescences, but distinguished by its straight, rigid, slightly concave and narrower leaves with yellow or reddish-brown margins (vs. leaves twisted, flexible, strongly concave, broader, and with orange or reddish-brown margins in *Y. rupicola*) (Hess & Robbins 2002). The protologue indicated that the distribution of *Y. reverchonii* on the Edwards Plateau (Texas) lies between *Y. rupicola* and *Y. thompsoniana*, and Webber (1953) reported apparent hybrids of *Y. reverchonii* with both species. The available molecular data is inconclusive about the relationships of *Y. reverchonii*: Clary (1997) (cited by Hess & Robbins 2002) found it close to *Y. thompsoniana* and *Y. rupicola*, while Pellmyr & al. (2007) and Smith & al. (2008a) found a position close to *Y. rostrata* (AFLP data), or to *Y. constricta* or *Y. intermedia* (chloroplast DNA sequence data), and *Y. rupicola* is well separated from *Y. reverchonii* in both datasets (*Y. thompsoniana* not sampled). The distribution in N Coahuila, Mexico, reported by Matuda & Piña Luján (1980: 120), is omitted by Hess & Robbins (2002) and Hawker (2016) and needs verification. Bolliger (2010) shows an artificial hybrid with *Y. filamentosa*.



**Fig. 6** *Yucca rigida*. (Copyright: U. Eggli)

**Y. rigida** (Engelmann) Trelease (Annual Rep. Missouri Bot. Gard. 13: 65, tt. 35, 36: fig. 1, 84: fig. 1, 1902). **Nom. illeg.**, ICN Art. 53.1. **Type:** Mexico, Durango (*Gregg* 477 [MO 148683]).—**Lit:** Matuda & Piña Luján (1980: 122–125, with ills.); Hochstätter (2004a: 47–49, ills. pp. 142, 144–146); Flores-Hernández & al. (2011: with ills.). **Distr:** Mexico (C & SE Chihuahua, SW Coahuila, E Durango); stony ravines and slopes in desert scrub, 1100–1600 m; flowers March to May. **I:** Earle (1964); Piña Luján (1980: 281); Starr (2000: 13); Irish & Irish (2000: t. 91); Johnson (2000: 19); Hochstätter (2003a: 20–22); Guillot Ortiz & Meer (2008: 110). – Fig. 6.

≡ *Yucca rupicola* var. *rigida* Engelmann (1873); **incl.** *Yucca luminosa* Govaerts (2014) (*nom. inval.*, ICN Art. 29.1).

[3a] Caulescent, stems to 3–5 m, 20–45 cm Ø, **Br** none or few, 3–5 or more, stems usually with a long skirt of dried deflected leaves often reaching down to the ground; **Ros** asymmetrical, 0.5–1 m Ø; **L** spreading, linear, slightly broadened in the middle, slightly canaliculate, thin, 30–60 × 2–3 cm, yellowish-green and glaucous to nearly pale blue, margins yellowish, finely denticulate, tip slender but very pungent, brown or grey; **Inf** erect, paniculate, peduncle 30–70 cm, flowering

part 0.6–1.2 m, with its base within the rosette leaves, ovoid, dense; part-**Inf** 28–40, glabrous; **Fl** globose to campanulate; **Tep** narrowly oblong, acuminate, 40–50 × 16–22 mm, creamy-white or greenish-white; **Fil** 16–22 mm; **Ov** ± 13 × 5 mm; **Sty** short, ± 2 mm; **Sti** lobed; **Fr** erect dry capsules, oblong, not constricted, rough, 35–70 × 18–25 mm, strongly beaked; **Se** 4–5 × 5–7 mm, dull black.

The protologue of the basionym cites Gregg, “scape . . . 5-10 feet high” as type. The Engelmann herbarium at MO “contains two specimens” (Trelease 1902: 65), *Gregg A* (= MO 148684) and *Gregg 477* (= MO 148683), which represent different gatherings with different collection numbers, but were nevertheless cross-labelled later. The specimen *Gregg 477* with the hand-written label “5 to 10 +” is the holotype. The neotypification by Hochstätter (2004a: 47) is thus superfluous, and moreover ineffective under ICN Art. 7.11.

The established name *Y. rigida* (Engelmann) Trelease is unfortunately a later homonym of *Y. ×rigida* Deleuil ex André 1883, and therefore illegitimate. Govaerts (2014+) used the replacement name *Y. luminosa*, but the name was not formally published and is therefore invalid. In order to stabilize current use, a proposal to conserve Trelease’s name is in progress.

Molecular AFLP data (Pellmyr & al. 2007; Smith & al. 2008a) show the species as well-supported sister to the other species of Sect. *Rupicolae* sampled in those studies; chloroplast sequence data (Smith & al. 2008a) show various different placements. A habitat study in the municipio of Mapimí, Durango, revealed a population density of 980 plants/ha, and that stem height and diameter increase with increasing altitude (Flores-Hernández & al. 2011).—The species becomes increasingly popular as landscape plant in the SW USA and is “perhaps the most beautiful and elegant of all yuccas” (Johnson 2000: 16).

**Y. rostrata** Engelmann ex Trelease (Annual Rep. Missouri Bot. Gard. 13: 68, tt. 40–42, 84: fig. 3, 93: fig. 2, 1902). **Type** [lecto]: Mexico, Coahuila (*Palmer* s.n. in 1880 [MO 148694,

GH]).—**Lit**: Matuda & Piña Luján (1980: 125–127, with ill.); Hochstätter (2000: 29–30, ill. pp. 82–83); Hess & Robbins (2002). **Dist**: USA (SW Texas: Brewster County), Mexico (C, E & S Chihuahua, N, C, W & S Coahuila, E Durango?); rocky mountain slopes, canyon bottoms, plains and moderate slopes with desert scrub, 300–800 m; flowers March to May. **I**: Hochstätter (1999: 215–218); Irish & Irish (2000: t. 92); Starr (2000: 13), Boeuf (2007a: 75); Guillot Ortiz & Meer (2008: 110); Boeuf & al. (2009: 98–99).

[3a] Arborescent, stems erect, 1.8–3.6 (–4.5) m, 18–32 cm Ø, mostly simple or occasionally with up to 3 branches; **Ros** frequently asymmetrical, with >100 leaves, solitary or forming colonies; **L** linear, often twisted, flat to canaliculate, broadest considerably above the middle, smooth on both faces, 25–60 × 1.2–1.7 cm, glaucous, margins lemon-yellow, hyaline, finely denticulate, **terminal Sp** very pungent; **Inf** erect, paniculate, peduncle 0.3–1 m, glabrous or glabrescent, flowering part 0.6–2 m, ellipsoid to ovoid, arising just within or beyond the rosette leaves, densely many-flowered; part-**Inf** 28–40, up to 38 cm, sparsely pubescent; **Fl** pendent, globose to campanulate; **Tep** narrowly ovate, sharply acuminate, 42–52 × 11–20 mm, white; **Fil** 17–20 mm; **Ov** ± 19–20 × 4–6 mm; **Sty** 6–14 mm, white; **Sti** lobed; **Fr** erect, ovoid to ellipsoid, rarely constricted, 40–70 × 18–25 mm, tip with a strong and curved beak; **Se** 4–5 × 6–7 mm, rather dull black.

The protologue cited material from Bigelow and Palmer. McKelvey (1947: 78) designated *Palmer* s.n. (MO 148694) as “Type”, which represents a lectotypification. The same selection was also made by Webber (1953: 38).

Closely related to *Y. thompsoniana*, which may represent just a N dwarfer variant (Webber 1953, Hess & Robbins 2002). It is best distinguished by its ± larger habit with larger inflorescences and longer and broader leaves with the widest part considerably above the middle, and smooth on both faces (vs. smaller-growing with smaller inflorescences and shorter and narrower leaves widest at or above the middle and ± scabrous on both faces in *Y. thompsoniana*). Specimens from Durango placed here need verification.

With early molecular data (chloroplast DNA restriction sites, Clary & Simpson 1995), *Y. rostrata* groups in an unresolved polytomy together with *Y. reverchonii*, *Y. rigida* and *Y. thompsoniana*. In recent molecular phylogenies (Pellmyr & al. 2007, Smith & al. 2008a), *Y. rostrata* is closest to *Y. reverchonii* (AFLP data), or to *Y. elata* (chloroplast DNA sequence data; *Y. thompsoniana* not sampled).

Recently, green-leaved populations from NE Coahuila placed in *Y. rostrata* (Boeuf & al. 2009: 99, Weissmüller 2017) and similar plants from N of the Big Bend National Park, Texas, placed in *Y. thompsoniana* (Boeuf 2007a: 118–119) became known and are also offered commercially in Europe. For the outdoor cultivation (hardy down to  $-15$  to  $-20$  °C) see Boeuf (2007a). Boeuf & al. (2010: 80) report variegated forms from European collections.

**Y. rupicola** Scheele (Linnaea 23: 143–144, 1850). **Type:** USA, Texas (*Lindheimer* 709 [MO 148731]).—**Lit:** Trelease (1902: 67–68, tt. 3–39); Matuda & Piña Luján (1980: 116, 119); Hochstätter (2000: 26–27, ills. p. 81); Hess & Robbins (2002); Diggs & al. (2006: 420–421, ill. p. 308); Hawker (2016: 386–391, with ills.). **Distr:** USA (S-C Texas: SE Edwards Plateau); rocky hillsides, limestone ledges and grassy plains, dense bush and open woodland, 400–900 m; flowers May to June. **I:** Curtis's Bot. Mag. 117: t. 7172 (1891); Hochstätter (1999: 209–210); Guillot Ortiz & Meer (2008: 111); Boeuf & al. (2009: 100–101).

**Incl.** *Yucca contorta* Regel (1858); **incl.** *Yucca lutescens* Carrière (1858); **incl.** *Yucca contorta* Carrière (1858) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca tortilis* hort. ex Carrière (1858) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca rupicola* var. *tortifolia* Engelmann (1873); **incl.** *Yucca tortifolia* Lindheimer ex Engelmann (1873) (*nom. inval.*, ICN Art. 36.1c).

[3a] Acaulescent, with branching subterranean rhizomes; **Ros** soon developing open colonies with 2–15 large heads; **L** < 100 per rosette, lanceolate, twisted, flaccid, flexible, strongly concave or flat but oblique or undulate, slightly striate, distinctly narrowing towards the

base, widest in the middle, (20–) 35–58 × 2–4 cm, dark green, margins hyaline dark orange or reddish-brown or occasionally yellow, minutely denticulate or wavy, tip pungent; **Inf** erect, paniculate, peduncle 30–150 cm, flowering part 25–100 cm, narrowly ovoid to narrowly pyramidal, 24–48 cm above the rosette leaves; part-**Inf** 8–16, 7–20 cm, glabrous to slightly floccose; **Fl** few, pendent, mainly campanulate, expanding but little, rarely somewhat globose and open; **Tep** ovate, sharply acuminate, 38–69 × 15–30 mm, white or greenish-white; **Fil** 18–32 mm; **Ov** 17–25 × 4–6 mm, tapering or somewhat abruptly terminating into the style; **Sty** 12–20 mm, white or greenish; **Sti** lobed; **Fr** erect dry capsules, ellipsoid or somewhat cylindrical, rarely constricted, 38–55 × 20–30 mm, beaked; **Se** thin, 6–8 × 7–8 mm, dull black.—**Cytology:** 2n = 60 (McKelvey & Sax 1933).

The protologue cites material of Lindheimer from a rocky plateau near New Braunfels, June, which, among the 14 *Y. rupicola* specimens of Lindheimer at MO, is only matched by MO 148731, as also indicated by a label of K. H. Clary (2003). The neotypification by Hochstätter (1999: 209) is thus superfluous.

This is the only species with twisted adult leaves (Hochstätter 2000, Hess & Robbins 2002, Boeuf 2009). For a discussion of the relationships of this species with *Y. pallida* and *Y. cernua*, see under *Y. pallida*.

**Y. schidigera** Roehl ex Ortgies (Gartenflora 20: 110, 1871). **Type** [neo]: USA, California (*Nuttall* s.n. [GH]).—**Lit:** Shreve & Wiggins (1964: 354); Benson & Darrow (1981: 56, figs. 3.18–3.22); Matuda & Piña Luján (1980: 81–83, with ills.); Turner & al. (1995: 411–412); Hess & Robbins (2002); Hawker (2016: 391–398, with ills.). **Distr:** S USA (S California, S Nevada, W Arizona), Mexico (adjacent N Baja California); gravelly mountain and valley slopes, desert or chaparral vegetation, 300–2050 m; flowers March to May. **I:** Hochstätter (1999: 81–85); Irish & Irish (2000: t. 94); Guillot Ortiz & Meer (2008: 111); Boeuf & al. (2009: 102–103). – Fig. 7.

**Incl.** *Yucca californica* Nuttall ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca*





**Fig. 7** *Yucca schidigera*. (Copyright: U. Eggli)

*mohavensis* Sargent (1896)  $\equiv$  *Sarcoyucca mohavensis* (Sargent) Lindinger (1933).

[1b] Stems caulescent, 1–8, erect, simple or sparingly branched, to 2.5–5 m, forming colonies of several rosettes; **L** numerous, erect, sword-shaped, thick, very rigid, for the greater part rather deeply canaliculate, broadest near the middle, glabrous, 33–130  $\times$  3–5 cm, yellowish-green, margins thick, with coarse somewhat curled fibres, apex stout-pungent; **Inf** erect, paniculate, peduncle to 40 cm, flowering part 30–60 cm, obovoid or ellipsoid and with flattened tip, entirely within or scarcely beyond the rosette leaves; part-**Inf** many, with numerous densely arranged flowers, glabrous or pubescent; **Fl** pendent, globose; **Tep** (broadly) lanceolate, spreading, 30–50 (–75)  $\times$  10–18 mm, white or cream-coloured, commonly tinged with lavender or purple; **Fil** 20–25 mm; **Ov** rather stout, apex abruptly tapered, 17–27  $\times$  7–12 mm; **Sty** 1–2 mm; **Sti** distinct; **Fr** pendent fleshy berries, variable, long and cylindrical, mostly constricted in the middle, 50–115  $\times$

30–40 mm, usually tapering from the swollen base to a rather blunt tip 60–85 mm long, first green, turning dark brown to nearly black; **Se** unwinged, rugose, 8–11 mm  $\varnothing$ , 6–9 mm thick, grey.

The protologue does not cite a type. The designation of *Nuttall* s.n. (GH), the type of *Y. californica*, as “Type” by Webber (1953: 25), represents a neotypification. In the molecular phylogeny of Pellmyr & al. (2007), the single sample analyzed of *Y. schidigera* groups within 7 samples of *Y. baccata*.

*Y. schidigera* dominates the Mohave Desert of the SW USA, and is often associated with *Y. brevifolia* (Boeuf & al. 2009: 103). It is frequently used for landscaping in the SW USA (Irish & Irish 2000). Boeuf & al. (2010: 82) report rare cases of spontaneous variegations originating in cultivation. In historical times, *Y. schidigera* was used by Native Americans as a source of fibre, food, and soap (Benson & Darrow 1981, Hess & Robbins 2002).

**Y.  $\times$ schottii** Engelm *pro sp.* (Trans. Acad. Sci. St. Louis 3: 46, 1873). **Type** [lecto]: USA, Arizona (*Schott* s.n. [NY]).—**Lit**: Lenz & Hanson (2000); Lenz & Hanson (2001); both with ill. **Distr**: S USA (Arizona, SW New Mexico?), N Mexico (N, E & SE Sonora, W-most Chihuahua); rocky slopes (volcanic and limestone) in oak woodland and pine-oak forests, 350–1500 m; flowers February to May. – Fig. 8.

$\equiv$  *Sarcoyucca schottii* (Engelm) Lindinger (1933); **incl.** *Yucca  $\times$ puberula* Torrey *pro sp.* (1858) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca brevifolia* A. Schott *ex* Engelm (1873) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca  $\times$ macrocarpa* Engelm *pro sp.* (1881); **incl.** *Yucca brevifolia* A. Schott *ex* Trelease (1902) (*nom. illeg.*, ICN Art. 53.1).

[1b  $\times$  1c  $\times$  3b] Lenz & Hanson (2000, 2001) clarified the nomenclatural and taxonomic confusion surrounding *Y. schottii*, and designated the above-cited lectotype (Lenz & Hanson 2000: 97). According to their interpretation, the name *Y. schottii* Engelm represents the earliest applicable name for hybrids and backcrosses between the fleshy-fruited *Y. baccata* and *Y. madrensis* and



**Fig. 8** ×*Yucca schottii*.  
(Copyright: U. Eggli)



the capsular-fruited *Y. elata*, and it is thus recognized as name for a collective hybrid species.

Hess & Robbins (2002) express doubts, however, on the possibility for crosses between baccate and capsular-fruited species. The common fleshy-fruited *Yucca* with long wide flexible blue-green leaves from the mountains of S Arizona, previously wrongly named *Y. schottii* auct. non Engelmann, is regarded as pertaining to *Y. madrensis*, where most treatments and published photographs named *Y. schottii* belong. In the molecular phylogeny of Pellmyr & al. (2007) 3 samples of *Y. schottii* are sister to a clade that consists of 7 samples of *Y. baccata* plus 1 sample of *Y. schidigera*, but the *Y. schottii* samples may belong to *Y. schottii* auct. = *Y. madrensis*.

Lenz & Hanson (2001) also include the widely recognized taxa *Y. baccata* var. *brevifolia* (here treated as *Y. baccata* ssp. *thornberi*) and most of its synonyms as well as *Y. grandiflora* in *Y. ×schottii*, but since their study covers a small area in S Arizony only and neither the full geographical range also including Mexico, nor a broader specimen set, both are upheld here pending more detailed studies.

**Y. tenuistyla** Trelease (Annual Rep. Missouri Bot. Gard. 13: 53–54, tt. 17: fig. 2, 18–19, 83: fig. 3, 92: fig. 1, 1902). **Type** [lecto]: USA, Texas (*Lindheimer* s.n. [MO 148758]).—**Lit**: Hess & Robbins (2002); Diggs & al. (2006: 422). **Distr**: USA (SE Texas); scrubland at the coast, brushland

in the Edwards Plateau and the South Texas Plains, in dry soil, 0–200 m; flowers May to June.

[3c] Stems none or short and erect, to 0.5 m; **Ros** forming open colonies; **L** lanceolate, mostly recurving, rigid, lower face convex, upper face flat, widest near the middle, long attenuate, lower face often somewhat scabrid, 40–70 × 1–2 cm, dark green, margins entire but filiferous, whitish, apex scarcely pungent; **Inf** erect, paniculate, peduncle 1–1.7 m, flowering part to 1 m, ovoid, arising beyond the rosette leaves, distance from the rosette leaf tips to the lowest inflorescence branches >2× the leaf length at full anthesis, glabrous or slightly pubescent; **Fl** pendent; **Tep** narrow, apex acute, ± 27–30 × 7–10 mm; **Fil** < 19 mm; **Ov** ± 12 × 4 mm, white; **Sty** oblong, often deeply lobed, ± 7 mm, white or green; **Sti** lobed; **Fr** erect dry capsules, cylindrical, stout, not constricted, 50–65 × 25–30 mm; **Se** thin, 8–10 × 7–8 mm, shiny black.

The protologue cites specimens of Lindheimer, Trelease, and Harvey, which constitute syntypes. McKelvey (1947: 133) designated the above-cited lectotype.

Very insufficiently known. *Y. tenuistyla* and *Y. louisianensis* were both regarded as possible synonyms of *Y. constricta* by McKelvey (1947), and the three taxa differ only tenuously. According to Hess & Robbins (2002) *Y. tenuistyla* is probably just a variant of *Y. flaccida*, and also includes *Y. louisianensis*. According to Diggs & al. (2006), *Y. constricta* is usually easily

distinguished in the field in being typically much taller with very numerous, straight, narrower leaves and constricted capsules.

**Y. thompsoniana** Trelease (Annual Rep. Missouri Bot. Gard. 22: 101–102, tt. 104–107, 1912). **Type:** USA, Texas (*Bigelow* s.n. [NY 688485, MO, NY]).—**Lit:** Webber (1953: 39–40, t. 21); Matuda & Piña Luján (1980: 127–130, with ills.); Hochstätter (2000: 28–29, ills. p. 82); Hess & Robbins (2002); Hawker (2016: 397–401, with ills.). **Distr:** USA (SW Texas), Mexico (NE Chihuahua, N & C Coahuila, C Nuevo León), usually on exposed rocky knolls and slopes, 200–1400 m; flowers April to May. **I:** Piña Luján (1980: 281); Hochstätter (1999: 212–214); Boeuf (2007a: 77, 118–119); Guillot Ortiz & Meer (2008: 111); Boeuf & al. (2009: 106–107).

**Incl.** *Yucca rostrata* fa. *integra* Trelease (1911); **incl.** *Yucca thompsoniana* fa. *viridis* Weissbeck & Boeuf (2007) (*nom. inval.*, ICN Art. 29.1 & Ex. 2).

[3a] Caulescent, stems erect, 0.7–2.5 m, to 30 cm Ø, single, with 1–5 comparatively long ascending or diffusive branches; **Ros** with >100 leaves, frequently asymmetrical, rather small, solitary or forming colonies; **L** linear, thin and flexible, flat or canaliculate to flat above and keeled below, striate, widest at or above the middle, ± scabrous on both faces, 20–30 (–45) × 0.7–1.2 cm, margins horny, minutely denticulate, yellow or orangish-red, apex sharply pointed; **Inf** erect, paniculate, racemose at the tip, peduncle (30–) 40–70 cm, flowering part 52–82 cm, narrowly ellipsoid to somewhat ovoid, arising 11–19 cm above the rosette leaves; part-**Inf** 20–34, 2–22 cm, glabrous or glabrescent; **Fl** pendent, globose to campanulate; **Tep** narrowly elliptic, sharply acuminate, conspicuously veined, glossy, 35–67 × 12–35 mm, white; **Fil** 17–33 mm; **Ov** slender, 4–6 mm Ø, usually tapering into the style; **Sty** 6–18 mm, white; **Sti** lobed; **Fr** erect dry capsules, ellipsoid or somewhat ovoid, rarely constricted, 35–70 × 20–25 mm, with a long beak; **Se** flat, thin, unwinged, 5–6 × 6–7 mm, dull black.

The protologue cites *Bigelow* August 10, 1852, as “type”, and according to the captions to the plates, t. 105 illustrates the type sheet at NY (=

NY 688485, confirmed by K. H. Clary (label in 2003)). Webber (1953) characterized *Y. thompsoniana* as a dwarfish form of *Y. rostrata*, perhaps not worthy of recognition at species rank. He also suggested that it may hybridize with *Y. reverchonii*. In the molecular chloroplast DNA restriction site phylogeny of Clary & Simpson (1995), *Y. thompsoniana* groups in an unresolved polytomy together with *Y. reverchonii*, *Y. rigida*, and *Y. rostrata*. For differences to *Y. rostrata*, see there. Heim (2012) raised an artificial hybrid with *Y. recurvifolia* (here treated as *Y. gloriosa* var. *tristis*).

**Y. treculiana** Carrière (Rev. Hort. (Paris) 1858: 580, 1858). **Type** [neo]: USA/Mexico (*Trécul* 1496 [P 02161277]).—**Lit:** Trelease (1902: 96–97, tt. 52–54); Webber (1953: 21–22, t. 6); Matuda & Piña Luján (1980: 75–79, with ills.); Robbins (1983: 22–28, 41–45); Hess & Robbins (2002); Diggs & al. (2006: 420–421, ills. pp. 308, 425); Hawker (2016: 401–403, with ills.). **Distr:** SE USA (W Texas), N Mexico (Chihuahua, Coahuila, Nuevo León, Tamaulipas, Durango, Zacatecas); grassy or rocky slopes or mesas, brushland, chaparral vegetation, 0–1600 m; flowers March to April. **I:** Curtis’s Bot. Mag. 86: t. 5201 (1860, as *Y. canaliculata*); Irish & Irish (2000: tt. 97–98); Johnson (2000: 19); Starr (2000: 13); Hochstätter (2001b: 78–81); Boeuf (2007a: 85); Boeuf & al. (2009: 110–111).

≡ *Sarcocoyucca treculiana* (Carrière) Lindinger (1933); **incl.** *Yucca spinosa* Kunth (1816); **incl.** *Yucca agavoides* hort. ex Carrière (1858); **incl.** *Yucca recurvata* hort. ex Carrière (1858) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca revoluta* hort. ex Carrière (1858) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca undulata* hort. ex Carrière (1858) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca aspera* Regel (1859); **incl.** *Yucca canaliculata* Hooker (1860) ≡ *Yucca treculiana* var. *canaliculata* (Hooker) Trelease (1902); **incl.** *Yucca canaliculata* var. *pendula* K. Koch (1862); **incl.** *Yucca undulata* K. Koch (1862) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca longifolia* Buckley (1863) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca argospatha* Verlot (1868); **incl.** *Yucca crassifila* Engelman (1873) (*nom. inval.*, ICN Art. 36.1c);

**incl.** *Yucca longifolia* Engelm (1873) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Yucca cornuta* hort. ex Baker (1880); **incl.** *Yucca concava* hort. ex Baker (1880) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Yucca treculiana* var. *glauca* Sprenger (1901); **incl.** *Yucca torreyi* Shafer (1908); **incl.** *Yucca torreyi* fa. *parviflora* McKelvey (1938); **incl.** *Yucca treculiana* var. *succulenta* McKelvey (1938).

[1c] Arborescent, stems 1–8, forming groups of variable height, simple or occasionally with 2–5 branches, to 7 m, 14–15 cm Ø, often forming colonies of several rosettes; **L** erect, rigid, canaliculate, thick, usually U- or V-shaped in cross-section, rather scabrous, 36–128 × 1.6–7 cm, yellowish- to bluish-green, old leaves hanging at various angles, giving an overall ragged appearance, margins entire, with sparse thin and straight coarse fibres, light brown, **terminal Sp** very acute; **Inf** erect, paniculate, peduncle 30 cm or more, flowering part 1.8 m, variable in shape, usually ovoid, arising mostly within the rosette leaves, exceeding the leaves for ½–¾ of its length, densely many-flowered, glabrous, rarely slightly pubescent; **Bra** large in the lower inflorescence parts; **Fl** pendent, globose; **Tep** ovate, apex rounded or acute, 27–81 × 10–34 mm, cream-coloured, occasionally tinged with purple; **Fil** 10–27 mm; **Ov** 13–33 × 4–10 mm; **Sty** 2–8 mm; **Sti** distinct; **Fr** pendent fleshy berries, cylindrical, terminal part conical, 44–187 × 18–46 mm; **Se** rough, 5–14 mm Ø, 1–5 mm thick.

The protologue does not cite a type. The designation of *Trecul* 1496 (P) as “Type” by Webber (1953: 21) represents a neotypification. The epithet is usually written ‘treculeana’, but the taxon is named for the French botanist A. A. L. Trécul.

*Y. spinosa* Kunth (1816), listed here as provisional synonym following Govaerts (2014+: accessed Jan. 2019) would have priority over the younger name *Y. treculiana* if it should definitely belong here, and a proposal to conserve the latter name would be necessary.

*Y. torreyi*, shown as closely related with *Y. treculiana* in the early molecular study of Clary & Simpson (1995), is the E entity within a broader concept of *Y. treculiana*, and included in the synonymy here following Robbins (1983) and Hess & Robbins (2002), whereas Matuda & Piña

Luján (1980), Benson & Darrow (1981), and Diggs & al. (2006) recognize it as distinct.

**Y. utahensis** McKelvey (Yuccas Southwest US, 2: 94, tt. 32–34, 1947). **Type:** USA, Utah (McKelvey 4167 [A]).—**Lit:** Webber (1953: 62–65); Reveal (1977: 533–534, as *Y. elata* var.); Welsh & al. (1987: 650); Hess & Robbins (2002); Hawker (2016: 403–408). **Dist:** SW USA (SE Nevada, SW Utah, NW Arizona); desert and desert hillsides, woodlands, and canyons, often on sandy places, 700–2200 m; flowers late April to June. **I:** Hochstätter (1999: 24, 26, as *Y. elata* var.); Boeuf & al. (2009: 112–113).

≡ *Yucca elata* var. *utahensis* (McKelvey) Reveal (1977) ≡ *Yucca elata* ssp. *utahensis* (McKelvey) Hochstätter (1999).

[3b] Caulescent or appearing acaulescent, not distinctly arborescent, stems often procumbent, usually 7 or more per colony, thick, 1.2–2.8 m; **Ros** forming large colonies with up to 10–15 rosettes; **L** numerous, linear-lanceolate, divergent, flexible, plano-convex or plano-keeled, widest near the middle, 20–70 × 0.7–2.2 cm, yellow-green, margins whitish, entire but finely filiferous, tip acuminate with a short spine; **Inf** erect, paniculate, sometimes distally racemose, peduncle 1–1.6 m, flowering part 1–1.5 m, narrowly ellipsoid, arising beyond the rosette leaves; part-**Inf** 10–20 cm, glabrous; **Bra** erect; **Ped** 13–25 mm; **Fl** pendent, campanulate; **Tep** broadly elliptic or ovate, 40–50 × 20–25 mm, creamy-white; **Fil** 20–25 mm; **Ov** 20–25 mm; **Sty** 5–10 mm, white; **Sti** lobed; **Fr** erect dry capsules, oblong-cylindrical, 50–60 × 20–25 mm; **Se** thin, dull black.

The taxon is treated very differently by different authors. The protologue suggested a close relationship with *Y. elata*, from which it differs primarily in growth habit, fruit size, and leaf width, although with some overlap. Webber (1953) regarded *Y. utahensis* as a hybrid population, but this view was rejected as unjustified by Reveal (1977: 534) who reduced the taxon to varietal rank under *Y. elata*, assigning (sub-) caulescent plants to *Y. elata* var. *utahensis* and acaulescent or infrequently caulescent plants with racemose inflorescences to *Y. angustissima*.

Welsh & al. (1987) recognized the taxon at species rank, noting that it is disjunct from *Y. elata*, and closer to *Y. (angustissima var.) kanabensis*. DNA evidence of Clary (1997) (cited by Hess & Robbins 2002) suggested a close relationship with *Y. elata*. Lenz & Hanson (2001: 169) referred the taxon to the synonymy of *Y. elata*. However, species rank for *Y. utahensis* is strongly supported by molecular data (Pellmyr & al. 2007, Smith & al. 2008a: fig. 2b, c) where the sample of *Y. utahensis* (as *Y. elata utahensis*) is sister to *Y. angustissima* [var.] *kanabensis* (thus confirming Welsh) and clearly separate from six samples of *Y. elata*, which form a distinct clade.

**Y. valida** Brandegee (Proc. Calif. Acad. Sci., Ser. 2, 2: 208, t. 11., 1889). **Type:** Mexico, Baja California (Brandegee s.n. [UC]).—**Lit:** Shreve & Wiggins (1964: 354); Matuda & Piña Luján (1980: 96–99, with ills.); Turner & al. (1995: 413–414); Hochstätter (2004a: 31–32, ills. pp. 116–118). **Distr:** Mexico (Baja California, Baja California Sur); Pacific coastal plains and gentle slopes, to 850 m; flowers March to April. **I:** Piña Luján (1980: 280); Hochstätter (2003d: 211); Boeuf & al. (2009: 114–115).

≡ *Yucca ×schottii* var. *valida* (Brandegee) M. E. Jones (1930) ≡ *Sarcocoyucca valida* (Brandegee) Lindinger (1933).

[1b] Arborescent and stems 3–12 m tall, 50–60 cm Ø, ± branched upwards, or shrub-forming and branched nearly from the base, surculose, stems with a skirt of dried deflected leaves for 1–2 m below the rosettes; **L** many, spreading, lanceolate, rigid, thin, smooth, 15–35 (–50) × 1.5–2.5 (–3) cm, yellowish-green, margins grey to brownish, strongly filiferous, fibres thick, curved, tip stout-pungent; **Inf** erect, paniculate, peduncle short, flowering part short, 30–60 cm, hidden within the leaves for ¼–½; **part-Inf** ascending-spreading, 10–20 cm, puberulent to glabrous; **Ped** 15–20 mm; **Fl** pendent, broadly campanulate, scented; **Tep** elliptic-lanceolate, acute to obtuse, 25–30 mm, creamy-white; **Fil** 10–12 mm, densely papillate-puberulent; **Ov** oblong, ± 13 × 4 mm, tip abruptly conical; **Sty** short, ± 2 mm; **Sti** nearly sessile; **Fr** fleshy berries, oblong, 25–45 mm, turning black upon

drying; **Se** with rugose margin, 3–7 mm Ø, 1–1.5 mm thick.

An important and characteristic constituent of the fog-influenced Pacific coastal desert scrub formations of the Baja California Peninsula, occurring from near El Rosario in the N to the vicinity of Ciudad Constitución in the S (Rebman & al. 2016: 272). Plants from the Cape region formerly included here were described as a distinct separate species, *Y. capensis* (see there). The close relationship between the two taxa is supported by AFLP molecular data, but not by chloroplast DNA sequence data (Pellmyr & al. 2007, Smith & al. 2008a).

## References

- Addicott, J. F. & Bao, T. (1999) Limiting the costs of mutualism: Multiple modes of interaction between Yuccas and Yucca Moths. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 266(1415): 197–202. <https://doi.org/10.1098/rspb.1999.0622>
- Addicott, J. F. & Tyre, A. J. (1995) Cheating in an obligate mutualism: How often do Yucca Moths benefit Yuccas? Oikos 72(3): 382–394. <https://doi.org/10.2307/3546124>
- Afferni, M. (2003) *Yucca recurvifolia* Salisbury naturalizzata “Torrelaghesa”. Piante Grasse 23(3): 100–104, ills.
- Almeida, J. D. de (2018) New additions to the exotic vascular flora of continental Portugal. Fl. Medit. 28: 259–278. <https://doi.org/10.7320/FIMedit28.259>
- Althoff, D. M. (2008) A test of host-associated differentiation across the ‘parasite-continuum’ in the tri-trophic interaction among Yuccas, Bogus Yucca Moths, and parasitoids. Molec. Ecol. 17(17): 3917–3927. <https://doi.org/10.1111/j.1365-294X.2008.03874.x>
- Althoff, D. M. (2014) Shift in egg-laying strategy to avoid plant defense leads to reproductive isolation in mutualistic and cheating Yucca Moths. Evolution 68(1): 301–307, map, ills. <https://doi.org/10.1111/evo.12279>
- Althoff, D. M. (2016) Specialization in the Yucca-Yucca Moth obligate pollination mutualism: A role for antagonism? Amer. J. Bot. 103(10): 1803–1809, map, ills. <https://doi.org/10.3732/ajb.1600053>
- Althoff, D. M. [et al. 2004], Segraves, K. A. & Sparks, J. P. (2004) Characterizing the interaction between the Bogus Yucca Moth and Yuccas: Do Bogus Yucca Moths impact Yucca reproductive success? Oecologia 140(2): 321–327. <https://doi.org/10.1007/s00442-004-1584-5>
- Althoff, D. M. [et al. 2005], Segraves, K. A. & Pellmyr, O. (2005) Community context of an obligate mutualism: Pollinator and florivore effects on Yucca filamentosa. Ecology 86(4): 905–913, ills. <https://doi.org/10.1890/04-1454>



- Athoff, D. M. [et al. 2012], Segraves, K. A., Smith, C. I., Leebens-Mack, J. & Pellmyr, O. (2012) Geographic isolation trumps coevolution as a driver of *Yucca* and *Yucca* Moth diversification. *Molec. Phylogen. Evol.* 62(3): 898–906, maps. <https://doi.org/10.1016/j.ympev.2011.11.024>
- Athoff, D. M. [et al. 2013], Xiao, W., Sumoski, S. & Segraves, K. A. (2013) Florivore impacts on plant reproductive success and pollinator mortality in an obligate pollination mutualism. *Oecologia* 173: 1345–1354. <https://doi.org/10.1007/s00442-013-2694-8>
- André, E. (1883) Les nouveaux Yuccas de M. Deleuil. *Rev. Hort.* (Paris) 55: 109–111. <http://biodiversitylibrary.org/page/49653612>
- Aragón-Gastélum, J. L. [et al. 2018], Flores, J., Jurado, E., Ramírez-Tobías, H. M., Robles-Díaz, E., Rodas-Ortiz, J. P. & Yáñez-Espinosa, L. (2018) Potential impact of global warming on seed bank, dormancy and germination of three succulent species from the Chihuahuan Desert. *Seed Sci. Res.* 28(4): 312–318. <https://doi.org/10.1017/S0960258518000302>
- Arteaga, M. C. [et al. 2015], Bello-Bedoy, R., Luz, J. L. L. de la, Delgadillo, J. & Dominguez, R. (2015) Phenotypic variation of flowering and vegetative morphological traits along the distribution for the endemic species *Yucca capensis* (Agavaceae). *Bot. Sci.* 93(4): 765–770. <https://doi.org/10.17129/botsci.214>
- Asensi, A. [et al. 2016], Díez-Garretas, B. & Pereña, J. (2016) Alien plants of coastal dune habitats in southern Spain. *Pl. Biosystems* 150(3): 477–483, map. <https://doi.org/10.1080/11263504.2014.973463>
- Aymerich, P. (2015) Sobre la naturalización de *Yucca gloriosa* L. en el norte de Cataluña. *Bouteloua* 20: 16–21, ills.
- Baker, J. G. (1870) The known forms of *Yucca*—1. *Gard. Chron.* 1870: 828, ills. <http://biodiversitylibrary.org/page/26127668>
- Baker, J. G. (1880) A synopsis of *Aloineae* and *Yuccoideae*. *J. Linn. Soc., Bot.* 18(108): 148–194, (109): 195–241, keys. <http://biodiversitylibrary.org/page/230676>
- Bao, T. & Addicott, J. F. (1998) Cheating in mutualism: Defection of *Yucca baccata* against its *Yucca* Moths. *Ecol. Letters* 1(3): 155–159. <https://doi.org/10.1046/j.1461-0248.1998.00032.x>
- Barriada-Bernal, L. G. [et al. 2018], Aquino-González, L. V., Méndez Lagunas, L. L., Rodríguez-Ramírez, J. & Sandoval-Torres, S. (2018) Caracterización física y nutricional de frutos de Yuca (*Yucca mixteca*). *Agrociencia* (Chapingo) [Ser. 3] 52(3): 347–359. <http://dialnet.unirioja.es/servlet/articulo?codigo=6423183>
- Bechtold, M. & Metorn, W. (2005) Am Fundort von *Echinocereus rigidissimus* subsp. *rubispinus* (Lau 088) in der Serra Obscura. *Kakt. and. Sukk.* 56(2): 29–38, ills.
- Behan, T. (2012) *Yucca cernua* Keith. Ein Erfahrungsbericht mit einer noch recht neuen und unbekanntem Art. *Wüstengarten* 3: 11–15, ills.
- Benson, L. & Darrow, R. A. (1981) *Trees and shrubs of the southwestern deserts*. Tucson (US): University of Arizona Press.
- Bhattacharya, G. N. & Dutta, R. (1978) Chromosome studies in two species of *Yucca*. *Proc. Indian Sci. Congr. Assoc.* (III, C) 65: 91.
- Boeuf, T. (2007a) *Yucca & Co.* Winterharte Wüstengärten in Mitteleuropa anlegen und pflegen. Berlin (DE): Medemia.
- Boeuf, T. (2007b) *Yucca rostrata* und *Yucca linearifolia* in Freilandkultur. *Kakt. and. Sukk.* 58(8): 197–203, ills.
- Boeuf, T. (2009) *Yucca*-Palmen in Mitteleuropa - Teil 1 / Teil 2 und Schluss. *Avonia* 27(3): 95–101, (4): 149–154, ills.
- Boeuf, T. (2016) *Yucca necopina* Shinnners—Portrait einer nahezu unbekanntem Art. *Wüstengarten* 6: 57–66, ills., map.
- Boeuf, T. (2018) *Yucca*-Sorten (Karl Foerster). <http://www.gartenyucca.de/gartenyucca/sorten/>, accessed Dec. 2018.
- Boeuf, T. & Heim, A. (2014) “Alte” und “neue” panaschierte Sorten und ihre Gartentauglichkeit. *Avonia* 32(1): 17–30, ills.
- Boeuf, T. [et al. 2008a], Heim, A. & Weissbeck, S. (2008a) Panaschierte Yuccas. Eine Aufstellung von aktuell bekannten, “buntblättrigen” *Yucca*-Formen. *Avonia* 26(4): 99–107, ills.
- Boeuf, T. [et al. 2008b], Weissbeck, S. & Horn, K. (2008b) Blütenstände in der Gattung *Yucca* (Asparagaceae). *Kakt. and. Sukk.* 59(12): 331–340, ills.
- Boeuf, T. [et al. 2009], Bechtold, M. & Horn, K. (2009) Halbsträucher und Schopfbäume. *Yucca* und *Hesperoyucca*. Pforzheim (DE): Deutsche Kakteen-Gesellschaft.
- Boeuf, T. [et al. 2010], Heim, A. & Weissbeck, S. (2010) Faszination bunt. Die Welt der panaschierten Yuccas. Münster (DE): Natur und Tier-Verlag GmbH.
- Bolliger, T. (2010) *Yucca filamentosa* × *Yucca reverchonii*. *Kakt. and. Sukk.* 61(5): 127–131, ills.
- Borchert, M. I. & DeFalco, L. A. (2016) *Yucca brevifolia* fruit production, predispersal seed predation, and fruit removal by rodents during two years of contrasting reproduction. *Amer. J. Bot.* 103(5): 830–836. <https://doi.org/10.3732/ajb.1500516>
- Brittingham, S. & Walker, L. R. (2000) Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. *West. North Amer. Naturalist* 60(4): 374–383. <https://scholarsarchive.byu.edu/wnan/vol60/iss4/3/>
- Cambrón-Sandoval, V. H. [et al. 2013], Malda-Barrera, G., Suzán-Azpiri, H. & Díaz-Salim, J. F. (2013) Comportamiento germinativo de semillas de *Yucca filifera* Chabaud con diferentes periodos de almacenamiento. *Cact. Suc. Mex.* 58(3): 82–88, ills.
- Campbell, R. S. & Keller, J. G. (1932) Growth and reproduction of *Yucca elata*. *Ecology* 13(4): 364–374. <https://doi.org/10.2307/1932313>
- Carlquist, S. (2012) Monocot xylem revisited: New information, new paradigms. *Bot. Rev. (Lancaster)* 78: 87–153, ills. <https://doi.org/10.1007/s12229-012-9096-1>
- Carrière, E. A. (1859) *Essai d’une classification des diverses espèces et variétés du genre Yucca*. *Rev. Hort.* (Paris),



- sér. 4, 1859: 385–391. <http://biodiversitylibrary.org/page/49745660>
- Chabaud, J. (1876) Floraison d'un *Yucca filifera*. Rev. Hort. (Paris) 48: 432–434, ill. <http://biodiversitylibrary.org/page/49655543>
- Cheeke, P. R. (2000) Actual and potential applications of *Yucca schidigera* and *Quillaja saponaria* saponins in human and animal nutrition. Proc. Phytochem. Soc. Eur. 45: 241–254. [https://doi.org/10.1007/978-94-015-9339-7\\_25](https://doi.org/10.1007/978-94-015-9339-7_25)
- Clary, K. H. (1997) Phylogeny, character evolution, and biogeography of *Yucca* L. (*Agavaceae*) as inferred from plant morphology and sequences of the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA. Austin (US): University of Texas; Ph.D. thesis.
- Clary, K. H. & Simpson, B. B. (1995) Systematics and character evolution of the genus *Yucca* L. (*Agavaceae*): Evidence from morphology and molecular analyses. Bol. Soc. Bot. México 56: 77–88. <https://doi.org/10.17129/botsci.1466>
- Cole, W. S. jr. [et al. 2017], James, A. S. & Smith, C. I. (2017) First recorded observations of pollination and oviposition behavior in *Tegeticula antithetica* (*Lepidoptera: Prodoxidae*) suggest a functional basis for coevolution with Joshua Tree (*Yucca*) hosts. Ann. Entomol. Soc. Amer. 110(4): 390–397. <https://doi.org/10.1093/aesa/sax037>
- Crabb, B. A. & Pellmyr, O. (2006) Impact of the third trophic level in an obligate mutualism: Do *Yucca* plants benefit from parasitoids of *Yucca* Moths?. Int. J. Pl. Sci. 167(1): 119–124. <https://doi.org/10.1086/497844>
- Darwell, C. T. & Althoff, D. M. (2017) The relative contributions of competition and abiotic tolerances in determining the geographical distributions of four closely related *Yucca* species in Texas. J. Biogeogr. 44(6): 1373–1382, maps. <https://doi.org/10.1111/jbi.12907>
- Davis, D. R. (1967) A revision of the moths of the subfamily *Prodoxinae* (*Lepidoptera: Incurvariidae*). Bull. US Nation. Mus. 255: 1–170. <https://doi.org/10.5479/si.03629236.255.1>
- Deleuil, J.-B. (1880) Hybridation des Yuccas. Rev. Hort. (Paris) 52: 225–227. <http://biodiversitylibrary.org/page/49743850>
- Diggs, G. M. [et al. 1999], Lipscomb, B. L. & O'Kennon, R. J. (1999) Shinners & Mahler's Illustrated Flora of North Central Texas. Fort Worth (US): Botanical Research Institute of Texas.
- Diggs, G. M. [et al. 2006], Lipscomb, B. L., Reed, M. D. & O'Kennon, R. J. (2006) Illustrated flora of East Texas. Volume 1: Introduction, pteridophytes, gymnosperms and monocotyledons. Fort Worth (US): Botanical Research Institute of Texas & Austin College.
- Doweld, A. B. (2013) Proposal to conserve the name *Lepidophloios* against *Yuccites* (fossil *Lycopodiophyta*, *Lepidodendropsida*). Taxon 62(4): 839–840. <https://doi.org/10.12705/624.18>
- Earle, H. (1964) *Yucca rigida*. Saguaro Bull. 18(4): 39–40, ills. <http://biodiversitylibrary.org/page/54633741>
- Earle, H. (1968) *Yucca intermedia* McKelvey. Saguaro Bull. 22(1): 8–9, ill. <http://biodiversitylibrary.org/page/54640217>
- Engelmann, G. (1871) *Yucca* and *Agave* [additions]. In: Watson, S. (ed.): United States Geological Exploration of the Fortieth Parallel. Clarence King. Botany; pp. 496–497. Washington D.C. (US): Government Printing Office. <https://biodiversitylibrary.org/page/6207964>
- Engelmann, G. (1873) Notes on the genus *Yucca*. Trans. Acad. Sci. St. Louis 3(1): 17–54. <https://biodiversitylibrary.org/page/26377690>
- Engelmann, G. (1874) Notes on the genus *Yucca*. No. 2. Trans. Acad. Sci. St. Louis 3(1): 210–214. <https://biodiversitylibrary.org/page/26377904>
- Espejo Serna, A. & López Ferrari, A. R. (1993) Las monocotiledoneas Mexicanas, una sinopsis florística: 1. Lista de referencias: parte 1. *Agavaceae*, etc. México D.F. (MX): Consejo Nacional de la Flora de México.
- Esque, T. C. [et al. 2015], Medica, P. A., Shryock, D. F., Falco, L. A. de, Webb, R. H. & Hunter, R. B. (2015) Direct and indirect effects of environmental variability on growth and survivorship of pre-reproductive Joshua Trees, *Yucca brevifolia* Engelm. (*Agavaceae*). Amer. J. Bot. 102(1): 85–91, ills. <https://doi.org/10.3732/ajb.1400257>
- Euro+Med (2006+) Euro+Med PlantBase—the information resource for Euro-Mediterranean plant diversity. Berlin (DE): <http://ww2.bgbm.org/EuroPlusMed/>
- Faber, H. (2015) *Yucca schottii*—viel zu selten in Kultur. Wüstengarten 5: 21–36, ills.
- Ferguson, D. J. (1996) *Yucca linearis*, a unique species from the Chihuahuan Desert. Cact. Succ. J. (US) 68(3): 130–133, ills.
- Fernald, M. L. (1944) Overlooked species, transfers and novelties in the flora of eastern North America. Contr. Gray Herb. 150: 1–57, tt. 807–816. <http://biodiversitylibrary.org/page/40456232>
- Ferrer-Gallego, P. P. [et al. 2015], Guillot Ortiz, D. & Laguna Lumbreras, E. (2015) Tipificación del nombre lineano *Yucca gloriosa* (*Agavaceae*). Acta Bot. Malacit. 40: 230–232. <http://hdl.handle.net/10630/11142>
- Fisher, J. B. (1975) Eccentric secondary growth in *Cordylina* and other *Agavaceae* (Monocotyledonae) and its correlation with auxin distribution. Amer. J. Bot. 62: 292–302. <https://doi.org/10.1002/j.1537-2197.1975.tb12356.x>
- Flores-Hernández, A. [et al. 2011], Hernández-Herrera, J. A., Madinaveitia-Rios, H., Valenzuela-Núñez, L. M., Murillo-Amador, B., Rueda-Puente, E. O., García Hernández, J. L. & Ortiz-Cano, H. G. (2011) Evaluación de la población natural y hábitat de palma azul (*Yucca rigida*) en Mapimí, Durango, México. Trop. subtrop. Agroecosystems 14(1): 315–321. <http://www.redalyc.org/articulo.oa?id=93915703031>
- Fontaine, P. (2013) Un seigneur mexicain extraordinaire: *Yucca filifera* Chabaud 1876. Terra Seca 2013(3): 32–41, ills, map.
- García-Mendoza, A. J. (2003) Revisión de las *Agavaceae* (sensu stricto), *Crassulaceae* y *Liliaceae* incluidas en el

- PROY-NOM-059-ECOL-2000. Mexico (MX): Jardín Botánico, Instituto de Biología, UNAM, Proyecto W020, bases de datos SNIB-CONABIO.
- García-Mendoza, A. J. (2011) Flora del Valle de Tehuacán-Cuicatlán. 88. *Agavaceae*. Mexico (MX): Instituto de Biología, UNAM.
- Gentry, H. S. (1972) The *Agave* family in Sonora. Agricultural handbook No. 399. Washington D.C. (US): US Department of Agriculture. <http://naldc.nal.usda.gov/download/CAT87209091/PDF>
- Glass, C. & Foster, R. (1986) Mexican logbook. Abbey Garden spring expedition 1970: April 11th—May 19th. *Cact. Succ. J. (US)* 58(2): 60–63, ills.
- Godsoe, W. [ & al. 2008], Yoder, J. B., Smith, C. I. & Pellmyr, O. (2008) Coevolution and divergence in the Joshua Tree / *Yucca* Moth mutualism. *Amer. Naturalist* 171(6): 816–823. <https://doi.org/10.1086/587757>
- Gómez-Pompa, A. [ & al. 1971], Villalobos-Pietrini, R. & Chimal, A. (1971) Studies in the *Agavaceae* I. Chromosome morphology and number of seven species. *Madroño* 21(4): 208–221, ills. <http://www.jstor.org/stable/41423783>
- Good-Avila, S. V. [ & al. 2006], Souza, V., Gaut, B. S. & Eguiarte, L. E. (2006) Timing and rate of speciation in *Agave* (*Agavaceae*). *Proc. Nation. Acad. Sci. USA* 103(24): 9124–9129. <https://doi.org/10.1073/pnas.0603312103>
- Govaerts, R. H. A. (comp.) (2014+) World checklist of selected plant families [continuously updated]. Richmond (GB): Trustees of the Royal Botanic Gardens, Kew. <http://apps.kew.org/wcsp>
- Greulich, M. (2015) *Yucca endlichiana* Trelease in ihrem Habitat in der südlichen Sierra de la Paila. *Wüstengarten* 5: 3–12, ills.
- Groman, J. D. & Pellmyr, O. (2000) Rapid evolution and specialization following host colonization in a *Yucca* Moth. *J. Evol. Biol.* 13: 223–236. <https://doi.org/10.1046/j.1420-9101.2000.00159.x>
- Guillot Ortiz, D. & Meer, P. van der (2003) Las familias *Agavaceae* y *Aloaceae* en la Comunidad Valenciana. *Flora Montiber.* 23: 29–43, keys. <http://dialnet.unirioja.es/servlet/articulo?codigo=1394791>
- Guillot Ortiz, D. & Meer, P. van der (2008) El género *Yucca* L. en España. *Monogr. Revista Bouteloua* 2: 124 pp., ills., key.
- Hammel, B. E. [ & al. 2003], Grayum, M. H., Herrera, C. & Zamora, N. (eds.) (2003) Manual de plantas de Costa Rica. Vol. II. Gimnospermas y Monocotiledoneas (*Agavaceae*—*Musaceae*). St. Louis (US): Missouri Botanical Garden. <http://biodiversitylibrary.org/page/772431>
- Hart, A. (1977) *Yucca endlichiana* Trelease. *Ashingtonia* 2 (10): 216, ill.
- Hawker, J. L. (2016) Agaves, Yuccas and their kin. Seven genera of the Southwest, including the genera *Agave*, *Dasyllirion*, *Hechtia*, *Hesperaloe*, *Hesperoyucca*, *Nolina* and *Yucca*. Lubbock (US): Texas Tech University Press.
- Heim, A. (2011) *Yucca linearifolia*, eine für Mitteleuropa vielversprechende stammbildende Art. *Avonia* 29(3): 95–102, ills.
- Heim, A. (2012) *Yucca recurvifolia* × *thompsoniana* (ex “thompsonifolia”). Eine äusserst gartenwürdige Hybride. *Wüstengarten* 3: 56–60, ills.
- Heim, A. & Lorek, M. (2008) Pflanzenporträt *Yucca gloriosa*. *Hort. Exot.* 7: 3–5, ills.
- Hess, W. J. & Robbins, R. L. (2002) *Yucca* Linnaeus. In: *Flora of North America North of Mexico*, Volume 26: *Magnoliophyta: Liliidae: Liliales and Orchidales*; pp. 423–439, ills., key. New York (US)/Oxford (GB): Oxford University Press.
- Heyduk, K. [ & al. 2016], McKain, M. R., Lalani, F. & Leebens-Mack, J. (2016) Evolution of a CAM anatomy predates the origins of Crassulacean Acid Metabolism in the *Agavoideae* (*Asparagaceae*). *Molec. Phylogen. Evol.* 105: 102–113, ills. <https://doi.org/10.1016/j.ympev.2016.08.018>
- Hochstätter, F. (1998) Het geslacht *Yucca* (*Agavaceae*). Deel 1 / Deel 2. *Succulenta* 77(2): 69–84, (5): 220–229, ills., map, key.
- Hochstätter, F. (1999) Het geslacht *Yucca* (*Agavaceae*). Deel 2 (vervolg) / Deel 3 / Deel 4. *Succulenta* 78(1): 24–34, (3): 120–129, (5): 207–218, ills., maps, keys.
- Hochstätter, F. (2000) *Yucca* I (*Agavaceae*) in the southwest and midwest of the USA and Canada. Mannheim (DE): Published by the author.
- Hochstätter, F. (2001a) *Yucca* L. (*Agavaceae*): Vom Atlantik zu den Smoky Mountains und Blue Ridge. *Kaktusblüte* 2001: 7–12, ills.
- Hochstätter, F. (2001b) Het geslacht *Yucca* (*Agavaceae*). 7. Serie *Treculeana* McKelvey. *Succulenta* 80(2): 78–85, (3): 129–133, ills., maps.
- Hochstätter, F. (2002a) *Yucca* II (*Agavaceae*). Indehiscent-fruited species in the southwest, midwest and east of the USA. Mannheim (DE): Published by the author.
- Hochstätter, F. (2002b) The series of the genus / Die Serien von Genus *Yucca* L. (*Agavaceae*). *Cactaceae Rev.* 5(1): 17–20, ills.
- Hochstätter, F. (2002c) Het geslacht *Yucca* (*Agavaceae*). 10. Serie *Filamentosae*. *Succulenta* 81(1): 36–43, ills., key.
- Hochstätter, F. (2002d) Het geslacht *Yucca* (*Agavaceae*). 11. Serie *Gloriosae*. *Succulenta* 81(2): 89–94, ills., key; (3): 135 [erratum].
- Hochstätter, F. (2003a) Het geslacht *Yucca* (*Agavaceae*). Deel 12. *Yucca*'s in Mexico 1. *Succulenta* 82(1): 19–22, (2): 66–69, ills.
- Hochstätter, F. (2003b) Het geslacht *Yucca* (*Agavaceae*). Deel 13. *Yucca*'s in Mexico 2. *Succulenta* 82(3): 110–116, ills.
- Hochstätter, F. (2003c) Het geslacht *Yucca* (*Agavaceae*). Deel 14. *Yucca*'s in Mexico 3. *Succulenta* 82(4): 151–155, ills.
- Hochstätter, F. (2003d) Het geslacht *Yucca* (*Agavaceae*). Deel 15. *Yucca*'s in Mexico 4. *Succulenta* 82(5): 209–214, ills.

- Hochstätter, F. (2003e) Het geslacht *Yucca* (*Agavaceae*). Deel 16. *Yucca*'s in Mexico 5. *Succulenta* 82(6): 264–268, ill.
- Hochstätter, F. (2004a) *Yucca* III (*Agavaceae*). Mexico. Mannheim (DE): Published by the author.
- Hochstätter, F. (2004b) Het geslacht *Yucca* (*Agavaceae*). Deel 17. *Yucca*'s in Mexico 6. *Succulenta* 83(1): 39–41, ill.
- Hochstätter, F. (2008a) The smallest of the Bayonet plants. *CactusWorld* 26(2): 100–102, ill., key.
- Hochstätter, F. (2008b) *Yucca* news. *CactusWorld* 26(4): 233–236, ill.
- Hochstätter, F. (2009) Die kleinste der Bayonet-Pflanzen. Sektion *Endlichiana*. Eine Revision der kleinsten und sukkulentesten *Yucca*. *Kaktusblüte* 26: 48–50, ill.
- Hodgson, W. C. (2001) Food plants of the Sonoran Desert. Tucson (US): University of Arizona Press.
- Howes, F. N. (1946) Fence and barrier plants in warm climates. *Kew Bull.* 1(2): 51–87. <https://doi.org/10.2307/4109287>
- Hoxey, P. (2011) Lunch in the field. *Cact. Explorer* 1: 31–33, ill.
- Humphries, S. A. & Addicott, J. F. (2000) Regulation of the mutualism between *Yuccas* and *Yucca* Moths: Intrinsic and extrinsic factors affecting flower retention. *Oikos* 89(2): 329–339. <https://doi.org/10.1034/j.1600-0706.2000.890214.x>
- Hurrell, J. A. & Delucchi, G. (2009) *Agavaceae*. In: Hurrell, J. A. (ed.): *Flora Rioplatense. Sistemática, ecología y etnobotánica de las plantas vasculares rioplatenses. Parte 3 (Monocotiledóneas)*. Vol. 4; pp. 19–34. Buenos Aires (RA): Lola.
- Irish, M. & Irish, G. (2000) *Agaves, Yuccas and related plants. A gardener's guide*. Portland (US): Timber Press.
- James, C. D. [ & al. 1993], Hoffman, M. T., Lightfoot, D. C., Forbes, G. S. & Whitford, W. G. (1993) Pollination ecology of *Yucca elata*. *Oecologia* 93(4): 512–517. <https://doi.org/10.1007/BF00328959>
- Jensen, B. M. (2015) *Yucca* 'Anna', a new hybrid. *CactusWorld* 33(1): 15–18, ill.
- Jensen, B. M. (2018) Carl Sprenger (1846–1917). <http://www.bennyskaktus.dk/sprenger.htm>, accessed Dec. 2018.
- Johnson, M. B. (2000) Observations on some Chihuahuan Desert *Yuccas*. *Desert Pl.* 16(1): 14–19, ill. <http://repository.arizona.edu/handle/10150/554328>
- Karpov, P. (2004) Clonal propagation of *Yucca aloifolia* L. *Acta Univ. Latviensis, Biol.* 676: 177–182. <https://doi.org/10.13140/2.1.1355.9365>
- Kartesz, J. T. (1996) A synonymized checklist for the vascular flora of the United States, Canada, and Greenland. Internet version. Electronically published by the Biota of North America Program of the North Carolina Botanical Garden; <http://ils.unc.edu/botanical/gardens.html>, but no longer accessible as of December 2018.
- Keith, E. L. (2003) *Yucca cernua* (*Agavaceae*: series *Rupicola*), a new species from Newton and Jasper counties in eastern Texas. *Sida* 20(3): 891–898, ill., key. <http://www.jstor.org/stable/41968120>
- Kemp, P. R. & Gardetto, P. E. (1982) Photosynthetic pathway types of evergreen rosette plants (*Liliaceae*) of the Chihuahuan Desert. *Oecologia* 55(2): 149–156. <https://doi.org/10.1007/BF00384480>
- Koch, K. (1873) Die Mondblumen oder Yukken. Ein monographischer Versuch. *Monatsschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten* 16(5): 204–222. <http://biodiversitylibrary.org/page/33737728>
- Laferrière, J. E. (1990) The taxonomy and ethnobotany of *Yucca madrensis*. *Cact. Succ. J. (US)* 62(2): 95–96, ill.
- Lenz, L. W. (1992) An annotated catalogue of the plants of the Cape region, Baja California Sur, Mexico. Claremont (US): The Cape Press.
- Lenz, L. W. (1998) *Yucca capensis* (*Agavaceae*, *Yuccoideae*), a new species from Baja California Sur, Mexico. *Cact. Succ. J. (US)* 70(6): 289–296, ill., map.
- Lenz, L. W. (2007) Reassessment of *Yucca brevifolia* and recognition of *Yucca jaegeriana* as a distinct species. *Aliso* 24: 97–104, ill., maps. <https://doi.org/10.5642/aliso.20072401.07>
- Lenz, L. W. & Hanson, M. A. (2000) Typification and change in status of *Yucca schottii* (*Agavaceae*). *Aliso* 19(1): 93–98, ill. <https://doi.org/10.5642/aliso.20001901.07>
- Lenz, L. W. & Hanson, M. A. (2001) *Yuccas* (*Agavaceae*) of the international Four Corners: Southwestern USA and northwestern Mexico. *Aliso* 19(2): 165–179, maps, ill. <https://doi.org/10.5642/aliso.20001902.04>
- López-Pujol, J. & Guillot Ortiz, D. (2014a) Primeras citas de *Yucca recurvifolia* Salisb. en Cataluña, y una nueva cita de *Yucca gloriosa* L. *Bouteloua* 19: 95–98, ill.
- López-Pujol, J. & Guillot Ortiz, D. (2014b) *Yucca gigantea* Lem., primeras citas en Cataluña, y área potencial de naturalización en la Península Ibérica e Islas Baleares. *Bouteloua* 19: 212–220, ill., map.
- López-Ramírez, Y. [ & al. 2018], Palomeque-Carlín, A., Ortiz, L. I. C., Rosa, M. D. L. de la & Pérez-Molphe-Balch, E. (2018) Micropropagation of *Yucca* species. In: Loyola-Vargas, V. M. & Ochoa-Alejo, N. (eds.): *Plant cell culture protocols*; pp. 171–177. New York (US): Humana Press. [https://doi.org/10.1007/978-1-4939-8594-4\\_10](https://doi.org/10.1007/978-1-4939-8594-4_10)
- Lott, E. J. & García-Mendoza, A. (1994) *Agavaceae*. In: Davidse, G. & al. (eds.): *Flora Mesoamericana*, Volumen 6, *Alismataceae a Cyperaceae*; pp. 35–47, keys. México (MX): UNAM, Instituto de Biología / St. Louis (US): Missouri Botanical Garden / London (GB): Natural History Museum. <http://www.tropicos.org/Project/FM>
- Luna Ortiz, P. A. (2018) Diversidad genética de *Yucca capensis* (*Asparagaceae*), planta endémica de la Sierra de la Laguna. Ensenada (MX): Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California; M.Sc thesis.
- Magallán Hernández, F. [ & al. 2013a], Maruri Aguilar, B., Sánchez Martínez, E. & Hernández-Sandoval, L. (2013a) Rareza y belleza del estoquillo, una especie de *Yucca* endémica del semidesierto queretanihualguense. *Biodiversitas* 109: 7–11, ill.

- Magallán Hernández, F. [ & al. 2013b], Maruri Aguilar, B., Sánchez Martínez, E., Hernández-Sandoval, L., Robledo-Mejía, M. & Hernández-Martínez, M. (2013b) Evaluación del estado de conservación, uso y amenazas de *Yucca queretaroensis* Piña (*Agavaceae*) y la pertinencia de incluirla en los Apéndices de la CITES. Informe final, CONABIO proyecto JE005. Cadereyta (MX): Consejo de Ciencia y Tecnología de Querétaro, Jardín Botánico Regional de Cadereyta “Ing. Manuel González de Cosío”.
- Magallán Hernández, F. [ & al. 2014], Maruri Aguilar, B., Sánchez Martínez, E., Hernández-Sandoval, L., Luna-Zúñiga, J. & Robledo-Mejía, M. (2014) Consideraciones taxonómicas de *Yucca queretaroensis* Piña (*Agavaceae*), una especie endémica del semi-desierto Queretano-Hidalguense. *Acta Bot. Mex.* 108: 51–66, ills. <https://doi.org/10.21829/abm108.2014.196>
- Marr, D. L. & Pellmyr, O. (2003) Effect of pollinator-inflicted ovule damage on floral abscission in the *Yucca*-*Yucca* Moth mutualism: The role of mechanical and chemical factors. *Oecologia* 136(2): 236–243. <https://doi.org/10.1007/s00442-003-1279-3>
- Martin, P. S. [ & al. 1998], Yetman, D., Fishbein, M. E., Jenkins, P. D., Devender, T. R. Van & Wilson, R. K. (eds.) (1998) *Gentry's Rio Mayo plants: The tropical deciduous forest and environs of northwest Mexico*. Tucson (US): University of Arizona Press.
- Martin, W. C. & Hutchins, C. R. (1980) *A flora of New Mexico*. Volume 1. Vaduz (FL): J. Cramer.
- Massey, L. S. & Hamrick, J. L. (1998) Genetic diversity and population structure of *Yucca filamentosa* (*Agavaceae*). *Amer. J. Bot.* 85(3): 340–345. <https://doi.org/10.2307/2446326>
- Mattern, R. (1999) Auf der Suche nach *Yucca nana*. *Kakt. and. Sukk.* 50(5): 107–108, ills.
- Matuda, E. & Piña Luján, I. (1980) Las plantas mexicanas del género *Yucca*. Toluca (MX): Miscelanea Estado de México.
- Mays, H. (2005) Sukkulente aus den Huntington Botanical Gardens. *Avonia* 23: 44–47, ills. (incl. front cover).
- McKain, M. R. [ & al. 2016], McNeal, J. R., Kellar, P. R., Eguiarte, L. E., Pires, J. C. & Leebens-Mack, J. (2016) Timing of rapid diversification and convergent origins of active pollination within *Agavoideae* (*Asparagaceae*). *Amer. J. Bot.* 103(10): 1717–1729. <https://doi.org/10.3732/ajb.1600198>
- McKelvey, S. D. (1935) Notes on *Yucca*. *J. Arnold Arbor.* 16(2): 268–271. <http://www.jstor.org/stable/43782276>
- McKelvey, S. D. (1938) *Yuccas of the Southwestern United States*. Part I. Jamaica Plain (US): Arnold Arboretum of Harvard University.
- McKelvey, S. D. (1947) *Yuccas of the Southwestern United States*. Part II. Jamaica Plain (US): Arnold Arboretum of Harvard University.
- McKelvey, S. D. & Sax, K. (1933) Taxonomic and cytological relationships of *Yucca* and *Agave*. *J. Arnold Arbor.* 14: 76–81. <https://www.jstor.org/stable/43780651>
- McKinney, K. K. & Hickman, J. C. (1993) *Yucca*. In: Hickman, J. C. (ed.): *The Jepson Manual*. Higher plants of California; p. 1210. Berkeley etc. (US): University of California Press.
- McVaugh, R. (1989) *Flora Novo-Galiciana*. A descriptive account of the vascular plants of Western Mexico. Vol. 15: *Bromeliaceae* to *Dioscoreaceae*. Ann Arbor (US): University of Michigan Herbarium.
- Mitich, L. W. (1977) Uses of the genus *Yucca*. *Excelsa* 7: 45–56, ills.
- Morales-Rangel, A. [ & al. 2015], Cambrón-Sandoval, V. H., Bustos-Ulloa, D., Villegas-Olguín, M. A., Malda-Barrera, G. & Suzán-Azpiri, H. (2015) Ensayo de densidades de plantación en procedencias de *Yucca filifera* Chabaud en jardín común. *Cact. Suc. Mex.* 60(4): 100–111, ills.
- Neese, E. & Welsh, S. L. (1986) New variety of *Yucca harrimaniae* (*Agavaceae*) from Utah. *Great Basin Naturalist* 45(4): 789–790. <http://biodiversitylibrary.org/page/8885711>
- North, G. B. & Baker, E. A. (2007) Water uptake by older roots: Evidence from desert succulents. *HortScience* 42(5): 1103–1106.
- North, G. B. [ & al. 2004], Martre, P. & Nobel, P. S. (2004) Aquaporins account for variations in hydraulic conductance for metabolically active root regions of *Agave deserti* in wet, dry, and rewetted soil. *Pl. Cell Environm.* 27(2): 219–228. <https://doi.org/10.1111/j.1365-3040.2003.01137.x>
- North, G. B. [ & al. 2008], Brinton, E. K. & Garrett, T. Y. (2008) Contractile roots in succulent monocots: Convergence, divergence and adaptation to limited rainfall. *Pl. Cell Environm.* 31: 1179–1189, ills. <https://doi.org/10.1111/j.1365-3040.2008.01832.x>
- Ondrovic, R. & Ondrovic, S. (2016) *Yucca*. Vorkommen, Bestimmen und Pflegen aller Arten aus Nordamerika. Remagen-Oberwinter (DE): Verlag Kessel.
- Ondrovic, S. (2018) Im Land der Gummistiefel. Ein Besuch bei *Yucca elephantipes*. *Avonia* 36(4): 234–239, ills.
- Patel, S. (2012) *Yucca*: A medicinally significant genus with manifold therapeutic attributes. *Nat. Prod. & Bioprospect.* 2(6): 231–234. <https://doi.org/10.1007/s13659-012-0090-4>
- Pellmyr, O. (2003) *Yuccas, Yucca Moths, and coevolution: A review*. *Ann. Missouri Bot. Gard.* 90(1): 35–55, ills., map. <https://doi.org/10.2307/3298524>
- Pellmyr, O. (2012) Pollen load in an active pollinator, the *Yucca* Moth *Tegeticula yuccasella* (*Prodoxidae*). *J. Lepidopterists' Soc.* 66(1): 50–51, ill. <https://doi.org/10.18473/lepi.v66i1.a5>
- Pellmyr, O. & Huth, C. J. (1994) Evolutionary stability of mutualism between *Yuccas* and *Yucca* Moths. *Nature (London)* 372(6503): 257–260. <https://doi.org/10.1038/372257a0>
- Pellmyr, O. & Leebens-Mack, J. (1999) Forty million years of mutualism: Evidence for Eocene origin of the *Yucca*—*Yucca* Moth association. *Proc. Nation. Acad. Sci. USA* 96(16): 9178–9183. <https://doi.org/10.1073/pnas.96.16.9178>
- Pellmyr, O. & Segaves, K. A. (2003) Pollinator divergence within an obligate mutualism: Two *Yucca* Moth



- species (*Lepidoptera*; *Prodoxidae*: *Tegeticula*) on the Joshua Tree (*Yucca brevifolia*; *Agavaceae*). *Ann. Entomol. Soc. Amer.* 96(6): 716–722, ills., map. [https://doi.org/10.1603/0013-8746\(2003\)096\[0716:PDWAOM\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2003)096[0716:PDWAOM]2.0.CO;2)
- Pellmyr, O. [et al. 2007], Segraves, K. A., Althoff, D. M., Balcázar-Lara, M. & Leebens-Mack, J. (2007) The phylogeny of *Yuccas*. *Molec. Phylogen. Evol.* 43: 493–501, map. <https://doi.org/10.1016/j.ympev.2006.12.015>
- Pellmyr, O. [et al. 2008], Balcázar-Lara, M., Segraves, K. A., Althoff, D. M. & Littlefield, R. J. (2008) Phylogeny of the pollinating *Yucca* Moths, with revision of Mexican species (*Tegeticula* and *Parategeticula*; *Lepidoptera*, *Prodoxidae*). *Zool. J. Linn. Soc.* 152(2): 297–314, ills. <https://doi.org/10.1111/j.1096-3642.2007.00361.x>
- Perry, J. C. [et al. 2004], Mondor, E. B. & Addicott, J. F. (2004) An indirect mutualism: Ants deter seed predators for ovipositing in *Yucca* fruit. *Canad. J. Zool.* 82(5): 823–827. <https://doi.org/10.1139/z04-039>
- Piña Luján, I. (1980) Geographic distribution of the genus *Yucca*. *Cact. Succ. J. (US)* 52(6): 277–281, ills.
- Piña Luján, I. (1990) Nuevas aportaciones a *Yucca queretaroensis* Piña sp. nov. *Cact. Suc. Mex.* 35(3): 61–62, ills.
- Pinkava, D. J. & Baker, M. A. (1985) Chromosome and hybridization studies of *Agaves*. *Desert Pl.* 7(2): 93–100, ills. <http://repository.arizona.edu/handle/10150/554212>
- Potter-Bassano, G. (1991) *Yucca baccata*: From the beginning. *Arid Lands Newslett.* 31(fall): 24–29, ills. <http://hdl.handle.net/10150/228186>
- Powell, J. A. (1984) Biological interrelationships of moths and *Yucca schottii*. Los Angeles (US): University of California Press.
- Powell, J. A. (2001) Longest insect dormancy: *Yucca* Moth larvae (*Lepidoptera*: *Prodoxidae*) metamorphose after 20, 25, and 30 years in diapause. *Ann. Entomol. Soc. Amer.* 94(5): 677–680. [https://doi.org/10.1603/0013-8746\(2001\)094\[0677:LIDYML\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2001)094[0677:LIDYML]2.0.CO;2)
- Powell, J. A. & Mackie, R. A. (1966) Biological interrelationships of moths and *Yucca whipplei*. *Univ. Calif. Publ. Entomol.* 42: 1–59.
- Proctor, G. R. & Acevedo-Rodríguez, P. (2005) *Agavaceae*. In: Acevedo-Rodríguez, P. & Strong, M. T. (eds.): *Monocotyledons and Gymnosperms of Puerto Rico and the Virgin Islands*; pp. 116–125. Washington D.C. (US): Department of Botany, National Museum of Natural History. <http://www.fs.usda.gov/treesearch/pubs/30275>
- Rebman, J. P. [et al. 2016], Gibson, J. & Rich, K. (2016) Annotated checklist of the vascular plants of Baja California, Mexico. *Proc. San Diego Soc. Nat. Hist.* 45: 1–352, map.
- Rentsch, J. D. & Leebens-Mack, J. (2012) Homoploid hybrid origin of *Yucca gloriosa*: Intersectional hybrid speciation in *Yucca* (*Agavoideae*, *Asparagaceae*). *Ecol. & Evol.* 2(9): 2213–2222, ills., map. <https://doi.org/10.1002/ece3.328>
- Rentsch, J. D. & Leebens-Mack, J. (2014) *Yucca aloifolia* (*Asparagaceae*) opts out of an obligate pollination mutualism. *Amer. J. Bot.* 101(12): 2062–2067, ills. <https://doi.org/10.3732/ajb.1400351>
- Reveal, J. L. (1977) *Agavaceae*. In: Cronquist, A. & al. (eds.): *Intermountain Flora*, 6: 526–538, ills., keys. New York (US): The New York Botanical Gardens/Columbia University Press.
- Reynolds, M. B. J. [et al. 2012], DeFalco, L. A. & Esque, T. C. (2012) Short seed longevity, variable germination conditions, and infrequent establishment events provide a narrow window for *Yucca brevifolia* (*Agavaceae*) recruitment. *Amer. J. Bot.* 99(10): 1647–1654, ills. <https://doi.org/10.3732/ajb.1200099>
- Riha, J. (2013) [Czech:] *Yucca endlichiana* Trelease—Patilla *Yucca* of the Desierto de Chihuahua. *Kaktusy* 49(3): 102–105, ills.
- Riley, C. V. (1872) The fertilization of the *Yucca* plant by *Pronuba yuccasella*. *Canad. Entomol.* 4(10): 182. <https://biodiversitylibrary.org/page/30569177>
- Riley, C. V. (1873) On a new genus in the Lepidopterous family *Tineidae*, with remarks on the fertilization of *Yucca*. *Trans. Acad. Sci. St. Louis* 3: 55–64, ills. <https://biodiversitylibrary.org/page/26377749>
- Riley, C. V. (1874) On the oviposition of the *Yucca* Moth. *Trans. Acad. Sci. St. Louis* 3(14): 208–209. <https://biodiversitylibrary.org/page/26377902>
- Riley, C. V. (1878) Further remarks on *Pronuba yuccasella* and on the pollination of *Yucca*. *Trans. Acad. Sci. St. Louis* 3: 568–573. <https://biodiversitylibrary.org/page/26378272>
- Riley, C. V. (1880) The true and bogus *Yucca* Moth, with remarks on the pollination of *Yucca*. *Amer. Entomol.* 3: 141–145. <https://biodiversitylibrary.org/page/49962573>
- Riley, C. V. (1881) Further notes on the pollination of *Yucca* and on *Pronuba* and *Prodoxus*. *Proc. Amer. Assoc. Advancem. Sci.* 29: 617–739.
- Riley, C. V. (1892) The *Yucca* Moth and *Yucca* pollination. Part I. Part II. *Annual Rep. Missouri Bot. Gard.* 3: 99–158, tt. 34–43. <https://biodiversitylibrary.org/page/675451>
- Robbins, R. L. (1983) A systematic study of indehiscent-fruited *Yuccas* in the Chihuahuan Desert. Lubbock (US): Texas Tech University; Ph.D. thesis.
- Robbins, R. L. (2001) *Agavaceae*. In: Steven, W. D. & al. (eds.): *Flora de Nicaragua*, *Introducción*, *Gimnospermas y Angiospermas* (*Acanthaceae—Euphorbiaceae*); pp. 41–47. St. Louis (US): Missouri Botanical Garden. <http://www.tropicos.org/Name/42000378?projectId=7>
- Rocha, M. [et al. 2006], Good-Ávila, S. V., Molina-Freaner, F., Arita, H. T., Castillo, A., García-Mendoza, A., Silva-Montellano, A., Gaut, B. S., Souza, V. & Eguiarte, L. E. (2006) Pollination biology and adaptive radiation of *Agavaceae*, with special emphasis on the genus *Agave*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 329–344, maps. <https://doi.org/10.5642/aliso.20062201.27>
- Roosbroeck, J. van (2017) *Yucca lacandonica*. *Enkele wetenswaardigheden. Succulenta* 69(2): 71–72, ills.



- Royer, A. M. [& al. 2016], Streisfeld, M. A. & Smith, C. I. (2016) Population genomics of divergence within an obligate pollination mutualism: Selection maintains differences between Joshua Tree species. *Amer. J. Bot.* 103(10): 1730–1741, map, ills. <https://doi.org/10.3732/ajb.1600069>
- Sáez, L. [& al. 2016], Serapio, J., Gómez-Bellver, C., Ardenghi, N. M., Guillot, D. & Rita, J. (2016) New records in vascular plants alien to the Balearic Islands. *Orsis* 30: 101–131. <https://doi.org/10.5565/rev/orsis.38>
- Satô, D. (1935) Analysis of the karyotypes in *Yucca*, *Agave* and the related genera with special reference to the phylogenetic significance. *Jap. J. Genet.* 1: 272–278.
- Schneckenburger, S. (2001) Carl Albert Purpus (1851–1941). Ein deutscher Pflanzensammler in Amerika. Darmstadt (DE): Technische Universität Darmstadt.
- Schönherr, W. (2017) *Yucca nana* oder *Yucca harri-maniana*?—Standortbetrachtungen. *Wüstengarten* 7: 31–46, ills., map.
- Segraves, K. A. (2008) Florivores limit cost of mutualism in the *Yucca*—*Yucca* Moth association. *Ecology* 89(11): 3215–3221, ills. <https://doi.org/10.1890/07-1993.1>
- Segraves, K. A. [& al. 2005], Althoff, D. M. & Pellmyr, O. (2005) Limiting cheaters in mutualism: Evidence from hybridization between mutualist and cheater *Yucca* Moths. *Proc. Roy. Soc., Biol. Sci., Ser. B*, 272: 2195–2201, ills., map. <https://doi.org/10.1098/rspb.2005.3201>
- Sheldon, S. (1980) Ethnobotany of *Agave lechuguilla* and *Yucca carnerosana* in Mexico's Zona Ixtlera. *Econ. Bot.* 34(4): 376–390. <https://doi.org/10.1007/BF02858314>
- Shreve, F. & Wiggins, I. L. (1964) *Vegetation and flora of the Sonoran Desert*. Vols. I+II. Stanford (US): Stanford University Press.
- Sivinski, R. (2008) Some observations on the dry, dehiscent-fruited *Yuccas* in New Mexico. *New Mexico Botanist* 43: 1–4. <https://www.npsnm.org/pubpdfs/43.pdf>
- Smith, C. (2004) *Yuccas: Giants among the Lilies*. Working (GB): National Council for the Conservation of Plants and Gardens.
- Smith, C. I. [& al. 2008a], Pellmyr, O., Althoff, D. M., Balcázar-Lara, M., Leebens-Mack, J. & Segraves, K. A. (2008a) Pattern and timing of diversification in *Yucca* (*Agavaceae*): Specialized pollination does not escalate rates of diversification. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 275: 249–258. <https://doi.org/10.1098/rspb.2007.1405>
- Smith, C. I. [& al. 2008b], Godsoe, W. K. W., Tank, S., Yoder, J. B. & Pellmyr, O. (2008b) Distinguishing coevolution from covariation in an obligate pollination mutualism: Asynchronous divergence in Joshua Tree and its pollinators. *Evolution* 62(10): 2676–2687. <https://doi.org/10.1111/j.1558-5646.2008.00500.x>
- Smith, G. F. & Figueiredo, E. (2016) Widely cultivated, large-growing *Yuccas*: Notes on *Yucca elephantipes* Regel ex Trel., *Yucca gigantea* Lem., and *Yucca guatemalensis* Baker (*Agavaceae*). *Bradleya* 34: 28–37, ills. <https://doi.org/10.25223/brad.n34.2016.a18>
- Smith, G. F. [& al. 2012], Figueiredo, E. & Crouch, N. R. (2012) A first record of *Yucca aloifolia* L. (*Agavaceae* / *Asparagaceae*) naturalized in South Africa with notes on its uses and reproductive biology. *Haseltonia* 17: 87–93, ills., map. <https://doi.org/10.2985/1070-0048-17.1.11>
- Smith, S. D. & Ludwig, J. A. (1976) Reproductive and vegetative growth patterns in *Yucca elata* Engelm. (*Liliaceae*). *Southw. Naturalist* 21(2): 177–184. <http://www.jstor.org/stable/3669953>
- Snell, R. S. & Addicott, J. F. (2008a) Direct and indirect effects of ants on seed predation in moth / *Yucca* mutualisms. *Ecoscience* 15(3): 305–314. <https://doi.org/10.2980/15-3-3116>
- Snell, R. S. & Addicott, J. F. (2008b) Limiting the success of stem borers (*Prodoxus quinquepunctellus*) in *Yuccas*: Indirect effects of ants, aphids, and fruit position. *Ecol. Entomol.* 33(1): 119–126. <https://doi.org/10.1111/j.1365-2311.2007.00946.x>
- Sorrie, B. A. & LeBlond, R. J. (2008) Noteworthy collections from the southeastern United States. *J. Bot. Res. Inst. Texas* 2(2): 1353–1361. <http://www.jstor.org/stable/41971783>
- Spracklin, P. (2015) *Yucca queretaroensis* × *filifera* Naturhybriden? *Wüstengarten* 5: 59–64, ills.
- Sprenger, C. (1920a) Mitteilungen über meine *Yucca*-Hybriden und -Formen, gezüchtet in den Jahren 1897 bis 1907. *Mitt. Deutsch. Dendrol. Ges.* 29: 96–138, tt. 21–22. <http://biodiversitylibrary.org/page/14076617>
- Sprenger, C. (1920b) Beobachtungen an einigen *Yucca*-Arten. *Mitt. Deutsch. Dendrol. Ges.* 29: 138–149. <http://biodiversitylibrary.org/page/14076661>
- Starr, G. (2000) Intriguing Chihuahuan Desert *Yuccas* in cultivation. *Desert Pl.* 16(1): 10–13, ills. <http://repository.arizona.edu/handle/10150/554339>
- Starr, T. N. [& al. 2013], Gadek, K. E., Yoder, J. B., Flatz, R. & Smith, C. I. (2013) Asymmetric hybridization and gene flow between Joshua Trees (*Agavaceae*: *Yucca*) reflect differences in pollinator host specificity. *Molec. Ecol.* 22: 437–449, maps. <https://doi.org/10.1111/mec.12124>
- Stevenson, D. W. (1980) Radial growth in *Beaucarnea recurvata*. *Amer. J. Bot.* 67(4): 476–489. <http://www.jstor.org/stable/2442287>
- Svensson, G. P. [& al. 2005], Hickman jr, M. O., Bartram, S., Boland, W., Pellmyr, O. & Raguso, R. A. (2005) Chemistry and geographic variation of floral scent in *Yucca filamentosa* (*Agavaceae*). *Amer. J. Bot.* 92(10): 1624–1631. <https://doi.org/10.3732/ajb.92.10.1624>
- Svensson, G. P. [& al. 2006], Pellmyr, O. & Raguso, R. A. (2006) Strong conservation of floral scent composition in two allopatric *Yuccas*. *J. Chem. Ecol.* 32(12): 2657–2665, map. <https://doi.org/10.1007/s10886-006-9189-6>
- Svensson, G. P. [& al. 2011], Pellmyr, O. & Raguso, R. A. (2011) Pollinator attraction to volatiles from virgin and pollinated host flowers in a *Yucca* / moth obligate mutualism. *Oikos* 120(10): 1577–1583. <https://doi.org/10.1111/j.1600-0706.2011.19258.x>
- Szarek, S. R. & Troughton, J. H. (1976) Carbon isotope ratios in Crassulacean Acid Metabolism plants. *Pl. Physiol. (Lancaster)* 58: 367–370. <https://doi.org/10.1104/pp.58.3.367>

- Tidwell, W. D. & Parker, L. R. (1990) *Protoyucca shadishii* gen. et sp. nov., an arborescent monocotyledon with secondary growth from the middle Miocene of north-western Nevada, USA. *Rev. Palaeobot. Palynol.* 62 (1–2): 79–96. [https://doi.org/10.1016/0034-6667\(90\)90018-E](https://doi.org/10.1016/0034-6667(90)90018-E)
- Trelease, W. (1898) Miscellaneous observations on *Yucca*. *Annual Rep. Missouri Bot. Gard.* 9: 141–146, tt. 40–43. <http://biodiversitylibrary.org/page/676433>
- Trelease, W. (1902) The *Yuccaeae*. *Annual Rep. Missouri Bot. Gard.* 13: 27–133, tt. 1–99. <https://doi.org/10.5962/bhl.title.20018>
- Trelease, W. (1907) Additions to the genus *Yucca*. *Annual Rep. Missouri Bot. Gard.* 18: 225–230, 6 tt. <http://www.biodiversitylibrary.org/item/15221#page/236/>
- Trelease, W. & Gray, A. (eds.) (1887) The botanical works of the late George Engelmann. Edited by W. Trelease and A. Gray, collected for Henry Shaw. Cambridge (US): John Wilson & Son, University Press. <https://doi.org/10.5962/bhl.title.95463>
- Tröger, A. [et al. 2019], Svensson, G. P., Althoff, D. M., Segraves, K. A., Raguso, R. A. & Francke, W. (2019) The pattern of straight chain hydrocarbons released by *Yucca* flowers (*Asparagaceae*). *J. Chem. Ecol.* 45 (1): 46–49. <https://doi.org/10.1007/s10886-018-1037-y>
- Turner, R. M. [et al. 1995], Bowers, J. E. & Burgess, T. L. (1995) Sonoran Desert plants. An ecological atlas. Tucson (US): University of Arizona Press.
- Tyre, A. J. & Addicott, J. F. (1993) Facultative non-mutualistic behaviour by an “obligate” mutualist: “Cheating” by *Yucca* Moths. *Oecologia* 94(2): 173–175. <https://doi.org/10.1007/BF00341314>
- Ullrich, B. (1991) *Yucca desmetiana* Baker (*Agavaceae*). *Kakt. and. Sukk.* 42(10): centre page pullout 1991/30.
- USDA (2001) The PLANTS database. Baton Rouge (US): National Plant Data Center. Electronically published at <http://plants.usda.gov>
- Utah Native Plant Society (2003–2016) Utah rare plant guide (a work in progress). Salt Lake City (US): Utah Native Plant Society, published on the web at [http://www.utahrareplants.org/rpg\\_species.html](http://www.utahrareplants.org/rpg_species.html)
- Vander Wall, S. B. [et al. 2006], Esque, T., Haines, D., Garnett, M. & Waitman, B. A. (2006) Joshua Tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. *Ecoscience* 13(4): 539–543. [https://doi.org/10.2980/1195-6860\(2006\)13\[539:JTYBSA\]2.0.CO;2](https://doi.org/10.2980/1195-6860(2006)13[539:JTYBSA]2.0.CO;2)
- Véliz Pérez, M. E. & Archila Morales, F. (2015) *Yucca lacandonica* (*Agavaceae*), a new record for Guatemala. *Int. Cact.-Advent.* 106–107(7): 49–53, ills., map, key.
- Verloove, F. & Alves, P. (2016) New vascular plant records for the western part of the Iberian Peninsula (Portugal and Spain). *Folia Bot. Extremadurensis* 10: 5–23. <http://dialnet.unirioja.es/servlet/articulo?codigo=6419382>
- Villavicencio, M. A. & Pérez-Escandón, B. E. (1995) Tipos de fruto de *Yucca filifera* y formas asociadas de *Tegeticula yuccasella* (*Lepidoptera*). *Bol. Soc. Bot. México* 57: 121–123, ills. <https://doi.org/10.17129/botsci.1481>
- Waitman, B. A. [et al. 2012], Vander Wall, S. B. & Esque, T. C. (2012) Seed dispersal and seed fate in Joshua Tree (*Yucca brevifolia*). *J. Arid Environm.* 81: 1–8, ills. <https://doi.org/10.1016/j.jaridenv.2011.12.012>
- Wallen, D. R. & Ludwig, J. A. (1978) Energy dynamics of vegetative and reproductive growth in Spanish Bayonet (*Yucca baccata* Torrey). *Southw. Naturalist* 23(3): 409–422. <https://doi.org/10.2307/3670249>
- Walter, H. (1931) Die Hydratur der Pflanze und ihre physiologisch-ökologische Bedeutung (Untersuchungen über den osmotischen Wert). Jena (DE): Verlag von Gustav Fischer.
- Walters, M. [et al. 2011], Figueiredo, E., Crouch, N. R., Winter, P. J. D., Smith, G. F., Zimmermann, H. G. & Mashope, B. K. (2011) Naturalised and invasive succulents of southern Africa. *Abc-Taxa* 11: x + 359 pp., ills., maps, keys.
- Ward, D. B. (2004) Native or not: Studies of problematic species. No. 2: Mound-Lily *Yucca: Yucca gloriosa* (*Agavaceae*). *Palmetto* 22(3): 6–8, ills.
- Ward, D. B. (2006) A nomenclatural history of southeastern filiferous *Yucca*, with selection of a neotype for *Y. flaccida*. *Castanea* 71(1): 80–84, ills. <https://doi.org/10.2179/04-30.1>
- Ward, D. B. (2011) *Yucca filamentosa* and *Yucca flaccida* (*Agavaceae*) are distinct taxa in their type localities. *Castanea* 76(2): 222–228, ills. <https://doi.org/10.2179/10-017.1>
- Warren, S. D. [et al. 2016], Scott Baggett, L. & Warren, H. (2016) Directional floral orientation in Joshua Trees (*Yucca brevifolia*). *West. North Amer. Naturalist* 76(3): 374–378, ills. <https://doi.org/10.3398/064.076.0313>
- Watkins, G. M. (1936) Chromosome numbers and species characters in *Yucca*. *Amer. J. Bot.* 23(5): 328–333. <http://www.jstor.org/stable/2436092>
- Webber, J. M. (1953) *Yuccas of the Southwest*. Washington D.C. (US): US Department of Agriculture. <http://archive.org/details/yuccasofsouthwes17webb>
- Weissbeck, S. (2010) Aktuelle Erkenntnisse und Kulturerfahrungen sowie Methoden zur eindeutigen Identifizierung von *Yucca queretaroensis*. *Avonia* 28(3): 75–85.
- Weissbeck, S. (2011) *Yucca queretaroensis*. Biconvex Denticulate-Leaf *Yucca*. Aktuelle Erkenntnisse und Kulturerfahrungen sowie Methoden zur eindeutigen Identifizierung. *Wüstengarten* 2011: 4–18, ills.
- Weissbeck, S. (2012a) *Yucca recurvifolia* ‘Lemon Sun’ ex *Y. recurvifolia* “SW-09-002”. Eine Spontanmutation stellt sich vor. *Wüstengarten* 3: 16–22, ills.
- Weissbeck, S. (2012b) Leopold Graebener’s Hinterlassenschaft. *Yucca ×karlsruhensis* — Die älteste dokumentierte *Yucca*-Hybride der Welt. *Wüstengarten* 3: 61–73, ills.
- Weissmüller, M. (2017) *Yucca spec. nova?*—Das Geheimnis der grünen Yuccas von Coahuila. *Wüstengarten* 7: 47–62, ills.
- Welsh, S. L. (1975) Utah plant novelties in *Astragalus* and *Yucca*. *Great Basin Naturalist* 34(4): 305–310, ills. <http://biodiversitylibrary.org/page/7913971>

- Welsh, S. L. [ & al. 1987], Atwood, N. D., Goodrich, S. & Higgins, L. C. (eds.) (1987) A Utah Flora. Provo (US): Brigham Young University (Great Basin Naturalist Memoirs, No. 9). <http://biodiversitylibrary.org/page/7934093>
- Welsh, S. L. [ & al. 2008], Atwood, N. D., Goodrich, S. & Higgins, L. C. (eds.) (2008) A Utah Flora. Ed. 4. Provo (US): Brigham Young University.
- Wijnands, D. O. (1983) The botany of the Commelins. A taxonomical, nomenclatural and historical account of the plants depicted in the Moninckx Atlas and in the four books by Jan and Caspar Commelin on the plants in the Hortus Medicus Amstelodamensis 1682–1710. Rotterdam (NL): A. A. Balkema. <http://edepot.wur.nl/205789>
- Wolf, F. T. (1940) Macrosporogenesis and the development of the embryo sac in *Yucca aloifolia*. Bull. Torrey Bot. Club 67(9): 755–761. <https://doi.org/10.2307/2481526>
- Yoder, J. B. [ & al. 2010], Smith, C. I. & Pellmyr, O. (2010) How to become a Yucca Moth: Minimal trait evolution needed to establish the obligate pollination mutualism. Biol. J. Linn. Soc. 100(4): 847–855. <https://doi.org/10.1111/j.1095-8312.2010.01478.x>
- Yoder, J. B. [ & al. 2013], Smith, C. I., Rowley, D. J., Flatz, R., Godsoe, W., Drummond, C. & Pellmyr, O. (2013) Effects of gene flow on phenotype matching between two varieties of Joshua Tree (*Yucca brevifolia*; *Agavaceae*) and their pollinators. J. Evol. Biol. 26: 1220–1233, map, ills. <https://doi.org/10.1111/jeb.12134>
- Zamudio, S. & Galván Villanueva, R. (2011) La diversidad vegetal del estado de Guanajuato, México. In: Flora del Bajío y regiones adyacentes, Fascículo Complementario 27. Pátzcuaro (MX): Instituto de Ecología.
- Zimer, E. (2014) New first records for New Zealand naturalized and casual succulent flora. Xerophilia 4(1): 95–106, ills.



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**Part II**

**The Family Amaryllidaceae**







## Amaryllidaceae

U. Eggli, E. Van Jaarsveld, and S. Arroyo-Leuenberger

**Including** *Brunsvigiaceae* Horaninow.

**Including** *Cyrtanthaceae* Salisbury.

**Including** *Galanthaceae* G. Meyer.

**Including** *Gethyllidaceae* Rafinesque.

**Including** *Haemanthaceae* Salisbury.

**Including** *Leucojaceae* Batsch ex Borkhausen.

**Including** *Narcissaceae* Jussieu.

**Including** *Oporanthaceae* Salisbury.

**Including** *Pancratiaceae* Horaninow.

**Including** *Zephyranthaceae* Salisbury.

Perennial or biennial bulbous herbs with fleshy tunics, rarely rhizomatous (*Clivia*, *Scadoxus*); **R** contractile; **L** linear to oblong, sometimes ovate or tapering, slightly to rarely distinctly succulent; **Inf** umbellate with a usually well-developed scape, or rarely **Fl** solitary, with an involucre (= spathe) of 2 (–8) **Bra**; **Fl** bisexual, actinomorphic to zygomorphic; **Tep** 6 in 2 series; **St** 6 (rarely more); **Fil** free or united at the base, filiform; **Anth** dorsifixed or basifixed; **Ov** inferior,

3-locular, each with 1 to many ovules, placentation axile (rarely parietal); **Sty** terete; **Sti** capitate or tricuspidate or 3-branched; **Fr** 3-valved capsules, rarely fleshy; **Se** few to many, voluminous or flattish, angled or winged; endosperm fleshy.

**Order:** Asparagales

**Important Literature:** Meerow & Snijman (1998: synopsis); Meerow & al. (1999: molecular systematics); Meerow & al. (2000a: phylogeny American taxa); Meerow & al. (2000b: phylogeny); Meerow & Clayton (2004: phylogeny *Haemantheae*); Meerow & Snijman (2006: molecular phylogeny); Meerow (2010: evolution American taxa); Duncan & al. (2016: illustrated monograph S African taxa).

**Distribution:** Cosmopolitan, confined mainly to temperate, subtropical and tropical regions, more common in Mediterranean and Savanna regions.

A family with 59 genera and ±870 species, of which many are frequently cultivated. *Amaryllidaceae* is part of the lower core Asparagales. It has invariably been found to form a clade with *Alliaceae* and *Agapanthaceae*, and APG (2009) advocated a wide circumscription of the group (accepting the traditional families at the rank of subfamilies). A super-conservation proposal was published by Meerow & al. (2007) to allow the continued usage of the name *Amaryllidaceae* (vs. the prioritable *Alliaceae*). Recent molecular

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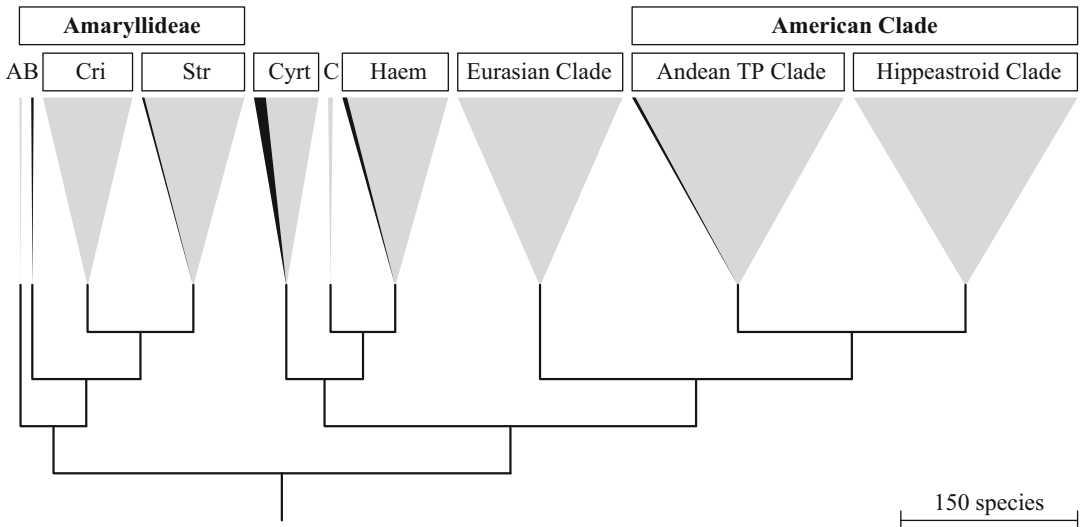
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**Fig. 1** Summary phylogeny of *Amaryllidaceae* based on Meerow & Snijman (2006); species numbers based on own counts, Stevens (2001+) and Nicolás García (pers. comm.) (870 species total). A = *Amaryllidinae*, Andean TP =

Andean Tetraploid Clade, B = *Boophoninae*, C = *Calostemateae*, Cri = *Crininae*, Cyrt = *Cyrtantheae*, Stru = *Strumarinae*. (Copyright: U. Eggli)

phylogenies found reasonable support for *Agapanthaceae* as sister to a clade formed by *Alliaceae* plus *Amaryllidaceae* s.s. (Seberg & al. 2012, Steele & al. 2012).

Meerow & al. (2000a) and Meerow & al. (2000b) divide the *Amaryllidaceae* s.s. into 14 tribes and imply an African origin with a derived Eurasian clade. The American genera form a well-defined sister group relative to the Eurasian genera, and fall in 2 subclades, the “Andean clade” (here belongs tribe *Stenomesseae*) and a Hippeastroid clade. – Fig. 1.

The underground organs of most clades are bulbs, but bulb and rhizome geophytes can occur in close systematic neighbourhood, e.g. in the African tribe *Haemantheae* (*Clivia* with rhizomes and *Haemanthus* with bulbs) (Meerow & Clayton 2004). Many species contain toxic norbelladine alkaloids which are unique for the family.

**Succulence:** Undisputed leaf succulence is found in the S American genus *Rauhia*, but varying degrees of weak leaf succulence occur also in scattered species of the genera *Boophone*, *Brunsvigia*, *Cyrtanthus* and *Haemanthus* from

the savanna regions of RSA (Eastern Cape, KwaZulu-Natal and Mpumalanga) with mainly epigeous bulbs. However, most bulbous species from seasonally arid regions could be interpreted as being succulent to some extent, esp. when they produce flowers during the dry season. The bat-pollinated epiphytic *Hippeastrum calyptratum* is sometimes also regarded as succulent, but the leaves are merely slightly fleshy, and the plants are not specifically adapted to cope with water stress.

In addition, many species have somewhat fleshy roots. Distinctly succulent and thick (to 2 cm Ø) roots are described for the S African *Clivia mirabilis* by Duncan & al. (2016: 129–130), and they are thought to “provide water storage capacity enabling plants to survive summer drought”.

**Horticultural Importance:** *Amaryllidaceae* have a fairly pronounced horticultural importance, esp. because the many spring-flowering bulbs of *Galanthus*, *Leucojum* or *Narcissus*, while hybrids and cultivars of *Hippeastrum* (= the “Amaryllis” of the horticultural trade) or *Clivia* are widely cultivated as indoor plants.

## Key to genera with succulents

<b>1a</b>	<b>L</b> usually 2, opposite, hairy or glabrous; <b>Fr</b> fleshy berries	<i>Haemanthus</i>
<b>1b</b>	<b>L</b> 2 or more, glabrous; <b>Fr</b> dry capsules	2
<b>2a</b>	<b>Spathe</b> valves 2–4; <b>Se</b> flattened, usually appearing winged	<i>Cyrtanthus</i>
<b>2b</b>	<b>Spathe</b> valves 2 (rarely more); <b>Se</b> globose	3
<b>3a</b>	<b>Fl</b> ± 100 per <b>Inf</b> ; <b>Per</b> 1–2 (–3) cm, actinomorphic	<i>Boophane</i>
<b>3b</b>	<b>Fl</b> ≤ 30 per <b>Inf</b> ; <b>Per</b> 4–15 cm	4
<b>4a</b>	<b>L</b> tongue-shaped; <b>Per</b> pink or red; <b>Inf</b> caducous at fruiting time	<i>Brunsvigia</i>
<b>4b</b>	<b>L</b> oval to oblong, very fleshy, pseudopetiolate; <b>Per</b> greenish-whitish; <b>Inf</b> persistent at fruiting time	<i>Rauhia</i>

## References

- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>.
- Duncan, G. [ & al. 2016 ], Jeppe, B. & Voigt, L. (2016) *The Amaryllidaceae of southern Africa*. Hatfield (ZA): Umदाus Press.
- Meerow, A. W. (2010) Convergence or reticulation? Mosaic evolution in the canalized American *Amaryllidaceae*. In: Seberg, O. & al. (eds.): *Diversity, phylogeny and evolution in the monocotyledons*; pp. 145–168. Aarhus (DK): Aarhus University Press. <http://www.researchgate.net/publication/261239102>.
- Meerow, A. W. & Clayton, J. R. (2004) Generic relationships among the baccate-fruited *Amaryllidaceae* (tribe *Haemantheae*) inferred from plastid and nuclear non-coding DNA sequences. *Pl. Syst. Evol.* 244(3–4): 141–155. <https://doi.org/10.1007/s00606-003-0085-z>.
- Meerow, A. W. & Snijman, D. A. (1998) *Amaryllidaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 83–110, ills., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_11](https://doi.org/10.1007/978-3-662-03533-7_11).
- Meerow, A. W. & Snijman, D. A. (2006) The never-ending story: Multigene approaches to the phylogeny of *Amaryllidaceae*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 355–366. <https://doi.org/10.5642/aliso.20062201.29>.
- Meerow, A. W. [ & al. 1999 ], Fay, M. F., Guy, C. L., Li, Q.-B., Zaman, F. Q. & Chase, M. W. (1999) Systematics of *Amaryllidaceae* based on cladistic analysis of plastid *rbcL* and *trnL-F* sequence data. *Amer. J. Bot.* 86(9): 1325–1345. <http://www.amjbot.org/content/86/9/1325.abstract>.
- Meerow, A. W. [ & al. 2000a ], Guy, C. L., Li, Q.-B. & Yang, S.-L. (2000a) Phylogeny of the American *Amaryllidaceae* based on nrDNA ITS sequences. *Syst. Bot.* 25(4): 708–726. <https://doi.org/10.2307/2666729>.
- Meerow, A. W. [ & al. 2000b ], Fay, M. F., Chase, M. W., Guy, C. L., Li, Q.-B., Snijman, D. A. & Yang, S.-L. (2000b) Phylogeny of *Amaryllidaceae*: Molecules and morphology. In: Wilson, K. L. & Morrison, D. A. (eds.): *Monocots: Systematics and evolution*; pp. 372–386. Melbourne (AU): CSIRO.
- Meerow, A. W. [ & al. 2007 ], Reveal, J. L., Snijman, D. A. & Dutilh, J. H. (2007) (1793) Proposal to conserve the name *Amaryllidaceae* against *Alliaceae*, a “super-conservation” proposal. *Taxon* 56(4): 1299–1300. <https://doi.org/10.2307/25065925>
- Seberg, O. [ & al. 2012 ], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ills. <https://doi.org/10.3732/ajb.1100468>.
- Steele, P. R. [ & al. 2012 ], Hertweck, K. L., Mayfield, D., McKain, M. R., Leebens-Mack, H. & Pires, J. C. (2012) Quality and quantity of data recovered from massively parallel sequencing: Examples in Asparagales and *Poaceae*. *Amer. J. Bot.* 99(2): 330–348. <https://doi.org/10.3732/ajb.1100491>.





## Boophone AMARYLLIDACEAE

E. Van Jaarsveld

**Boophone** Herbert (Appendix, 18, 1821). **Type:** *Haemanthus toxicarius* Aiton [*nom. illeg.*; = *Amaryllis disticha* Linné *fil.* (ICBN 2006: 256)]. — **Amaryllideae** — **Boophoninae** — **Lit:** Duncan & al. (2016: 48–63, 662 [key] (S African taxa)). **Distr:** Widespread in Africa from Sudan to RSA. **Etym:** Gr. ‘bouphonos’, killing cattle; for the poisonous nature of the plants.

**Incl.** *Boophane* Herbert (1821) (*nom. inval.*, Art. 61.1). **Type:** *Haemanthus toxicarius* Aiton [*nom. illeg.*; = *Amaryllis disticha* Linné *fil.* (ICBN 2006: 256)].

**Incl.** *Buphane* Herbert (1825) (*nom. inval.*, Art. 61.1). **Type:** *Amaryllis disticha* Linné *fil.*

**Incl.** *Buphone* Herbert (1825) (*nom. inval.*, Art. 61.1). **Type:** *Amaryllis disticha* Linné *fil.*

Perennials with thickly tunicated bulbs to 30 cm Ø, mainly above-ground; **L** distichous, erect when young becoming spreading with age, variable in shape, narrowly lanceolate, ensiform, strap-shaped or tongue-shaped, leathery, sometimes undulate, glaucous-green to green; **Inf** densely umbellate, many-flowered; scape short, firm, somewhat laterally compressed; **Bra** 2, triangular; **Per** consisting of a short subcylindrical

tube and spreading slender **Tep** lobes; **St** from the throat of the perianth tube; **Fil** straight, filiform; **Anth** oblong, dorsifixed, versatile; **Ov** inferior, turbinate, 3-locular, each locule with 1 to few ovules; **Sty** simple, obscurely 3-lobed; **Fr** dry capsules, triquetrous, obtriangular, indehiscent or loculicidally 3-valved; **Se** globose.

A small genus of only 2 species. The spelling of the generic name was much in dispute and various spellings are encountered in the literature. The spelling as here used has been conserved (Barrie 2006: 798). Both species of the genus are sometimes referred to as succulents. The inflorescences easily detach when the fruits are ripe, dispersing the seeds when blown away as a whole by wind. The seeds are recalcitrant and should be sown fresh.

**B. disticha** (Linné *fil.*) Herbert (Appendix, 18, 1821). **Type:** UPS. — **Distr:** SE Sudan to RSA; widespread in grassland, Karoo vegetation and dry savanna. **I:** Wyk & al. (1997: 60) Duncan & al. (2016: 54–57). – Fig. 1

≡ *Amaryllis disticha* Linné *fil.* (1782) ≡ *Brunsvigia disticha* (Linné *fil.*) Sweet (1826) ≡ *Haemanthus distichus* (Linné *fil.*) Linné *fil. ex* Savage (1937); **incl.** *Haemanthus ciliaris* Linné (1762) ≡ *Brunsvigia ciliaris* (Linné) Ker-Gawler (1817); **incl.** *Haemanthus toxicarius* Linné *fil. ex* Aiton (1789) (*nom. illeg.*, Art. 52.1) ≡ *Brunsvigia toxicaria* (Linné *fil. ex* Aiton) Ker-Gawler (1821) (*nom. illeg.*, Art. 52.1) ≡ *Boophone toxicaria*

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**Fig. 1** *Boophone disticha* (Copyright: E. J. Van Jaarsveld)

(Linné *fil. ex* Aiton) Herbert (1825) (*nom. illeg.*, Art. 52.1)  $\equiv$  *Amaryllis toxicaria* (Linné *fil. ex* Aiton) D. Dietrich (1840) (*nom. illeg.*, Art. 52.1); **incl.** *Haemanthus sinuatus* Schultes & Schultes *fil.* (1830) (*nom. inval.*, Art. 32.1d); **incl.** *Boophone intermedia* M. Roemer (1847); **incl.** *Boophone longipedicellata* Pax (1889); **incl.** *Haemanthus robustus* Pax (1892); **incl.** *Brunsvigia rautanenii* Baker (1903); **incl.** *Haemanthus lemairei* De Wildeman (1921).

Bulb solitary, above-ground, subglobose, to 30 cm  $\varnothing$ , thickly tunicated, outer tunics brown and firm; **R** terete, fleshy; **L** 15–30  $\times$  5–10 cm, green, oblong, coriaceous, margin straight, tip obtuse; scape firm, to 25 cm, to 3 cm  $\varnothing$ ; **Fl** numerous, in dense umbels, creamy-yellow becoming reddish with age; **Bra** suberect, pink or red, to 14  $\times$  8.5 cm; **Ped** 5–10 cm; **Per** tube 5–7 mm, 6-angled with deep grooves between the angles, free parts of the tepals to 3.5 cm, cucullate, to 4 mm wide near the tips narrowed to 2 mm at the base; **St**  $\pm$  as long as the tepals; **St** exerted to 1 cm beyond the perianth; **Fil** slender, erect, attached to the tepals; **Sty** to 1 cm longer than the stamens; **Ov** obconical, sharply angled.

The synonymous *Haemanthus ciliaris* Linné 1762 would have nomenclatural priority, but the combination under *Boophone* is pre-occupied by *B. ciliaris* (Linné) Herbert, now regarded as a synonym of the non-succulent *Crossyne guttata* (Linné) D. & U. Müller-Doblies. The taxon is widely used in traditional popular medicine as treatment for painful wounds, headaches, skin disorders, inflammations, rheumatism, and anxiety, and of the 8 known alkaloids, 4 have been shown to be biologically active (Neergaard & al. 2009). In addition, the bulbs have also been used to prepare arrow poison (Roberts & Wink 1998: 64), and were widely used as such by Bushmen as one of several ingredients (Smith 1966). Animals suffering poisoning show a mad and confused behaviour, resembling acute drunkenness. A complete overview of traditional usage, phytochemistry and pharmacology is given by Nair & van Staden (2014).

**B. haemanthoides** F. M. Leighton (J. South Afr. Bot. 13: 59–61, fig. 4, 1947). **Type:** RSA, Western Cape (*Leighton* 2361 [BOL]). — **Lit:** Duncan & al. (2016: 58–63, with ill.). **Dist:** SW Namibia, RSA (Northern Cape, Western Cape); coastal regions, autumn-flowering.

**Incl.** *Boophone disticha* var. *ernesti-ruschii* Dinter & G. M. Schulze (1941)  $\equiv$  *Boophone haemanthoides* ssp. *ernesti-ruschii* (Dinter & G. M. Schulze) G. D. Duncan & C. C. Tsang (2016); **incl.** *Boophone ernesti-ruschii* Dinter ex Sölch (1960) (*nom. inval.*, Art. 32.1d).

Bulb solitary, glabrous, above-ground, ovoid to globose, to 18 cm  $\varnothing$ , thickly tunicated, outer tunics brown and firm; **R** terete, fleshy; **L** 15–30  $\times$  5–10 cm, green, oblong, coriaceous, margin straight, tip obtuse; scape firm, to 25 cm, to 3 cm  $\varnothing$ ; **Fl** numerous, in dense umbels, creamy-yellow becoming reddish with age; **Bra** suberect, pink or red, to 14  $\times$  8.5 cm; **Ped** 5–10 cm; **Per** tube 5–7 mm, 6-angled with deep grooves between the angles, free parts of the tepals to 3.5 cm, cucullate, to 4 mm wide near the tips narrowed to 2 mm at the base; **St**  $\pm$  as long as the tepals; **St** exerted to 1 cm beyond the perianth; **Fil** slender, erect, attached to the tepals; **Sty** to 1 cm longer than the stamens; **Ov** obconical, sharply angled.

## References

- Barrie, F. R. (ed.) (2006) Proposals to conserve or reject. Report of the General Committee: 9. *Taxon* 55(3): 795–800. <https://doi.org/10.2307/25065657>
- Duncan, G. [et al. 2016], Jeppe, B. & Voigt, L. (2016) The *Amaryllidaceae* of southern Africa. Hatfield (ZA): Umdaus Press.
- Nair, J. J. & Staden, J. van (2014) Traditional usage, phytochemistry and pharmacology of the South African medicinal plant *Boophone disticha* (L.f.) Herb. (*Amaryllidaceae*). *J. Ethnopharmacol.* 151(1): 12–16, ill. <https://doi.org/10.1016/j.jep.2013.10.053>.
- Neergaard, J. S. [et al. 2009], Andersen, J., Pedersen, M. E., Stafford, G. I., Staden, J. van & Jäger, A. K. (2009) Alkaloids from *Boophone disticha* with affinity to the serotonin transporter. *South Afr. J. Bot.* 75(2): 371–374. <https://doi.org/10.1016/j.sajb.2009.02.173>.
- Roberts, M. F. & Wink, M. (1998) Alkaloids: Biochemistry, ecology, and medicinal applications. New York (US)/London (GB): Plenum Press. <https://doi.org/10.1007/978-1-4757-2905-4>
- Smith, C. A. (1966) Common names of South African plants. Pretoria (ZA): Government Printer/Department of Agricultural Technical Services, Botanical Research Institute (= Botanical Survey Memoir No. 35).
- Wyk, B-E. van [et al. 1997], Oudtshoorn, B. van & Gericke, N. (1997) Medicinal plants of South Africa. Pretoria (ZA): Briza Publications.





## Brunsvigia AMARYLLIDACEAE

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**Brunsvigia** Heister (Beschr. neu. Geschl., 3, 1755). **Type:** *Brunsvigia orientalis* Aiton ex Ecklon. — **Amaryllideae** — **Strumariinae** — **Lit:** Dyer (1950: revision); Dyer (1951: revision); Duncan & al. (2016: 64–107, 662–663 [key] (S African taxa)). **Distr:** Tanzania, Malawi, Botswana, Namibia, Lesotho, Swaziland, RSA. **Etym:** Honouring the House of Braunschweig [Brunswick]-Lüneburg.

Perennial herbs with underground or above-ground bulbs to 20 cm Ø, usually thickly tunicated; **L** 2 to many per season, variously shaped, usually broad, appearing after the flowers; **Inf** few- to many-flowered umbels; scape firm, to 35 cm, deciduous at fruiting time; spathe valves 2 (= **Bra**); **Ped** elongating and spreading after anthesis; **Per** zygomorphic or almost actinomorphic with short tube, segments spreading-recurved; **St** arising from the perianth tube, ± declinate or erect; **Ov** turbinate, with many superposed ovules in each locule; **Sty** filiform, declinate; **Sti** capitate; **Fr** dry capsules, obtuse or acute, 3-angled, dehiscent loculicidally or breaking unevenly; **Se** subglobose.

A genus of ±20 species in S and SE Africa. The species with above-ground fleshy bulbs are considered succulent and are treated below. They

are all from arid winter rainfall regions and occur in Succulent Karoo vegetation.

**B. herrei** F. M. Leighton ex W. F. Barker (J. South Afr. Bot. 29: 165, t. 32, 1963). **Type:** RSA, Northern Cape (*Herre* 3368 [NBG]). — **Lit:** Duncan & al. (2016: 84–85, with ills.). **Distr:** S Namibia, RSA (Northern Cape); Succulent Karoo, mountains in Namaqualand Blomveld vegetation, autumn-flowering.

Bulb to ±15 cm Ø, above-ground to partly underground, globose and covered with brownish cartilaginous tunics; **L** 6, to 20 × 9 cm, erect at first becoming spreading, oblong, smooth, glaucous, margins narrowly reddish, tip obtuse; scape green, slightly laterally compressed, to 23 cm, 15 mm Ø; **Bra** ovate, pale greenish-fawn, to 6 × 2.5 cm; umbel to 40-flowered, globose and head-like; **Ped** pale green, to 18 cm, 5 mm Ø at the base; **Per** pale pink, actinomorphic; **Tep** to 5.5 × 1.2 cm, oblong, obtuse, tube 3 mm long, deep pink; **St** declinate, the longest somewhat shorter than the perianth, the others ½ as long; **Fil** adnate to the perianth tube; **Sty** becoming longer than the stamens; **Ov** to 6 mm Ø, obtusely angled when young; **Fr** and **Se** not seen.

**B. radula** (Jacquin) W. T. Aiton (Hort. Kew., ed. 2, 2: 230, 1811). **Type:** [lecto — icono]: Jacquin, Hort. Schönbr. 1: 35, t. 68, 1797. — **Lit:** Snijman (2012); Duncan & al. (2016: 100–101, with ills.). **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo,

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Knersvlakte Dolomite Vygieveld vegetation, limestone outcrops.

≡ *Amaryllis radula* Jacquin (1797) ≡ *Coburgia radula* (Jacquin) Herbert ex Steudel (1840).

Bulb to ±25 cm Ø, below ground, globose and with short neck, covered with dry brownish tunics; **L** 2–3, to 8 × 3.5 cm, tongue-shaped to oblong, appressed to the ground, obtuse, tip obtuse, thick, upper face and margin with papillae with enlarged bases, lower face smooth, pale green; **Inf** 1–2; scape to 10 cm, 5 mm Ø, slightly laterally compressed; **Bra** ovate-oblong, reddish, to 2 cm; umbel 3- to 5-flowered; **Ped** to 5 cm, 5 mm Ø; **Per** flesh-coloured to pink; **Tep** to 3 cm, linear-lanceolate, spreading, recurved, undulate, the lower often subtending stamens and style; **St** declinate, ± as long as the tepals; **Sty** slightly

longer than the stamens; **Ov** roundish, obtusely angled; **Fr** 3-angled; **Se** not seen.

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## References

- Duncan, G. [et al. 2016], Jeppe, B. & Voigt, L. (2016) The *Amaryllidaceae* of southern Africa. Hatfield (ZA): Umdaus Press.
- Dyer, R. A. (1950) A revision of the genus *Brunsvigia*. Pl. Life (Stanford) 6: 63–83.
- Dyer, R. A. (1951) A revision of the genus *Brunsvigia*. Pl. Life (Stanford) 7: 44–64.
- Snijman, D. A. (2012) A revision of the *Brunsvigia radula*-group (*Amaryllidaceae: Amaryllideae*) of species in South Africa, including the description of *Brunsvigia gariepensis*, a new species from Bushmanland in Northern Cape. South Afr. J. Bot. 79(1): 106–116, ills, maps, key. <https://doi.org/10.1016/j.sajb.2011.12.005>.

## Cyrtanthus AMARYLLIDACEAE

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**Cyrtanthus** Aiton (Hort. Kew. 1: 414, 1789). **Type:** *Crinum angustifolium* Linné *fil.* — **Cyrtantheae** — **Lit:** Dyer (1939: synopsis); Nordal (1979: revision E Africa); Reid & Dyer (1984: synopsis S Africa); Snijman & Meerow (2010: molecular phylogeny & evolution); Duncan & al. (2016: 196–315, 665–668 [key] (S African taxa)). **Distr:** S Africa extending to E Africa (Kenya); mainly summer-rainfall regions. **Etym:** Gr. ‘kyrtos’, curved; and Gr. ‘anthos’, flower; for the curved flower tube.

**Incl.** *Vallota* Salisbury *ex* Herbert (1821). **Type:** *Vallota purpurea* Herbert [*nom. illeg.*, ≡ *Crinum speciosum* Linné *fil.*].

**Incl.** *Anoiganthus* Baker (1878). **Type:** *Cyrtanthus breviflorus* Harvey.

Plants bulbous, evergreen or deciduous; bulbs tunicate, above-ground or underground, solitary, dividing or offsetting to form dense groups; **L** ascending, straight or curved, oblong, lorate or linear, green to glaucous; **Inf** umbellate, 1- to many-flowered with up to 4 spathe valves; scape ascending, usually hollow; **Fl** tube narrow, shorter or longer than the lobes, widening towards the mouth; **St** inserted in the throat of the tube; **Anth**

dorsifixed, versatile; **Ov** 3-locular, with numerous ovules in each locule; **Sty** filiform; **Sti** 3-lobed; **Fr** oblong loculicidal capsules; **Se** flat.

A mainly S African genus with ±55 species, some of them frequently cultivated. The genus was found to be monophyletic by Snijman & Meerow (2010), and consists of 3 poorly to well-supported major lineages (recognized as informal groups) which agree with cytological findings, but not with morphological data. 10 taxa from arid to semi-arid sheer cliff-faces or rocky habitats have succulent above-ground or semi-underground bulbs. The flowers are mainly red but also yellow or mottled, depending on the species. Of the species treated below, those with tubular flowers (red or yellow) are pollinated by sunbirds. *C. flammosus* and *C. montanus* have a flower construction that makes it likely that the butterfly *Meneris* (*Aeropetes*) *tulbaghia* (Table Mountain Beauty) is involved (Johnson & Bond 1994). Switches between floral syndromes have likely played an important role in the evolution of the genus, and ornithophily likely evolved in parallel in all primary clades (Snijman & Meerow 2010).

Several species of *Cyrtanthus* are valued horticulturally.

**C. falcatus** R. A. Dyer (Herbertia 6: 75, t. 138: Fig. 1, 1939). **Type:** RSA, KwaZulu-Natal (*Carter* s.n. [NH 30339]). — **Distr:** RSA (KwaZulu-Natal: Drakensberg); sheer cliff-faces in Foothill Moist Grassland vegetation, 1500–2000 m,

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**Fig. 1** *Cyrtanthus flammosus* (Copyright: E. Van Jaarsveld)

spring-flowering and summer-growing. **I:** Dyer (1971); Duncan & al. (2016: 232–233).

Deciduous, cluster-forming; bulbs above-ground, ovoid to globose, to 8 cm Ø, offsetting from the base, tapering to a neck to 12 cm long; tunics densely arranged, brown to grey, membranous; **L** to 4, linear, falcate, 35 × 3 cm, leathery, green, apex acute; **Inf** to 30 cm, scape glaucous, 15 mm Ø near the base and ±10 mm distally, characteristically recurved at the top with a pendent umbel of up to 10 flowers; spathe valves 4–5 × 1.25 cm, linear-lanceolate, soon withering; **Ped** to 14 mm; **Fl** 6–10, pendulous, greenish to red, zygomorphic, 7 cm long, **Per** tube to 4 cm, gradually dilated to 1 cm Ø at the throat, outer face greenish, buff, lobes reddish, obovate-oblong, the outer 2.5 × 1.2 cm, shortly cucullate at the throat, inner lobes 1.3 cm broad, slightly retuse at the apex; **St** arising from the base of the perianth lobes; **Anth** yellow; **Ov** to 1 cm.

Easily cultivated in containers or hanging baskets; propagation by seed or division.

**C. flammosus** Snijman & Van Jaarsveld (Flow. Pl. Afr. 54: 100–103, t. 2120, 1995). **Type:** RSA, Eastern Cape (*Van Jaarsveld & al.* 13803 [NGB, PRE]). — **Distr:** RSA (Eastern Cape); sheer cliff-faces in Gamtoos Thicket vegetation, all-year rainfall region. **I:** Duncan & al. (2016: 236–237). – Fig. 1

Evergreen, to 25 cm; bulb solitary, ovoid, partly exposed or completely above-ground, to 4 cm Ø; tunics fleshy, withering papery, brown;

**L** 2–4, ascending, 13–29 × 1.5–2 cm, glaucous, fleshy; **Inf** 1-flowered, scape erect, to 17 cm; spathe valves suberect, lanceolate, 5.5 × 1 cm; **Per** tube 4–5 cm; **Tep** spreading, broadly obovate, 4–5 × 3–3.5 cm, fire-red; **Fil** free for 2–2.5 cm, cream to pale green; **Anth** 1.5 cm, yellow, pollen yellow; **Ov** 1–1.5 × 0.6 cm; **Sty** declinate; **Sti** branches 5 mm; **Fr** not seen.

**C. flanagani** Baker (in Thiselton-Dyer, Fl. Cap. 6: 532, 1897). **Type:** RSA, KwaZulu-Natal (*Flanagan* 1824 [K, BOL, PRE]). — **Distr:** RSA (Eastern Cape, KwaZulu-Natal, Free State), Lesotho; sheer cliff faces in Ukahlamba Basalt Grassland vegetation, 2750–3000 m. **I:** Duncan & al. (2016: 238–239).

Deciduous, cluster-forming; bulbs halfway above-ground, ovoid to globose, to 3 cm Ø, offsetting from the base, tapering to a neck to 11 cm long; tunics densely arranged, brown, membranous; **L** up to 4, linear, 20 × 1.9 cm, leathery, lorate, falcate, green, obtuse; **Inf** to 20 cm, scape compressed; spathe valves white with red veins, 5 × 1.1 cm at the base; **Bra** white, 2 cm, linear-filiform; **Ped** to 2.5 cm; **Per** yellow, ascending, trumpet-shaped, tube 4.6 × 0.6 cm Ø at the throat, lobes ascending, 1.5 cm, the outer 0.9 cm broad and slightly hooded, the inner 0.8 cm broad, not hooded; **St** not exerted; **Ov** 0.8 cm, cylindrical-oblong, faintly 3-lobed; **Sty** shortly 3-lobed.

**C. herrei** (F. M. Leighton) R. A. Dyer (Flow. Pl. Afr. 33: t. 1281 + text, 1959). **Type:** RSA, Northern Cape (*Herre* s.n. [BOL]). — **Distr:** Extreme S Namibia, RSA (Northern Cape); sheer cliffs in Succulent Karoo vegetation, winter-rainfall region. **I:** Duncan & al. (2016: 250–251). – Fig. 2

≡ *Cryptostephanus herrei* F. M. Leighton (1932).

Bulbs large, above-ground, clustering, obclavate, to 6 cm Ø; **R** succulent, terete; **L** synanthous, distichous, lorate, to 45 × 5 cm, leathery, glaucous, apex obtuse; **Inf** to 40 cm, to 28-flowered; scape glaucous; spathe valves to 8 × 1.3 cm, linear-lanceolate, soon withering; **Ped** to 4 cm; **Fl** pendulous; **Per** zygomorphic, to 5.5 cm, tube to 4 cm, red,



**Fig. 2** *Cyrтанthus herrei* (Copyright: U. Eggli)

lobes yellowish-green; **St** fused to the perianth, free part of **Fil** to 6 mm; **Anth** yellow; **Ov** to 8 mm; **Se** black, winged.

**C. inaequalis** O'Brien (Gard. Chron., ser. 3, 37: 261, ill., 1905). **Type:** RSA, Western Cape (*Anonymus* s.n. [[lecto — icono]: l.c., fig. 110: part 1]). — **Distr:** RSA (Western Cape, Eastern Cape); sheer quartzitic sandstone cliffs in Gamka Thicket vegetation, summer- and winter-rainfall region. **I:** Duncan & al. (2016: 254–255).

Bulb above-ground, globose, 4–7 × 6–8 cm, purplish-green, solitary or forming groups, bulbiferous from the base; tunics withering papery, brown; **L** 2–3, evergreen, glaucous, linear-oblancoate, leathery, 30–40 × 1 cm, upper face channelled, apex subacute; **Inf** 40–45 cm, 3- to 5-flowered, scape glaucous; **Bra** 6.5 × 0.8 cm, triangular-lanceolate, acuminate, soon withering; **Ped** 3.5–4.8 cm; **Per** orange-red, zygomorphic, labiate, 6.5–9 cm long, tubular, curved, tube 2–3.5 mm Ø at the base expanding to 7–10 mm at the throat, infundibuliform, the 4 upper lobes linear-lanceolate, together forming

a hood, the 2 lower lobes lanceolate, 25 × 6 mm; **St** basally fused to the perianth, free part 1.3 cm; **Anth** yellow, 7 mm, oblong; **Sty** 7.2–7.8 cm, 3-lobed; **Ov** oblong-triangular, 0.6 × 0.4 cm.

The **lectotype** given above is formally **designated here**.

**C. junodii** Beauverd (Bull. Herb. Boissier, sér. 2, 7: 437, 1907). **Type:** RSA, Limpopo (*Junod* s.n. [G?]). — **Distr:** RSA (Limpopo: Wolkberg); S-facing sandstone cliffs in Strydpoort Summit Sourveld vegetation, 1500–2000 m, summer-flowering. **I:** Duncan & al. (2016: 256–257).

Deciduous, forming clumps 20–45 cm Ø; bulbs halfway to completely above-ground, ovoid, 3–7 × 3–6 cm, sprouting from the base, tapering to a neck; tunics densely arranged, reddish-brown, membranous, becoming papery and greyish-brown; **L** 1–6, lorate, to 25–38 × 2–2.8 cm, leathery, purplish at the base, green above, gently recurved, sometimes somewhat twisted sideways near the apex, surface smooth, obscurely striate, apex acute; **Inf** 22–50 cm, 6- to 9-flowered; scape green; spathe valves 2, erect, ovate-lanceolate, 3–5 × 1.5–1.9 cm, yellowish-brown; **Ped** variable in length, 1.5–4 cm, shorter than the spathe valves, ascending, reddish-brown; **Fl** horizontally spreading, secund, somewhat pendulous; **Per** tubular, curved, dilating towards the throat, 3.5–5.5 cm, tube 4 mm wide at the base, dilating to 10–12 mm, red, yellow at the tip of the lobes, lobes 8–12 × 4–6 mm; **St** biseriate, arising from the throat, not exerted; **Sty** yellowish, exerted; **Sti** trifid, lobes ±2 mm.

**C. labiatus** R. A. Dyer (Bothalia 13(1–2): 135, ill., 1980). **Type:** RSA, Eastern Cape (*Bayliss* 5660 [PRE]). — **Distr:** RSA (Eastern Cape); sheer cliff-faces in Gamka Thicket vegetation, all-year rainfall region, summer-flowering. **I:** Duncan & al. (2016: 258–259).

Bulb above-ground, globose, 4–7.5 × 6–7.5 cm, purplish-green, solitary or forming groups, bulbiferous from the base, withering with papery brown tunics; **L** 2–4, evergreen, lorate-elliptic to strap-shaped, 18–30 × 1.4–2 cm, apex obtuse; **Inf** 12–30 cm, up to 8-flowered, scape to 2.3 cm Ø, glaucous; **Bra** 5 × 0.5 cm, triangular-lanceolate,

soon withering; **Ped** 2–2.5 cm; **Per** red, zygomorphic, bilabiate, 5–6 cm, tubular-curved, tube 1 cm, infundibuliform, with 4 upper linear-oblong lobes forming a hood and 2 lower lobes; **St** fused to the perianth, free for the last 1 cm; **Anth** yellow, 3 mm, oblong; **Sty** 4 cm, **Sti** 3-lobed; **Ov** oblong-triangular, 6 × 4 mm.

Easily propagated from bulbils.

**C. montanus** R. A. Dyer (Flow. Pl. Afr. 44: t. 1756 + text, 1977). **Type:** RSA, Eastern Cape (*Skinner* s.n. [PRE 37061]). — **Distr:** RSA (Eastern Cape); sheer cliff-faces in Gamka Thicket vegetation, rainfall all year, summer-flowering. **I:** Duncan & al. (2016: 276–277).

Bulb above-ground, globose, 6.5 × 7 cm, purplish-greenish, solitary or forming groups, bulbiferous from the base; tunics withering grey-brown, papery; **L** 2–4, evergreen, lorate-elliptic, to 30 × 2 cm, ascending, glaucous; **Inf** to 10 cm, to 10-flowered; **Bra** 2, linear-lanceolate, to 5 cm, with smaller bracteoles subtending the flowers; **Ped** to 3 cm; **Per** red, erect, to 5 cm, tube infundibuliform, to 1.5 cm; **OTep** linear-lanceolate, to 0.9 cm wide; **ITep** to 1.1 cm wide; **St** biseriate; **Fil** 9–11 mm; **Ov** oblong, to 6 mm; **Sty** filiform; **Sti** tricuspiate; **Fr** oblong; **Se** compressed, black.

Easily propagated from bulbils.

**C. obliquus** Aiton (Hort. Kew. 1: 414, 1789). **Type:** RSA (*Masson?* s.n. [not located]). — **Distr:** RSA (Western Cape, Eastern Cape, KwaZulu-Natal); coastal areas in Fynbos and Indian Ocean Coastal Belt vegetation; summer-flowering. **I:** Phillips & Pole Evans (1921b); Duncan & al. (2016: 280–281).

**Incl.** *Crinum obliquum*. Linné *fil.* (1782); **incl.** *Amaryllis umbella*. L'Heritier (1789); **incl.** *Timmia obliqua*. J. F. Gmelin (1791).

Bulb above-ground, globose, 8–10 cm Ø, solitary or dividing to form small groups; tunics withering dark brown, papery; **L** 6–12, evergreen, ascending, distichous, lorate, semi-fleshy and twisted, 18–48 × 3.5–5 cm, grey-green, apex obtuse; **Inf** 28–77 cm, 6- to 12-flowered, scape cylindrical but slightly flattened, 1.3–2.5 cm Ø; spathe valves 3–4 × 1–1.2 cm, ovate to

acuminate; **Ped** 2 cm; **Fl** pendent, funnel-shaped, mottled green, yellowish and red; **Per** tube 4.5 cm long and 2.4 cm Ø at the throat; **OTep** 2.5 cm long, oblong; **ITep** 2.4 cm, obovate; **St** from near the base of the perianth tube; **Fil** 3 cm; **Anth** 4 mm; **Ov** subglobose, 5 mm; **Sti** faintly 3-lobed; **Fr** oblong, 2.7–3 cm; **Se** oblong, flattened, 1.2–1.3 cm, black.

Easily propagated from seed or division.

**C. sanguineus** (Lindley) Hooker *fil.* (Curtis's Bot. Mag. 86: t. 5218 + text, 1860). **Type** [neo]: RSA, Eastern Cape (*Ryder* 105 [K]). — **Lit:** Nordal (1979); Duncan & al. (2016: 292–293, with ills.). **Distr:** Sudan, Kenya, Tanzania, Zimbabwe, Moçambique, RSA (Eastern Cape, KwaZulu-Natal); sheer cliffs in Eastern Valley Bushveld vegetation or rocky regions in savannas, summer-flowering.

≡ *Gastronema sanguineum* Lindley (1848).

Easily grown from seed or division.

**C. sanguineus** ssp. **ballyi** Nordal (Norweg. J. Bot. 26: 190, 1979). **Type:** Kenya (*Bally* B5135 [EA, K]). — **Distr:** Kenya (Nairobi National Park); open grassy *Acacia* savanna, 1650 m.

Differs from ssp. *sanguineus*: **L** appearing after flowering, 0.4–1.2 cm broad; **Ped** 2–4.4 cm; **Per** bright red, or crimson to scarlet, 5–10 cm; **St** uniseriate.

**C. sanguineus** ssp. **minor** Nordal (Norweg. J. Bot. 26: 190, 1979). **Type:** Kenya (*Champion* s.n. [K]). — **Distr:** S Sudan, N Kenya, W Tanzania; grassy regions among boulders.

Differs from ssp. *sanguineus*: **Ped** 0.4–1.2 cm; **Per** pinkish-mauve, 3.5–4 cm; **St** biseriate.

**C. sanguineus** ssp. **salmonoides** (P. R. O. Bally & Carter) Nordal (Norweg. J. Bot. 26: 190, 1979). **Type:** Kenya (*Bally* 8482 [K, G]). — **Distr:** Kenya (Nairobi area: Ngong Hills); grassland, 2100 m.

≡ *Cyrtanthus salmonoides* P. R. O. Bally & Carter (1962).

Differs from ssp. *sanguineus*: Bulb 4 cm Ø; **L** absent or present at anthesis, to 30 cm;



**Ped** 0.3–1.5 cm; **Per** pink to salmon-pink, 6.5–9.5 cm; **St** uniseriate or biseriate.

**C. sanguineus** ssp. **sanguineus** — **Distr:** Sudan, Kenya, Tanzania, Zimbabwe, Moçambique, RSA (Eastern Cape, KwaZulu-Natal); sheer cliffs in Eastern Valley Bushveld vegetation or rocky regions in savannas, summer-flowering. **I:** Phillips & Pole Evans (1921a); Duncan & al. (2016: 292–293).

Bulb halfway above-ground, ovoid, 2–7 cm Ø, solitary or dividing to form small groups, evergreen; tunics brown to grey, scarious, forming a distinct neck with parchment-like scales; **L** 1–4, lanceolate, 30–35 × 0.9–1.7 cm, green, with a prominent midrib on the lower face and a distinct petiole 1–6 cm long; **Inf** 1–2 per plant, to 28 cm, 1- to 4-flowered, scape terete, to 1 cm Ø at the base; spathe valves 2, 4. 4–8.5 cm, lanceolate; **Ped** 2–5 cm; **Fl** ascending-spreading, bright red or pink; **Per** tube 3.5–12.5 cm, campanulate in the upper ½, 2.5 cm Ø at the throat, cylindrical in the lower ½; **Tep** lobes 4–5 × 1.8 cm; **St** included or slightly exserted; **Fil** 2.5 cm; **Anth** 5 mm; **Ov** oblong-triangular; **Sty** overtopping the anthers; **Sti** 3, slender, recurved.

**C. sanguineus** ssp. **wakefieldii** (Sealy) Nordal (Norweg. J. Bot. 26: 189, 1979). **Type:** Tanzania, Songea Distr. (*Milne-Redhead & Taylor* 10735 [K, BR, EA]). — **Distr:** Kenya, Tanzania; *Brachystegia* woodland (savanna), rocky slopes, coast to 1300 m. **I:** Nordal (1979: 187).

≡ *Cyrтанthus sanguineus* var. *wakefieldii* Sealy (1965).

Differs from ssp. *sanguineus*: Bulb 3–4 cm Ø; **L** 10–40 cm; **Ped** 0.3–2.5 cm; **Per** pink or salmon-pink to rose-vermillion, 8–10.5 cm.

## References

- Duncan, G. [ & al. 2016], Jeppe, B. & Voigt, L. (2016) The *Amaryllidaceae* of southern Africa. Hatfield (ZA): Umdaus Press.
- Dyer, R. A. (1939) Description, classification and phylogeny. A review of the genus *Cyrтанthus*. *Herbertia* 6: 65–103.
- Dyer, R. A. (1971) *Cyrтанthus falcatus*. *Flow. Pl. Afr.* 41 (3–4): t. 1632 + 3 pp. text.
- Johnson, S. D. & Bond, W. J. (1994) Red flowers and butterfly pollination in the fynbos of South Africa. In: Arianoutsou, M. & Groves, R. (eds.): *Plant-animal interactions in Mediterranean-type ecosystems*; pp. 137–148. Dordrecht (NL): Kluwer Academic Publishers. [https://doi.org/10.1007/978-94-011-0908-6\\_13](https://doi.org/10.1007/978-94-011-0908-6_13).
- Nordal, I. (1979) Revision of the genus *Cyrтанthus* (*Amaryllidaceae*) in East Africa. *Norweg. J. Bot.* 26: 183–192.
- Phillips, E. P. & Pole Evans, I. B. (ed.) (1921a) *Cyrтанthus sanguineus*. *Flow. Pl. South Afr.* 1: t. 25 + 1 p. text.
- Phillips, E. P. & Pole Evans, I. B. (ed.) (1921b) *Cyrтанthus obliquus*. *Flow. Pl. South Afr.* 1: t. 35 + 2 pp. text.
- Reid, C. & Dyer, R. A. (1984) A review of the southern African species of *Cyrтанthus*. La Jolla (US): American Plant Life Society (= *Plant Life*, Supplement 1).
- Snijman, D. A. & Meerow, A. W. (2010) Floral and macroecological evolution within *Cyrтанthus* (*Amaryllidaceae*): Inferences from combined analyses of plastid ndhF and nrDNA ITS sequences. *South Afr. J. Bot.* 76: 217–238. <https://doi.org/10.1016/j.sajb.2009.10.010>.





## Haemanthus AMARYLLIDACEAE

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**Haemanthus** Linné (Spec. Pl. [ed. 1], 325, 1753). **Type:** *Haemanthus coccineus* Linné [lectotype, designated by Hitchcock & Green, Stand. Spec. Linnean Gen., 1929]. — **Haemantheae** — **Lit:** Snijman (1984: monograph); Conrad & al. (2006: molecular phylogeny); Bay-Smidt & al. (2011: molecular phylogeny); Duncan & al. (2016: 398–463, 671–672, ill. synopsis). **Distr:** Namibia, RSA, Lesotho, Swaziland. **Etym:** Gr. ‘haima, haimatos’, blood; and Gr. ‘anthos’, flower; for the dark red flowers of some species.

**Incl.** *Leucodesmis* Rafinesque (1838). **Type:** *Haemanthus pubescens sensu* Rafinesque.

**Incl.** *Perihema* Rafinesque (1838). **Type:** *Haemanthus coarctatus* Jacquin.

**Incl.** *Serena* Rafinesque (1838). **Type:** *Haemanthus carneus* Ker Gawler [lectotype, designated by Snijman, J. South Afr. Bot. 12 (Suppl.): 17, 1984].

**Incl.** *Diacles* Salisbury (1866). **Type:** *Haemanthus pubescens sensu* Ker Gawler [lectotype, designated by Snijman, J. South Afr. Bot. 12(Suppl.): 17, 1984].

**Incl.** *Melicho* Salisbury (1866). **Type:** *Haemanthus amarylloides* Jacquin [lectotype,

designated by Bjørnstad & Friis, Norweg. J. Bot. 19: 187–206, 1972].

Deciduous or rarely evergreen bulbous geophytes; bulbs usually underground, rarely above-ground or half exposed, variable, usually ovoid to pyriform with fleshy tunics in successive horizontal layers; **L** few, often 2, distichous, fleshy, strap-shaped, patent to ascending; **Fl** in dense umbels to 10 cm Ø; scape compressed; spathe valves firm, fleshy, white to red, broadly ovate; **Per** with short cylindrical tube, lobes spreading to ascending, longer than the tube; **St** 6, fused to the throat of the tube; **Fil** filiform; **Anth** oblong, dorsifixed; **Ov** inferior, globose; **Sty** filiform, **Sti** tricuspidate; **Fr** soft fleshy globose berries; **Se** ovoid, fleshy, wine-red to green.

A genus of 22 species confined mainly to the winter rainfall regions in S Africa with a concentration in Namaqualand.

*Haemanthus* has been found to be monophyletic in recent molecular phylogenetic studies, and is sister to *Scadoxus* (Bay-Smidt & al. 2011). The same study found the genus to consist of 2 well defined clades, corresponding to summer-rainfall taxa with white to pale pink flowers mainly in the Eastern Cape, and, respectively, to winter-rainfall taxa with red to pale pink flowers, mainly in the Western Cape. The summer-rainfall species *H. montanus* is sister to the winter-rainfall group (Bay-Smidt & al. 2011).

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**Fig. 1** *Haemanthus albiflos*. (Copyright: U. Eggli)

Only a few taxa are somewhat succulent. They are native to the summer rainfall region in E RSA and are easily cultivated in containers, but only *H. albiflos* is seen frequently in cultivation.

**H. albiflos** Jacquin (Pl. Hort. Schoenbr. 1: 31, t. 59, 1797). **Type**: [icono]: l.c., t. 59. — **Distr**: RSA (Western Cape, Eastern Cape, KwaZulu-Natal); Albany Thicket vegetation and dry Eastern Valley Bushveld vegetation (savanna biome), autumn- to spring-flowering. **I**: Duncan & al. (2016: 404–405). – Fig. 1.

≡ *Haemanthus pubescens* var. *albiflos* (Jacquin) Ker Gawler (1826) ≡ *Haemanthus virescens* var. *albiflos* (Jacquin) Herbert (1837); **incl.** *Haemanthus pubescens* auct. pl. (s.a.) (*nom. illeg.*, Art. 53.1); **incl.** *Haemanthus virescens* var. *intermedius* Herbert (1837) ≡ *Haemanthus intermedius* (Herbert) M. Roemer (1847); **incl.** *Haemanthus leucanthus* Miquel (1861); **incl.** *Haemanthus ciliaris* Salisbury (1866) (*nom. inval.*, Art. 32.1c); **incl.** *Haemanthus albo-maculatus* Baker (1878); **incl.** *Haemanthus albiflos* var. *brachyphyllus* Baker (1888); **incl.** *Haemanthus albiflos* var. *burchellii* Baker (1888).

Evergreen; bulbs ovoid, to 8 cm broad, clustering, above-ground to halfway underground; tunics truncate at the top, green when exposed to light; **L** strap-shaped to elliptic, appressed to the ground or spreading, flat or canaliculate, smooth or slightly pubescent, apex obtuse to acute; **Inf** 5–35 cm; scape compressed, to 14 mm wide; umbel compact, laterally compressed, to 7 cm wide with 4–8 semi-erect spathe valves; **Fl** to 50,

white; **Ped** to 1 cm; **Per** funnel-shaped, to 23 mm, tube to 7 mm with spreading oblong segments 10–18 × 1–2.5 mm; **Ov** globose, to 3 mm Ø; **Fr** ovoid, to 1 cm Ø, white to red.

**H. avasimontanus** Dinter (Repert. Spec. Nov. Regni Veg. 19(11–13): 186, 1923). **Type** [syn]: Namibia (*Dinter* 4465 [B]). — **Lit**: Craib (2010: with ill.). **Distr**: C Namibia (Auas Mts.); dry savanna, mainly S-facing cliffs on schist ledges, flowering in February. **I**: Duncan & al. (2016: 414–415).

Bulbs winter-deciduous, medianly compressed, to 4.5 cm broad, proliferating from the base by bulblets and forming clusters in rock crevices, usually underground but occasionally exposed, outer tunics becoming brownish and papery; **L** 2, ascending, synanthous, lorate, 35–40 × 4–4.5 cm, glabrous, soft in texture, margin smooth, apex acute; scape 25–35 cm, 7 mm Ø; **Inf** narrowly obconical, ±4.5 cm diam; spathe valves 4–5, spreading, as long as the flowers, lanceolate, ±25–30 × 6 mm, brownish-white, membranous, tips acute; **Fl** 15–20, white; **Ped** 7–10 mm; **Per** ± 20 mm, tube 2.5–3 mm long, segments slightly spreading, linear to lanceolate, ±17 × 1–2 mm, tips acute; **Fil** exerted for up to 3 mm, white; **Anth** 1 mm long, yellow; **Ov** ovoid, 2–3.5 mm; **Sty** as long as the stamens.

The specific epithet is frequently mis-spelled ‘avasmontanus’.

**H. deformis** Hooker *fil.* (Curtis’s Bot. Mag. 97: t. 5903 + text, 1871). **Type**: RSA, KwaZulu-Natal (*McKen* s.n. [[lecto — icono]: l.c., t. 5903]). — **Distr**: RSA (E-most Eastern Cape, KwaZulu-Natal); Eastern Valley Bushveld vegetation, coastal sheltered rocky regions to 1000 m. **I**: Snijman (1984: 65); Duncan & al. (2016: 428–429).

**Incl.** *Haemanthus baurii* Baker (1885); **incl.** *Haemanthus mackenii* Baker (1888).

Evergreen; bulbs solitary or in small clusters, above-ground to halfway underground, laterally compressed, to 16 × 10 cm, tunics truncate at the top, green when exposed; **L** 2–4, broadly oblong, often broader than long, to 24 × 30 cm, appressed to the ground, glabrous to pubescent, margin ciliate, tip obtuse; **Inf** 1–3, almost sessile to 6 cm,

umbel compact, with 6–7 semi-spreading spathe valves; **Fl** to 45, white; **Ped** to 7 mm; **Per** funnel-shaped, to 31 mm, tube 7–9 mm, segments to 23 mm; **Fr** ovoid, to 15 mm  $\varnothing$ , orange to red.

Closely related to *H. albiflos*.

**H. pauculifolius** Snijman & A. E. van Wyk (South Afr. J. Bot. 59(2): 247–250, ill., 1993).

**Type:** RSA, Mpumalanga (*Matthews* 624 [NBG, K, MO, PRE]). —**Distr:** RSA (Mpumalanga), Swaziland; Bushveld (savanna biome), mountainous rocky terrain. **I:** Duncan & al. (2016: 446–447).

Evergreen; bulbs ovoid, 4–5 cm  $\varnothing$ , clustering, above-ground to halfway underground, green, smooth; **L** 1–2, fleshy, strap-shaped to linear-lanceolate, canaliculate, tomentose, 7–10 (–30)  $\times$  2–4.5 cm, apex acute; **Inf** 5–19 cm; scape compressed, to 7 mm wide; umbel compact, compressed, to 3 cm wide, with 4 spathe valves; **Fl** to 19, white; **Ped** to 3 mm; **Per** funnel-shaped, to 35 mm, tube to 13 mm with spreading lanceolate segments 17–20  $\times$  3–4 mm; **Fr** globose, to 15 mm  $\varnothing$ , orange.

## References

- Bay-Smidt, M. G. K. [ & al. 2011], Jäger, A. K., Krydsfeldt, K., Meerow, A. W., Stafford, G. I., Staden, J. van & Rønsted, N. (2011) Phylogenetic selection of target species in *Amaryllidaceae* tribe *Haemantheae* for acetylcholinesterase inhibition and affinity to the serotonin reuptake transport protein. South Afr. J. Bot. 77: 175–83. <https://doi.org/10.1016/j.sajb.2010.07.016>.
- Conrad, F. [ & al. 2006], Reeves, G., Snijman, D. A. & Hedderson, T. A. J. (2006) Generic relationships within the tribe *Haemantheae* (*Amaryllidaceae*) based on plastid DNA sequence data. In: Ghazanfar, S. A. & Beentje, H. (eds): Taxonomy and ecology of African plants, their conservation and sustainable use; pp. 73–83. Richmond (GB): Royal Botanic Gardens, Kew.
- Craib, C. (2010) The rediscovery of *Haemanthus avasmontanus* (*Amaryllidaceae*) in Namibia. *Herbertia* [ser. 3], 64: 67–83, ill.
- Duncan, G. [ & al. 2016], Jeppe, B. & Voigt, L. (2016) The *Amaryllidaceae* of southern Africa. Hatfield (ZA): Umdaus Press.
- Snijman, D. A. (1984) A revision of the genus *Haemanthus* L. (*Amaryllidaceae*). J. South Afr. Bot. 12(Suppl.): 138 pp., ill., key, maps.







## Rauhia AMARYLLIDACEAE

### S. Arroyo-Leuenberger

**Rauhia** Traub (Pl. Life (Stanford) 13: 73, 1957).  
**Type:** *Rauhia peruviana* Traub. — **Andean Clade**  
— **Stenomesseae** — **Lit:** Ravenna (1969: synopsis).  
**Distr:** Peru; Andean rocky slopes. **Etym:** For  
Werner Rauh (1913–2000), German botanist in  
Heidelberg, and specialist of Madagascan succu-  
lents and bromeliads.

Bulbous perennials; bulbs tunicate, under-  
ground, solitary; **L** ascending, hysteranthous  
(in cultivation usually evergreen), distichous,  
oval to oblong, glaucous, fleshy, pseudopetiolate;  
**Inf** lateral, umbellate; scape erect, solid; **Bra** sub-  
erect, lanceolate; **Fl** declinate or horizontal,  
greenish-whitish, tube funnel-shaped; **Tep** oblan-  
ceolate, spreading; **St** inserted in the throat of the  
perianth tube, without staminal cup; **Anth**  
dorsifixed; **Ov** with numerous ovules in each locu-  
le; **Sty** slightly declinate; **Sti** capitate; **Fr** loculi-  
cidal capsules.

This small genus consists of 3 species and is  
known only from Peru. Only *R. multiflora* is  
encountered in cultivation; the other 2 are insuffi-  
ciently known and perhaps conspecific. All  
appear to be evergreen in cultivation.

**R. decora** Ravenna (Pl. Life (Stanford) 37:  
77, 1981). **Type:** Peru, Amazonas (*Ravenna*

3060 [Herb. Ravenna, K]). — **Distr:** Peru (Ama-  
zonas); 500–1000 m.

Bulb ovoid  $\pm 5.5$  cm  $\varnothing$ , tunics fleshy, withering  
papery, brown; **L** 2–6, 20–30  $\times$  8–12 cm; **Inf** 8-  
to 25-flowered; scape to 20–34 cm; **Bra** 2, free to the  
base, broadly ovate,  $\pm 3.8$  cm; **Ped** 6.5–7.5 cm;  
**Per** tube  $\pm 2.2$  cm; **Tep** 4–5 cm, greenish-whitish;  
shorter **Fil**  $\pm 6.2$  cm, longer  $\pm 6.7$  cm; **Ov**  
0.9–1.5  $\times$  0.5 cm; **Sty** declinate, longer than the  
stamens; **Sti** capitate-trilobate.

**R. multiflora** (Kunth) Ravenna (Pl. Life  
(Stanford) 25: 61, 1969). **Type:** Peru, Cajamarca  
(*Herb. Humboldt* 3582 [B]). — **Lit:** Leuenberger  
& Arroyo-Leuenberger (2006: typification).  
**Distr:** Peru (Cajamarca: Jaén); rocky slopes,  
500–1500 m. – Fig. 1.

$\equiv$  *Phaedranassa multiflora* Kunth (1850); **incl.**  
*Phaedranassa megistophylla* Kraenzlin (1917)  
 $\equiv$  *Rauhia megistophylla* (Kraenzlin) Traub (1966);  
**incl.** *Rauhia peruviana* Traub (1957); **incl.** *Rauhia*  
*occidentalis* Ravenna (2002).

Bulb ovoid,  $\pm 10$ –15 cm  $\varnothing$ , tunics fleshy,  
withering papery, brown; **L** 2–4, 20–30  $\times$   
9–15 cm, spreading; **Inf** 8- to 25-flowered; scape  
to 50–120 cm; **Bra** 2 (–3), free to the base,  
broadly ovate,  $\pm 3$  cm; **Ped** 3–9 cm; **Per**  
tube  $\pm 2.2$  cm; **Tep** 4–5 cm, greenish-whitish;  
**Fil** 2 shorter  $\pm 3.1$  cm, 4 longer  $\pm 3.6$  cm; **Sty**  
declinate, as long as or longer than the stamens;  
**Sti** capitate; **Ov** 0.5–1.2  $\times$  0.5 cm.

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**Fig. 1** *Rauhia multiflora*.  
(Copyright: U. Eggli)



**R. staminosa** Ravenna (Pl. Life (Stanford) 34: 68, 1978). **Type:** Peru, Amazonas (*Ravenna* 2091 [Herb. Ravenna]). — **Distr:** Peru (Amazonas); 500 – 1000 m.

Bulb ovoid, 8–10 cm Ø, tunics fleshy, withering papery, brown; **L** 2, 15–30 × 9–15 cm; **Inf** 8- to 24-flowered; scape 40–80 cm; **Bra** 2, free to the base, broadly ovate, 3.2–4 cm; **Ped** 4–9 cm; **Per** tube 1.4–1.7 cm; **OTep** 2–2.3 cm, greenish-whitish; **ITep** 1.8–2.15 cm; shorter **Fil** ± 4.6 cm, longer ± 6.5 cm; **Ov** 0.9–1.1 × 0.5 cm; **Sty** declinate, longer than the stamens; **Sti** capitate.

## References

- Leuenberger, B. E. & Arroyo-Leuenberger, S. (2006) Humboldt, Bonpland, Kunth and the type specimen of *Rauhia multiflora* (Amaryllidaceae) from Peru. *Willdenowia* 36: 601–609, ills. <https://doi.org/10.3372/wi.36.36157>.
- Ravenna, P. (1969) Contribution to South American *Amaryllidaceae*. II. *Pl. Life* (Stanford) 25: 55–76.

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**Part III**

**The Family Anthericaceae**







## Anthericaceae

E. Van Jaarsveld and U. Eggli

Perennial evergreen or geophytic herbs, rarely small shrubs; **R** variable, fibrous or more commonly thickened and succulent, sometimes tuberous or moniliform; rhizome creeping, often covered with old leaf bases, or rarely stems (semi-) erect and succulent; **L** spiral and rosulate, rarely reduced to 1, or distichous, with sheathing base, lamina flat, terete or trigonous, oblong, linear, glabrous to hairy, rarely succulent and xeromorphic, rigid to softly flaccid, margin often fimbriate; **Inf** lateral racemes or panicles, or condensed into clusters; peduncle bracteate; **Fl** 3-merous, hermaphroditic, actinomorphic or rarely slightly zygomorphic, usually small but conspicuous; **Per** stellate, rarely urceolate or campanulate; **Tep** 3 + 3, oblong, often white or yellowish; **St** 6; **Fil** free or connate basally, glabrous or papillate; **Anth** basifixed or dorsifixed-epipeltate, dehiscing longitudinally; **Ov** superior, 3-locular; **Sty** simple, terete, smooth; **Sti** 3-lobed; placentation axile; **Fr** loculicidal dry capsules; **Se** black, flat to angular or rounded, sometimes with an elaiosome.

**Order:** Asparagales

**Important Literature:** Conran (1998: synopsis).

**Distribution:** Worldwide except Antarctica, mainly tropics and subtropics.

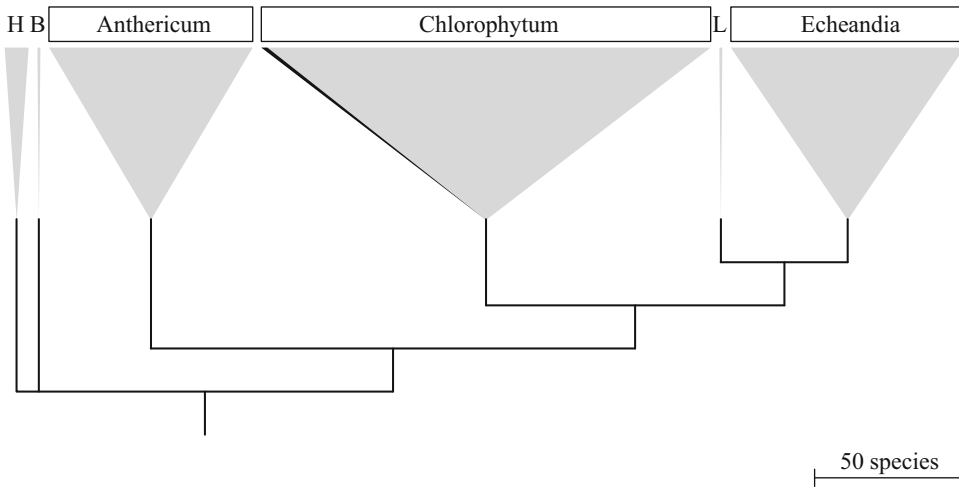
A small family of 8–9 genera and  $\pm 285$  species with a worldwide but mainly subtropical and tropical distribution with centres of diversity in Africa, SE Asia and S America. *Chlorophytum* is the largest genus with  $\pm 100$  (–150) species, followed by the closely related *Anthericum* with  $\pm 65$  species.

In traditional classifications, the family was included within *Liliaceae* s.l., but Bogler & al. (2006), Good-Avila & al. (2006) and Seberg & al. (2012) all found that the family represents a well-circumscribed lineage in sister-group position to the *Agavaceae*. APG (2009) favours a broad concept and includes *Anthericaceae* (together with *Agavaceae*) in *Asparagaceae* s.l., where the family would be placed in subfam. *Agavoideae* (Chase & al. 2009). Here, we follow the concept of Nyffeler & Eggli (2010), and accept *Anthericaceae* at family rank. Other workers have advocated a placement of *Anthericaceae* within a broadly circumscribed *Agavaceae* (e.g. Graham & al. (2006) or Pires & al. (2006)). – Fig. 1.

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**Fig. 1** Summary phylogeny of *Anthericaceae* based on Bogler & al. (2006) (285 species total, data from Maberley (2017) and own counts). B = *Behnia* (=

*Behniaceae*), H = *Herreria* (= *Herreriaceae*), L = *Leucocrinum*. (Diagram by Urs Eggli)

## References

- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>.
- Bogler, D. J. [& al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on *ndhF*, *rbcL*, and its sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>.
- Chase, M. W. [& al. 2009], Reveal, J. L. & Fay, M. F. (2009) A subfamilial classification for the expanded Asparagalean families *Amaryllidaceae*, *Asparagaceae* and *Xanthorrhoeaceae*. *Bot. J. Linn. Soc.* 161(2): 132–136. <https://doi.org/10.1111/j.1095-8339.2009.00999.x>.
- Conran, J. G. (1998) *Anthericaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 114–121, *ills.*, *key*. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_13](https://doi.org/10.1007/978-3-662-03533-7_13).
- Good-Avila, S. V. [& al. 2006], Souza, V., Gaut, B. S. & Eguiarte, L. E. (2006) Timing and rate of speciation in *Agave* (*Agavaceae*). *Proc. Nation. Acad. Sci. USA* 103 (24): 9124–9129. <https://doi.org/10.1073/pnas.0603312103>.
- Graham, S. W. [& al. 2006], Zgurski, J. M., McPherson, M. A., Chemiawsky, D. M., Saarela, J. M., Horne, E. F. C., Smith, S. Y., Wong, W. A., O'Brien, H. E., Biron, V. L., Pires, J. C., Olmstead, R. G., Chase, M. W. & Rai, H. S. (2006) Robust inference of Monocot deep phylogeny using an expanded multigene plastid data set. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 3–21. <https://doi.org/10.5642/aliso.20062201.02>.
- Maberley, D. J. (2017) *Maberley's Plant-Book. A portable dictionary of plants, their classification and uses*. Ed. 4. Cambridge (GB): Cambridge University Press.
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>.
- Pires, J. C. [& al. 2006], Maureira, I. J., Givnish, T. J., Sytsma, K. J., Seberg, O., Petersen, G., Davis, J. I., Stevenson, D. W., Rudall, P. J., Fay, M. F. & Chase, M. W. (2006) Phylogeny, genome size, and chromosome evolution of *Asparagales*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 287–304. <https://doi.org/10.5642/aliso.20062201.24>.
- Seberg, O. [& al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the *Asparagales* based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, *ills.* <https://doi.org/10.3732/ajb.1100468>.



## Chlorophytum ANTHERICACEAE

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**Chlorophytum** Ker Gawler (Curtis's Bot. Mag. 27: t. 1071 + text, 1807). **Type:** *Chlorophytum inornatum* Ker Gawler. — **Lit:** Obermeyer (1962: 690–711 [monograph S Africa]); Nordal & al. (1997: Fl. Tropical E Africa); Kativu & al. (2008: Fl. Zambesiaca); Lebrun and Stork (2014: 25–62, synopsis tropical Africa). **Distr:** Africa, Madagascar, Asia; forests, savanna and Karoo region. **Etym:** Gr. 'chloros', yellowish-green, pale green; and Gr. 'phyton', plant; for the leaves of some taxa.

**Incl.** *Hartwegia* Nees (1831). **Type:** *Hartwegia comosa* Nees [*nom. illeg.*, = *Anthericum sternbergianum* J. A. & J. H. Schultes].

**Incl.** *Hollia* Heynhold (1846) (*nom. illeg.*, Art. 53.1). **Type:** *Anthericum comosum* Thunberg.

**Incl.** *Asphodelopsis* Steudel *ex* Baker (1876). **Type:** not typified.

**Incl.** *Acrospira* Welwitsch *ex* Baker (1878) (*nom. illeg.*, Art. 53.1). **Type:** *Acrospira asphodeloides* Welwitsch *ex* Baker.

**Incl.** *Dasystachys* Baker (1878) (*nom. illeg.*, Art. 53.1). **Type:** *Dasystachys colubrina* Baker [lectotype, designated by Kativu & Nordal, Nordic J. Bot. 13(1): 62, 1993].

**Incl.** *Debesia* Kuntze (1891). **Type:** *Acrospira asphodeloides* Welwitsch *ex* Baker.

**Incl.** *Verdickia* De Wildemann (1902). **Type:** *Verdickia katangensis* De Wildemann.

Perennial evergreen or deciduous and geophytic herbs; **R** variable, mostly succulent, sometimes tuberous; rhizome creeping, often covered with old leaf bases; **L** rosulate, tufted, rarely reduced to 1, or subdistichous, lamina flat, oblong to linear, glabrous to hairy, margin often fimbriate; **Inf** terminal, racemose or paniculate; peduncle bracteate; **Ped** articulated near the middle; **Per** stellate, rarely urceolate or campanulate, white to blue; **Tep** 6, oblong, marcescent, midrib darkening, **OTep** narrower than **ITep**; **St** 6; **Fil** glabrous or papillate; **Anth** basifixed, introrse; **Ov** sessile or shortly stipitate, trigonous, with 6–30 biseriate ovules; **Sty** terete, smooth; **Sti** apical, minute; **Fr** loculicidal trilobate or 3-angled capsules; **Se** flat, rounded, black, shiny.

A large genus with  $\pm$  100 (–150) species occurring mainly in Africa, Madagascar and Asia. *C. comosum* s.l. ("Spider Plant") from South Africa is amongst the World's most commonly cultivated house plants. The genus is traditionally separated from *Anthericum* by its angled capsules (rounded in *Anthericum*) and flat (vs. angular) seeds. Kativu & Nordal (1993) have argued that *Anthericum* should be limited to species with unibracteate nodes and compact seeds, while *Chlorophytum* species have multi-bracteate nodes and thin seeds.

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Several taxa can be regarded as weakly developed succulents due to their fusiformly thickened roots (incl. *C. comosum*). Some have somewhat succulent rhizomes, or slightly fleshy leaves, but none of the latter appears to be in cultivation. The peculiar *C. suffruticosum* is notable for its stem succulence, and has been found to belong to a basal grade of species within the genus (Bjorå & al. 2008b).

**C. bulbinifolium** Hoell & Nordal (Bot. J. Linn. Soc. 157: 228, ill. (p. 229, 236), 2008). **Type:** Zambia, Northern Region (Hoell & Nordal 62 [O, K, SRGH]). — **Distr:** N Zambia (Northern Region); *Brachystegia* woodland, sandy soils, 1200 m; only known from the type locality.

Rhizomes to 10 cm, with a crown of fibres, with fusiform **R** 5–7 mm Ø; **L** in a basal **Ros**, to 12 cm × 0.5–1 mm, glabrous, filiform-semiterete, succulent, canaliculate; **Inf** to 35 cm, peduncle to 20 cm, naked, raceme to 15 cm; **Bra** green, ± 5 × 1 mm; **Fl** 1–2 (–4) per node; **Ped** ± 6 mm, articulated near the middle, green above and pale brown below the articulation; **Tep** white, persistent after anthesis; **OTep** 5–7 × 2 mm; **ITep** 4–5 mm, with 1–3 brownish veins; **Fil** ± 5 mm; **Anth** 2–3 mm; **Fr** trigonous, transversely ridged, to ± 4 × 5 mm, covered by the persistent **Per**; **Se** black, irregularly folded, ± 2 mm. — [U. Eggl].

**C. comosum** (Thunberg) Jacques (J. Soc. Imp. Centr. Hort. 8: 345, 1862). **Type:** RSA, Eastern Cape (Thunberg s.n. [UPS]). — **Lit:** Bjorå & al. (2008a). **Distr:** Widespread in Africa S of the Sahara, from W, C and E Africa (incl. Ethiopia) down to S RSA; in various habitats from coastal forest and thickets to rocks in more open areas, rarely even epiphytic, 0–2450 m; naturalized elsewhere in frost-free climates (e.g. Italy, Spain).

≡ *Anthericum comosum* Thunberg (1794) ≡ *Phalangium comosum* (Thunberg) Poirlet (1804) ≡ *Caesia comosa* (Thunberg) Sprengel (1825) ≡ *Hartwegia comosa* (Thunberg) Nees (1831) ≡ *Hollia comosa* (Thunberg) Heynhold (1846) (incorrect name, Art. 11.4); **incl.** *Anthericum planifolium* Thunberg (1818) (*nom. Illeg.*, Art. 53.1); **incl.** *Anthericum sternbergianum* Schultes & Schultes *fil.* (1829) ≡ *Chlorophytum*

*sternbergianum* (Schultes & Schultes *fil.*) Steudel (1840); **incl.** *Cordylina vivipara* hort. ex Steudel (1840); **incl.** *Phalangium viviparum* Reinwardt ex Kunth (1843); **incl.** *Chlorophytum burchellii* Baker (1876) ≡ *Chlorophytum elatum* var. *burchellii* (Baker) Baker (1897); **incl.** *Chlorophytum sparsiflorum* Baker (1876); **incl.** *Chlorophytum kirkii* Baker (1882); **incl.** *Chlorophytum bukobense* Engler (1895); **incl.** *Chlorophytum bukobense* var. *kilimandscharicum* Engler (1895); **incl.** *Chlorophytum miserum* Rendle (1895); **incl.** *Chlorophytum ramiferum* Rendle (1895); **incl.** *Chlorophytum delagoense* Baker (1897); **incl.** *Chlorophytum brevipes* Baker (1898); **incl.** *Chlorophytum gazense* Rendle (1911); **incl.** *Chlorophytum beniense* De Wildeman (1921); **incl.** *Chlorophytum ituriense* De Wildeman (1921); **incl.** *Chlorophytum elgonense* Bullock (1932); **incl.** *Chlorophytum limurense* Rendle (1932); **incl.** *Anthericum longituberosum* Von Poellnitz (1942); **incl.** *Anthericum vallis-trappii* Von Poellnitz (1942); **incl.** *Chlorophytum elatum* Poellnitz (1946); **incl.** *Chlorophytum glaucidulum* Poellnitz (1946); **incl.** *Chlorophytum glaucidulum* var. *pauper* Poellnitz (1946); **incl.** *Chlorophytum inopinum* Poellnitz (1946); **incl.** *Chlorophytum longum* Poellnitz (1946); **incl.** *Chlorophytum macrophyllum* var. *angustifolium* Poellnitz (1946); **incl.** *Chlorophytum magnum* Poellnitz (1946); **incl.** *Chlorophytum nemorosum* Poellnitz (1946); **incl.** *Chlorophytum paludicola* Poellnitz (1946); **incl.** *Chlorophytum rugosum* Poellnitz (1946); **incl.** *Chlorophytum turrutum*. Poellnitz (1946); **incl.** *Chlorophytum usambarense* Poellnitz (1946).

Perennial evergreen herbs to 80 cm tall and 1 m Ø; **R** fusiform, succulent, to 1 cm Ø; rhizome creeping, 1–1.5 cm Ø, often covered with old leaf bases; **L** 21–65 × 1–3.2 cm, in a dense basal **Ros**, lamina flat, linear, slightly fleshy, glabrous, canaliculate, bright green, margins entire, base sheathing, tips acute; **Inf** terminal spreading lax racemes, 30–100 cm; peduncle bracteate, 2–4 mm Ø; **Bra** linear-lanceolate, 2–4 cm, acuminate; **Fl** often replaced by propagules, which root and serve for vegetative reproduction; **Fil** in axillary fascicles; **Per** stellate, white; **Tep** oblong, to 10 mm, becoming reflexed; **St** 6; **Fil** glabrous;

**Sty** terete, smooth; **Sti** minute; **Fr** 3-angled emarginate capsules; **Se** flat, rounded, black, shiny.

*C. comosum* in its broad sense is a very variable complex of plants, and Nordal & al. (1997: 57–58) opt for a broad definition of the species. Traditionally, the complex was thought to consist of 2 species, *C. comosum* s.s. and *C. sparsiflorum* s.l. *C. comosum* was diagnostically circumscribed by inflorescences producing small plantlets (propagules for vegetative reproduction, making the plants esp. popular in horticulture), while *C. sparsiflorum* is lacking such plantlets. However, populations with both forms occurring together are known. In addition, considerable variation in many vegetative traits is known. The recent study of BJORÅ & al. (2008a) has shown that *C. comosum* s.l. has a polyphyletic origin, and that its delimitation is problematic — it appears likely that several segregates will have to be recognized. One such segregate is described as *C. rhizopendulum* by BJORÅ & al. (2008a) and it differs ecologically as well as morphologically (no tubers but long and thick rhizomes with green aerial roots).

The species is popular in horticulture as undemanding house plant, but is also used as garden plant in frost-free climates. Variegated plants are esp. frequently cultivated, either the cultivar ‘Variegatum’ with white margins, or ‘Vittatum’ with a white mid-stripe. ‘Mboyeti’ has leaves with undulating margins. Aymerich & Gustamante (2015) report that the species is rarely locally naturalized in Spain and Italy. — [E. Van Jaarsveld & U. Eggli]

**C. cremnophilum** Van Jaarsveld (Bradleya 32: 23–24, ill. (pp. 20–23), 2014). **Type:** RSA, Eastern Cape (*Van Jaarsveld* 25,079 [NMG]). — **Distr:** RSA (S Eastern Cape); pendent from E-facing sandstone cliffs.

Evergreen, slow growing, shrubby, to 1.5 m; rhizome to 25 mm Ø at the base, **R** fleshy, white, to 7 mm Ø, slightly tapering to both ends; **Bra** sparingly dichotomously branched, tips upcurving, 30–120 cm, 1.5–2.5 cm Ø, succulent, bare along the lower 1/3, green, leaf bases persistent for some time, finally leaving light coloured rings, sometimes with aerial roots; **L** 30–40 × 1.1–1.6 cm, spirally

in an apical rosette, amplexicaul, long-lived, leathery, linear-lanceolate and the lower part distinctly canaliculate, ascending-spreading, sometimes drooping, green, tip acuminate; **Inf** ascending to ascending-spreading, 90–137 cm; peduncle 7 mm Ø at the base, angular, 72 cm, panicle 69 cm, with 5–7 branches; lower **Bra** linear-triangular, 7.5 × 0.8 cm, acuminate, becoming smaller upwards and more triangular; **Fl** diurnal, 2–3 open together; **Per** stellate, 3 cm Ø, white; **OTep** sometimes slightly reflexed, linear-lanceolate, 15 × 4 mm, acute; **ITep** 16 × 7 mm, linear-obovate; **Fil** white, 10 mm; **Anth** 3 × 1 mm, the upper 1/3 coiled; **Ov** green, globose-trigonal, 2–2.5 mm Ø; **Sty** 15 mm, curved upwards; **Sti** minute, penicillate; **Fr** 3-lobed, 6.5 × ± 8 mm, globose in outline; **Se** black, flattened, 3–4 mm Ø with a pointed hilum, testa minutely granulate.

Similarly succulent stems are found in *C. suffruticosum*.

**C. suffruticosum** Baker (Gard. Chron., ser. nov. 24: 230, 1885). **Type:** Kenya (*Wakefield* s.n. [K]). — **Distr:** S Kenya, NE Tanzania; soil-pockets on rocks, 0–1150 m. **I:** Nordal & al. (1997: 41) – Fig. 1.

≡ *Anthericum suffruticosum* (Baker) Milne-Redhead (1936); **incl.** *Chlorophytum rhizomatosum* Baker (1885); **incl.** *Anthericum acuminatum* Rendle (1895); **incl.** *Anthericum campestre* Engler (1895); **incl.** *Dasystachys polyphylla* Baker (1898) ≡ *Chlorophytum polyphyllum* (Baker) Von Poellnitz (1946); **incl.** *Anthericum inexpectatum* Von Poellnitz (1942); **incl.** *Anthericum longisetosum* Von Poellnitz (1942).

**R**stock fleshy; stems solitary or little-branched, to 1.5 cm Ø, with semicircular ± horizontal but often irregularly arranged **L** scars, dull greenish, sometimes partly covered by fibrous remains of old **L** bases; **L** 45–60 × 1.5–2 cm, in apical **Ros**, ascending to erect, basally sheathing, linear, firm, glabrous, pale greyish-green, slightly succulent and canaliculate; **Inf** erect to drooping or irregular, normally unbranched, to 60 cm; peduncle terete, glabrous, to 30 cm; **Ped** short, ascending, articulate near the middle; **Bra** lanceolate, acuminate, lowermost to 1.3 cm; **Per** to 2 cm Ø, stellate; **Tep** white, outside with green midvein, 3-veined;





**Fig. 1** *Chlorophytum suffruticosum*. (Copyright: U. Eggli)

**Fil** much shorter than the tepals, **Anth** narrowly oblong, yellow; **Fr** and **Se** not described.

This peculiar and interesting stem-succulent is almost without parallel in the family, reminiscent of some species of *Velloziaceae* in vegetative appearance. The only other species with succulent conspicuous stems is the recently described *C. cremnophilum*. Nordal & al. (1997: 40) placed *C. suffruticosum* in the relationship of the stemless

*C. subpetiolatum*, and this position was recently corroborated by BJORÅ & al. (2008b).

## References

- Aymerich, P. & Gustamante, L. (2015) Nuevas citas de plantas alóctonas de origen ornamental en el litoral meridional de Cataluña. *Bouteloua* 20: 22–41, ills.
- BJORÅ, C. S. [ & al. 2008a], Hemp, A., Hoell, G. & Nordal, I. (2008a) A taxonomical and ecological analysis of two forest *Chlorophytum* taxa (*Anthericaceae*) on Mount Kilimanjaro, Tanzania. *Pl. Syst. Evol.* 274 (3–4): 243–253. <https://doi.org/10.1007/s00606-008-0032-0>
- BJORÅ, C. S. [ & al. 2008b], Hoell, G., Kativu, S. & Nordal, I. (2008b) New taxa of *Chlorophytum* (*Anthericaceae*) from southern tropical Africa with notes on their sister group relationships. *Bot. J. Linn. Soc.* 157(2): 223–238, ills. <https://doi.org/10.1111/j.1095-8339.2008.00811.x>
- Kativu, S. & Nordal, I. (1993) New combinations of African species in the genus *Chlorophytum* (*Anthericaceae*). *Nordic J. Bot.* 13(1): 59–65, ills. <https://doi.org/10.1111/j.1756-1051.1993.tb00016.x>
- Kativu, S. [ & al. 2008], Hoell, G., BJORÅ, C. S. & Nordal, I. (2008) *Anthericaceae*. In: Timberlake, J. R. & Martins, E. S. (eds.): *Flora Zambesiaca*; 13(1): 34–89, ills., key. Richmond (GB): Royal Botanic Gardens, Kew.
- Lebrun, J.-P. & Stork, A. L. (2014) Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (*Anthericaceae - Palmae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Nordal, I. [ & al. 1997], Kativu, S. & Poulsen, A. D. (1997) *Anthericaceae*. In: Polhill, R. M. (ed.): *Flora of Tropical East Africa*. Rotterdam (NL)/Brookfield (US): A. A. Balkema.
- Obermeyer, A. A. (1962) A revision of the South African species of *Anthericum*, *Chlorophytum* and *Trachyandra*. *Bothalia* 7(4): 669–767, keys, ills. <https://doi.org/10.4102/abc.v7i4.1679>

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**Part IV**

**The Family Araceae**





## Araceae

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**Including** *Arisaraceae* Rafinesque.  
**Including** *Caladiaceae* Salisbury.  
**Including** *Callaceae* Bartling.  
**Including** *Colocasiaceae* Vines.  
**Including** *Cryptocorynaceae* J. Agardh.  
**Including** *Dracontiaceae* Salisbury.  
**Including** *Lasiaceae* Vines.  
**Including** *Lemnaceae* Gray.  
**Including** *Monsteraceae* Vines.  
**Including** *Orontiaceae* Bartling.  
**Including** *Philodendraceae* Vines.  
**Including** *Pistiaceae* C. Agardh.  
**Including** *Pothaceae* Rafinesque.  
**Including** *Wolffiaceae* Bubani.

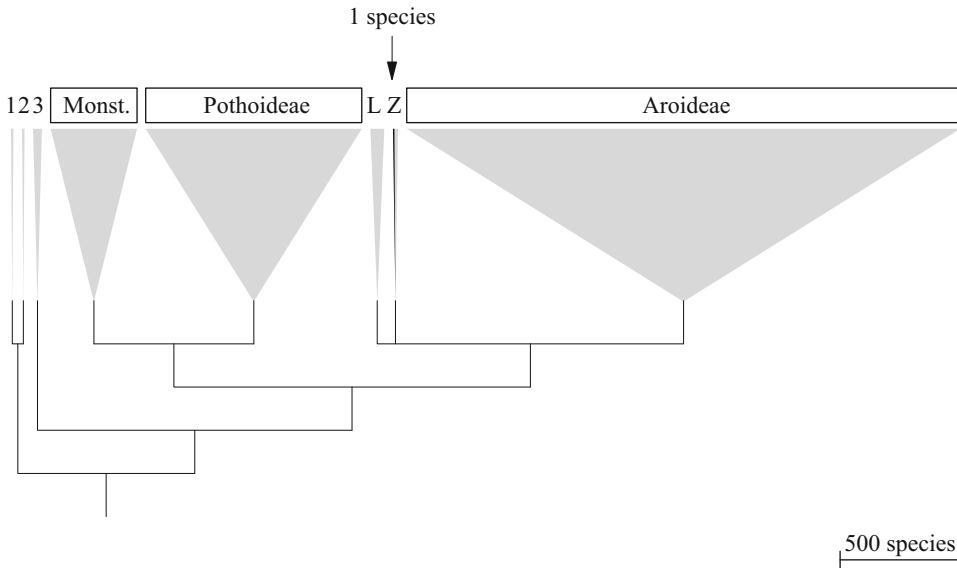
Dwarf to gigantic herbs, terrestrial, hemi-epiphytic or epiphytic, often geophytes or lithophytes, rarely floating (*Lemna*, *Pistia*) or submerged aquatic (*Jasarum*, *Cryptocoryne*); stems climbing, arborescent, erect, repent or subterranean, varying from subglobose tubers to very long rhizomes with elongate internodes; all tissues always with raphides, laticifers commonly present but absent in certain groups; **L** flat with petiole and lamina of very variable shape (except *Gymnostachys* with linear leaves), sometimes pinnatifid to pinnatisect, rarely pinnate, venation reticulate or parallel-pinnate (rarely strictly parallel); **Inf** pseudanthia consisting of

a spadix subtended and/or enveloped or surrounded by a spathe (= last leaf of the shoot, usually specialized in form and colour); spadix usually a dense fleshy spike with sessile (except *Pedicellarum*) minute ebracteate flowers; **Fl** bisexual or unisexual, when unisexual the female **Fl** forming the basal part and the male **Fl** the intermediate or apical part of the spadix (except *Spathicarpa*); **Fl** with or without perianth; **St** opposite to the tepals, free or connate into a synandrium; **Anth** extrorse (except *Zamioculcas*, *Pedicellarum*); **Ov** syncarpous, usually 1- to 3-locular (1- to 8-locular in *Spathicarpeae*, 2- to 47-locular in *Philodendron*), ovules anatropous to orthotropous or intermediate; **Sty** present or absent, often inconspicuous; **Sti** various, discoid to capitate, or  $\pm$  distinctly lobed, always wet at anthesis; **Fr** berries (basally dehiscent in *Lagenandra*), usually free and borne in  $\pm$  cylindrical dense infructescences (rarely syncarpous, *Syngonium*, *Cryptocoryne*); **Se** small to very large, globose to ellipsoid, sometimes reniform, testa very thin to very thick, smooth, ribbed, warty or rarely spiny; embryo minute to large, endosperm present or absent.

**Order:** Alismatales

**Important Literature:** Engler (1905: partial synopsis); Grayum (1990: evolution & phylogeny); Mayo & al. (1997: synopsis); Mayo & al. (1998: synopsis); Keating (2004: anatomy & classification); Tam & al. (2004: partial

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**Fig. 1** Summary phylogeny of Araceae (4150 species total, data from Stevens (2001 onwards, accessed May 2016). 1 = Gymnostachydoideae, 2 = Orontioideae, 3 =

Lemnoideae, L = Lasioideae, Monst. = Monsteroideae, Z = Zamioculcadoideae. (Copyright: U. Egli)

phylogeny); Cabrera & al. (2008: phylogeny); Nauheimer & al. (2012: phylogeny and evolution); Mayo & al. (2013: evolution); Henriquez & al. (2014: molecular phylogeny).

**Distribution:** Worldwide (except Antarctica), but mostly (>90%) in the tropics, especially in rainforests.

**Classification and History:** A family of 120 genera with  $\pm$  4150 species, representing a basal or near-basal lineage within the order Alismatales (Petersen & al. 2016). The circumscription of the family has remained largely uncontested, apart from the recent inclusion of the *Lemnaceae* on molecular grounds (Cabrera & al. 2008). The traditional *Araceae* can be divided in two large groups on the basis of flower morphology, i.e. all basal clades with hermaphroditic flowers on the one hand, and *Aroideae* s.l. with unisexual flowers on the other hand (Mayo & al. 1997, Mayo & al. 1998). Keating (2004) divides the family into 9 subfamilies, while Tam & al. (2004) found 5 major clades in their molecular phylogeny, and Cabrera & al. (2008) recognize 8 subfamilies – Fig. 1.

**Ethnobotany:** Several genera such as *Alocasia*, *Amorphophallus*, *Colocasia* (“Taro”), *Cyrtosperma* and *Xanthosoma* produce edible underground tubers or stems and have great importance as food plants in the tropics. *Monstera deliciosa* produces edible fruits, and some species are valued as houseplants, together with species from several other genera (*Anthurium*, *Dieffenbachia*, *Philodendron*, *Zantedeschia*, etc.).

**Succulence:** Succulence is uncommon in the family, and the only taxon with undisputed succulence is *Zamioculcas*. Several species of *Anthurium* have leathery leaves, and many tuberous (e.g. *Amorphophallus*, *Biarum*, *Eminium*) or rhizomatous members (e.g. *Stylochaeton* [some of its species with very fleshy roots], *Gonatopus* or *Synandropsadix*) have adaptations to seasonally dry conditions. The stems of *Philodendron warszewiczii* K. Koch & C. D. Bouché have been described as water-storing (Schulze & al. 1988), but are more fleshy-juicy without adaptations to water conservation.

The genera *Zamioculcas* and *Gonatopus* together form the subfamily *Zamioculcadoideae* (Bogner and Hesse 2005), which is distributed in



tropical E and SE Africa. It has an isolated position and is sister to subfamily *Aroideae* (Henriquez & al. 2014 and references cited there). *Zamioculcadoideae* (including tribe *Stylochaetoneae* with the only genus *Stylochaeton*, not succulent) are the only *Araceae* with unisexual flowers with a perigone.

## References

- Bogner, J. & Hesse, M. (2005) *Zamioculcadoideae*, a new subfamily of *Araceae*. *Aroideana* 28: 3–20.
- Cabrera, L. I. [& al. 2008], Salazar, G. A., Chase, M. W., Mayo, S. J., Bogner, J. & Dávila, P. (2008) Phylogenetic relationships of Aroids and Duckweeds (*Araceae*) inferred from coding and noncoding plastid DNA. *Amer. J. Bot.* 95(9): 1153–1165. <https://doi.org/10.3732/ajb.0800073>
- Engler, A. (1905) *Araceae—Pothoideae*. In: Engler, A. (ed.): *Das Pflanzenreich*, IV.23B. Leipzig (DE): W. Engelmann. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=575>
- Grayum, H. (1990) Evolution and phylogeny of the *Araceae*. *Ann. Missouri Bot. Gard.* 77: 628–697. <http://www.jstor.org/stable/2399668>
- Henriquez, C. L. [& al. 2014], Arias, T., Pires, J. C., Croat, T. B. & Schaal, B. A. (2014) Phylogenomics of the plant family *Araceae*. *Molec. Phylogen. Evol.* 75: 91–102, ills. <https://doi.org/10.1016/j.ympev.2014.02.017>
- Keating, R. C. (2004) Vegetative anatomical data and its relationship to a revised classification of the genera of *Araceae*. *Ann. Missouri Bot. Gard.* 91(3): 485–494. <http://www.jstor.org/stable/3298625>
- Mayo, S. J. [& al. 1997], Bogner, J. & Boyce, P. C. (1997) The genera of *Araceae*. Richmond (GB): Royal Botanic Gardens Kew.
- Mayo, S. J. [& al. 1998], Bogner, J. & Boyce, P. C. (1998) *Araceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 4: 26–74, ills., key. Berlin/Heidelberg (DE): Springer-Verlag. [https://doi.org/10.1007/978-3-662-03531-3\\_7](https://doi.org/10.1007/978-3-662-03531-3_7)
- Mayo, S. J. [& al. 2013], Bogner, J. & Cusimano, N. (2013) Recent progress in the phylogenetics and classification of *Araceae*. In: Wilkin, P. & Mayo, S. J. (eds.): *Early events in Monocot evolution*, pp. 208–242. Cambridge (GB): Cambridge University Press. <http://www.cambridge.org/9781107012769>
- Nauheimer, L. [& al. 2012], Metzler, D. & Renner, S. S. (2012) Global history of the ancient monocot family *Araceae* inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytol.* 195(4): 938–950, ills., maps. <https://doi.org/10.1111/j.1469-8137.2012.04220.x>
- Petersen, G. [& al. 2016], Seberg, O., Cuenca, A., Stevenson, D. W., Thadeo, M., Davis, J. I., Graham, S. & Ross, T. G. (2016) Phylogeny of Alismatales (Monocotyledons) and the relationship of *Acorus* (Acorales?). *Cladistics* 32: 141–159. <https://doi.org/10.1111/cla.12120>
- Schulze, E.-D. [& al. 1988], Mooney, H. A., Bullock, S. H. & Mendoza, A. (1988) Water contents of wood of tropical deciduous forest species during the dry season. *Bol. Soc. Bot. México* 48: 113–118.
- Tam, S.-M. [& al. 2004], Boyce, P. C., Upson, T. M., Barabé, D., Bruneau, A., Forest, F. & Parker, J. S. (2004) Intergeneric and infrafamilial phylogeny of subfamily *Monsteroideae* (*Araceae*) revealed by chloroplast trnL-F sequences *Amer. J. Bot.* 91(3): 490–498. <https://doi.org/10.3732/ajb.91.3.490>





## Zamioculcas ARACEAE

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**Zamioculcas** Schott (Syn. Aroid., 71, 1856).  
**Type:** *Zamioculcas loddigesii* Schott [*nom. illeg.*, = *Z. zamiifolia*]. — **Zamioculcadoideae** — **Lit:** Haigh and Boyce (2012: 22–24). **Distr:** Tropical E and SE Africa. **Etym:** For the genus *Zamia* (*Zamiaceae*); and from Arab. ‘qolqas’, ‘kulkas’, the name of the Taro plant (*Colocasia*); for the leaves, which resemble those of *Zamia*, and the placement in the same family as *Colocasia*.

Seasonally dormant or evergreen herbs with a short very thick rhizome 2–4 cm Ø; **L** few to many, erect, 40–80 cm, pinnate, leaflets deciduous leaving the persistent succulent petiole, petiole 10–35 cm, terete, basally thickened, 1–2 cm Ø, geniculate at the apex, sheath ligulate, free almost to the base, very short and inconspicuous, leaflets ± opposite, oblong-elliptic, 5–12 × 1.5–6 cm, coriaceous and thickish, dark glossy green, midvein thick, primary lateral veins pinnate, higher order venation reticulate; **Inf** 1–2 in each floral sympodium at ground-level; peduncle 3–20 cm, erect but recurved at fruiting time; spathe entirely persistent to fruiting stage, 5–10 cm, coriaceous, slightly constricted between tube and lamina, outside greenish, inside whitish, tube convolute, lamina longer than the tube, first expanded horizontally, later reflexed; spadix sessile, 5–8 cm, female zone subcylindrical, 1–2 × 0.7–1.5 cm Ø, separate from the male zone by a

short constriction with sterile flowers; male zone cylindrical, ellipsoid to clavate, fertile to apex, 4–6 × 1–1.5 cm Ø, falling off after anthesis; **Fl** unisexual; **Tep** 4 in 2 series, ± 3 mm, whitish, decussate, thickish; **male Fl** with 4 **St** shorter than the tepals; **Fl** free, oblong, thick, somewhat flattened; **Anth** introrse, pollen extruded in strands, pollen grains hamburger-shaped, large (c. 60 µm), fully zonate, exine fossulate-foveolate; pistillode clavate, as long as the tepals; **sterile Fl** with 4 **Tep** surrounding a clavate pistillode; **female Fl:** **Gy** equalling the tepals; **Ov** ovoid, 2-locular with 1 hemianatropous ovule per locule, placentation axile near the base of the septum; **Sti** large, discoid-capitate, ± 1.5 mm Ø; staminodes lacking; **Fr** a subglobose to ellipsoid infructescence at ground-level, to 3 cm Ø, berries depressed-globose, white, to 1.2 cm Ø, furrowed at the septum, 1- to 2-seeded, surrounded by the persistent tepals; **Se** ellipsoid, ± 8 × 4–5 mm, testa smooth, brown, raphe conspicuous, embryo large, endosperm almost absent. — **Cytology:** 2n = 34.

The only species of this monotypic genus is highly variable and is notable for the pronounced development of ‘leaf petiole succulence’. The upper part of the leaf abscises at a pre-formed layer at the top of the petiole. Crassulacean Acid Metabolism was reported by Holtum & al. (2007), and *Zamioculcas* is a flexible CAM-plant, with significant CAM appearing only during water stress conditions. It is the only taxon of the whole order Alismatales for which this mode of photosynthesis has been recorded so far. Its floral

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**Fig. 1** *Zamioculcas zamiifolia*. (Copyright: U. Eggli)

anatomy was studied by Barabé and Forget (1989), the palynology by Hesse & al. (2001).

The leaves are reported to be poisonous to goats (P. R. O. Bally, pers. comm.). The plants are used in the traditional medicine in Tanzania and Malawi.

**Z. zamiifolia** (Loddiges) Engler (Pflanzenr. IV. 23B: 305, Figs. 85, 1905). **Type:** [icono]: Bot. Cab. 15: t. 1408, 1829. — **Distr:** Kenya, Tanzania (incl. Pemba and Zanzibar), Malawi, Zimbabwe, Moçambique, RSA (KwaZulu-Natal); tropical moist lowland to submontane forests or savannas, often on stony ground, to 600 m. **I:** Obermeyer and Strey (1969) – Fig. 1.

≡ *Caladium zamiifolium* Loddiges (1829); **incl.** *Zamioculcas loddigesii* Schott (1856) (*nom. illeg.*, Art. 52.1); **incl.** *Zamioculcas lanceolata* Peter (1930).

Description as for the genus.

*Z. zamiifolia* is a common house-plant today in Europe and the USA, and it is produced in enormous numbers each year (Chen and Henny 2003) and sometimes marketed under the vernacular name “ZZ plant”. Plants can readily be propagated by detaching individual leaflets, which rapidly root. A variegated cultivar is also sometimes seen in cultivation.

## References

- Barabé, D. & Forget, S. (1989) Anatomie des fleurs fertiles et stériles de *Zamioculcas* (Araceae). Bull. Mus. Nation. Hist. Nat., Sect. B, Adansonia 10(4): 411–419, ills. <http://biodiversitylibrary.org/page/13738508>
- Chen, J. J. & Henny, R. J. (2003) ZZ: A unique tropical ornamental foliage plant. HortTechnol. 13(3): 458–462, ills. <http://horttech.ashspublications.org/content/13/3/458>
- Haigh, A. & Boyce, P. C. (2012) *Araceae*. In: Timberlake, J. R. & Martins, E. S. (eds.): Flora Zambesiaca, Volume 12, part 1; pp. 1–52, ills., keys. Richmond (GB): Royal Botanic Gardens, Kew, for Flora Zambesiaca Managing Committee.
- Hesse, M. [ & al. 2001], Bogner, J., Halbritter, H. & Weber, M. (2001) Palynology of the perigoniata *Aroideae*: *Zamioculcas*, *Gonatopus* and *Stylochaeton* (Araceae). Grana 40(1–2): 26–34. <https://doi.org/10.1080/00173130152591859>
- Holtum, J. A. M. [ & al. 2007], Winter, K., Weeks, M. A. & Sexton, T. R. (2007) Crassulacean Acid Metabolism in the ZZ plant, *Zamioculcas zamiifolia* (Araceae). Amer. J. Bot. 94(10): 1670–1676. <https://doi.org/10.3732/ajb.94.10.1670>
- Obermeyer, A. A. & Strey, R. G. (1969) *Zamioculcas zamiifolia*. Flow. Pl. Afr. 40(1–2): t. 1562 + 3 pp. text.

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**Part V**

**The Family Asparagaceae**







# Asparagaceae

E. Van Jaarsveld and U. Eggli

Perennial shrubs or subshrubs, often scrambling or climbing, with herbaceous to woody perennial or annual shoots; rhizome short, sympodial, **R** sometimes succulent and fusiform; stems wiry and tough, rarely twining, sometimes spiny, and **Sp** derived from modified lateral branches or leaves, usually with lateral branches transformed into leaf-like phylloclades, or modified stems (assimilatory structures) fasciculate, green, slender and needle-like; **L** often reduced to scale-like structures, spurred; **Fl** small, actinomorphic, solitary or in umbellate or racemose **Inf**, hermaphrodite or unisexual (then plants dioecious); **Te** 3 + 3, white, yellow or green, free and spreading or basally fused to form a campanulate perigone; male and hermaphrodite flowers with 3 + 3 **St**, **Fi** free or fused with the tepals; **Anth** introrse, dorsifixed; **Ov** superior, 3-locular, placentation axile with 2–12 ovules per locule; **Sty** short; **Sti** capitate or lobed; **Fr** globose red, blue or white berries; **Se** globose, black.

**Order:** Asparagales

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**Important Literature:** Kubitzki & Rudall (1998: synopsis).

**Distribution:** Widely distributed in the Old World, rare in the New World (only *Hemiphylacus* in Mexico).

The *Asparagaceae* s.s., in old traditional classifications included in the *Liliaceae*, are widely distributed in the Old World. They occur mainly in semi-arid to arid Mediterranean climates, and taxa with xeromorphic adaptations such as succulent tuberous roots are common. Photosynthesis occurs mainly with green branches and branchlets (phylloclades), and true leaves are reduced to scales. The small family embraces only 2 genera, *Asparagus* and *Hemiphylacus* (Kubitzki & Rudall 1998). *Hemiphylacus* (native to Mexico) counts 5 species (none succulent) and *Asparagus* embraces the majority of the ±200 (–290?) species of the family. Older treatments of the family recognized *Protasparagus* and *Myrsiphyllum* as separate genera (e.g. Obermeyer & al. (1992)), but the differences between them and *Asparagus* are only minor (Malcomber & Demissew 1993; Fellingham & Meyer 1995).

Recent years saw a movement towards expanding the circumscription of the family, and APG (2009) as well as Chase & al. (2009) proposed to subsume *Agavaceae*, *Anthericaceae*, *Eriospermaceae*, *Hyacinthaceae* and *Ruscaceae* (including *Dracaenaceae* and *Nolinaceae*) under a vastly expanded family *Asparagaceae*. Here we

follow Nyffeler & Eggli (2010) and Judd & al. (2016) and accept a narrow circumscription of *Asparagaceae*. A broadened *Asparagaceae* is phylogenetically not more correct than the traditional family concepts, which are therefore retained.

Economically important plants include *Asparagus officinalis* Linné (“Garden Asparagus”, used as vegetable) as well as *A. setaceus* (Kunth) Jessop (“Fern Asparagus”, used by florists for decoration). Only a few species of *Asparagus* can be considered succulent due to their succulent roots.

## References

- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>.
- Chase, M. W. [ & al. 2009], Reveal, J. L. & Fay, M. F. (2009) A subfamilial classification for the expanded Asparagalean families *Amaryllidaceae*, *Asparagaceae* and *Xanthorrhoeaceae*. *Bot. J. Linn. Soc.* 161(2): 132–136. <https://doi.org/10.1111/j.1095-8339.2009.00999.x>.
- Fellingham, A. C. & Meyer, N. L. (1995) New combinations and a complete list of *Asparagus* species in southern Africa (*Asparagaceae*). *Bothalia* 25(2): 205–209. <https://doi.org/10.4102/abc.v25i2.728>.
- Judd, W. S. [ & al. 2016], Campbell, C. S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J. (2016) *Plant systematics: A phylogenetic approach*. Ed. 4. Sunderland (US): Sinauer Associates.
- Kubitzki, K. & Rudall, P. J. (1998) *Asparagaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 125–129, ills., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_15](https://doi.org/10.1007/978-3-662-03533-7_15).
- Malcomber, S. T. & Sebsebe Demissew (1993) The status of *Protasparagus* and *Myrsiphyllum* in the *Asparagaceae*. *Kew Bull.* 48(1): 63–78. <http://www.jstor.org/stable/4115749>.
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>.
- Obermeyer, A. A. [ & al. 1992], Immelman, K. L. & Bos, J. J. (1992) *Dracaenaceae*, *Asparagaceae*, *Luzuriagaceae* and *Smilacaceae*. In: Leistner, O. A. (ed.): *Flora of Southern Africa*, Vol. 5, part 3. Pretoria (ZA): National Botanic Institute.



## Asparagus ASPARAGACEAE

E. Van Jaarsveld and U. Egli

**Asparagus** Linné (Spec. Pl. [ed. 1], 1: 313, 1753). **Type:** *Asparagus officinalis* Linné. — **Lit:** Jessop (1966: synopsis S Africa); Obermeyer (1984: revision S Africa, as *Myrsiphyllum*); Obermeyer & al. (1992: flora S Africa); Malcomber & Sebsebe Demissew (1993: classification); Norup & al. (2015: phylogeny). **Distr:** Old World excluding Australasia; invasive neophytes elsewhere (e.g. Australia, New Zealand). **Etym:** Lat., asparagus, cultivated asparagus.

**Incl.** *Myrsiphyllum* Willdenow (1808). **Type:** *Medeola asparagoides* Linné.

**Incl.** *Asparagopsis* (Kunth) Kunth (1850) (*nom. illeg.*, Art. 53.1). **Type:** *Asparagus aethiopicus* Linné.

**Incl.** *Hecatrix* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Medeola asparagoides* Linné.

**Incl.** *Protasparagus* Obermeyer (1983). **Type:** *Asparagus aethiopicus* Linné.

Shrubs, soft to woody sometimes spiny subshrubs, or scramblers, from a usually multi-stemmed tuberous base; stems often annual;

rhizome short, sympodial, mostly covered with persistent ascending cataphylls; **R** often swollen, fusiform and succulent, radiating from the rhizome, sometimes exposed but usually underground; stems ascending, sometimes with assimilating branchlets, sometimes modified into flat leaf-like phylloclades; phylloclades solitary or fascicled, deciduous to persistent, linear to ovate; **L** reduced and scale-like; **Inf** 1- to few-flowered, raceme-like; **Fl** small, white, yellowish or green, often inconspicuous, uni- or bisexual; **Tep** 3 + 3, all of similar shape, usually free or fused at the base into a campanulate perigone; male **Fl** with 3 + 3 **St**; **Fil** free; **Anth** dorsifixed, introrse, sterile in unisexual female flowers; **Ov** superior, trilocular; **Sty** short; **Sti** capitate or lobed; **Fr** globose berries, red, brown, blue or black, **Se** 1 to several, globose, black.

*Asparagus* is a large genus of  $\pm 200$  (–290?) species (Kubota & al. 2012), restricted to the Old World, and many are native to semiarid to arid climates, and xeromorphic in nature. The diversification hotspot is S Africa. (Norup & al. 2015). Many species have fleshy, succulent tubers disposed along their rhizomes, and are geophytic succulents. Seedlings of many species first develop rather weak above-ground growth, but have a comparatively huge succulent main root. Leaves are reduced to scales, and the photosynthetic organs are fascicled phylloclades of various shape (flattened and leaf like, terete, or angled). The spines, where present, are of different origins, and either represent the hardened spurs of the primary leaves, hardened phylloclades, or sterile

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spur branches (Kubitzki & Rudall 1998). The phylloclades are modified axillary shoots where genes usually associated with leaf development are co-opted into phylloclade development (Nakayama & al. 2012a, Nakayama & al. 2012b).

**Classification:** In earlier classifications (e.g. Obermeyer & al. 1992) 3 separate three genera *Asparagus*, *Protasparagus* and *Myrsiphyllum* were recognized, following Dahlgren & al. (1985). Later authors found this division untenable (Malcomber & Sebsebe Demissew 1993). All 3 genera are today subsumed under an expanded *Asparagus* s.l. but — contrary to Malcomber & Sebsebe Demissew (1993) who accepted only 2 subgenera — represent separate clades in the molecular phylogeny presented by Kubota & al. (2012):

- [1] Subgen. *Asparagus*: Flowers unisexual and plants dioecious, ovary locules with 2 ovules, phylloclades terete.
- [2] Subgen. *Protasparagus*: Flowers bisexual, tepals free, ovary locules with 4 to many ovules; spines usually present; phylloclades usually dorsiventrally flattened.
- [3] Subgen. *Myrsiphyllum*: Flowers bisexual, tepals fused in the lower  $\frac{1}{2}$ , ovary locules with 4 to many ovules; spines absent; phylloclades usually dorsiventrally flattened.

The phylogeny of Kubota & al. (2012) is not supported by the results of the more detailed study of Norup & al. (2015), which found 6 clades which can also be diagnosed morphologically. Since the re-classification based on this research has not yet been published, we continue to use the traditional classification as given above for the time being. Norup & al. (2015) moreover found that about  $\frac{1}{3}$  of the studied species are not monophyletic in their analyses, supporting earlier suggestions from other sources. Species delimitations in several groups are in need of further research as to variability and suitable defining traits.

The origin of the genus is likely S Africa, with subsequent dispersal throughout the Old World (Kubota & al. 2012). This biogeographic scenario is also supported by Norup & al. (2015).

**Terminology:** Depending on the literature consulted, the term “cladode” is used for the leaf-like photosynthetic structures. The terms “cladode” and “phylloclade” are frequently used indiscriminately, esp. in English-language publications, but for *Asparagus*, the term “phylloclade” should be used, since these structures represent modified short shoots, while “cladode” refers to a modified long shoot. [U. Eggli].

**Use and cultivation:** Some species are edible such as *A. officinalis* (“Garden Asparagus”, young shoots), *A. abyssinicus*, *A. lucidus* or *A. densiflorus* (tubers). Only a small selection of tuberous-rooted species is covered below as succulents. These are becoming more popular, and esp. those with exposed tuberous roots are attractive. Most are easily grown from seed and make attractive long-lived container and garden plants.

**A. asparagoides** (Linné) W. Wight (Century Dict. 11: 854, 1909). **Type:** [lecto — icono]: Tilli, Cat. Pl. Horti Pisani, 17, t. 12: fig. 1–2, 1723. — **Distr:** Tropical Africa to Namibia, Malawi, Zimbabwe and RSA; Succulent Karoo, thickets, savanna, flowers mid-winter to spring; invasive alien in Australia. **I:** Obermeyer & al. (1992: 72, fig. 14: 2, sub *Myrsiphyllum*).

≡ *Medeola asparagoides* Linné (1753) ≡ *Myrsiphyllum asparagoides* (Linné) Willdenow (1808) ≡ *Hecatris asparagoides* (Linné) Salisbury (1866); **incl.** *Medeola angustifolia* Miller (1768) (*nom. illeg.*, Art. 52.1) ≡ *Myrsiphyllum angustifolium* (Miller) Willdenow (1808) (*nom. illeg.*, Art. 52.1) ≡ *Asparagus medeoloides* var. *angustifolius* (Miller) Baker (1896) (*nom. illeg.*, Art. 52.1); **incl.** *Dracaena medeoloides* Linné fil. (1782) ≡ *Asparagus medeoloides* (Linné fil.) Thunberg (1794); **incl.** *Myrsiphyllum falciforme* Kunth (1850) ≡ *Asparagus medeoloides* var. *falciformis* (Kunth) Baker (1896); **incl.** *Asparagus kuisibensis* Dinter (1931).

[3] Scandent much-branched perennials with wiry twisted stems and shiny green ovate phylloclades, deciduous or semideciduous; rhizome cylindrical, with numerous lateral, fusiform, radially arranged **R** tubers, these to 6 × 2 cm but variable in size, close to the rhizome but not



overlapping; stems wiry, twisting, smooth or ridged, to 2 m; **Br** short, with beaded ridges; phylloclades variable in size and shape, ovate-acuminate, to 4 × 2 cm, flat or folded and curved, many-veined but mostly with 3 more pronounced veins on each face, margin smooth or minutely denticulate; **Ped** to 10 mm, articulated below the perianth; **Tep** to 10 mm, forming a tube in the lower ½, reflexed above; **St** erect, connivent; **Fil** expanded below into 2 small spreading teeth; **Anth** red; **Ov** pear-shaped, stipitate, narrowed into a **Sty** as long as the ovary, ovules to ± 6 in each locule; **Sti** short, spreading, ciliate; **Fr** globose, ± 1 cm Ø, usually many-seeded. — [E. Van Jaarsveld]

**A. crassicladius** Jessop (Bothalia 9: 75, 1966). **Type:** RSA, Eastern Cape (*Esterhuysen* 4670 [BOL]). — **Distr:** RSA (North-West, Eastern Cape: Uniondale to Somerset East); mainly in Albany Thicket vegetation and savanna.

≡ *Protasparagus crassicladius* (Jessop) Obermeyer (1983).

[2] Ascending scandent to spreading tufted shrubs to 2 m tall; rhizome broad and woody with fleshy roots, lateral roots producing fusiform tubers; stem woody, tortuous, slightly pubescent, becoming glabrous, with short recurved spines; phylloclades somewhat succulent, oval, acuminate, 1- to 12-nate, 1.2–2.5 cm long; **Inf** racemes, paired, to 6 cm; **Fl** 2–6 in fascicles; **Ped** 3–4 mm; **Tep** oblong, sometime slightly obovate, 3 mm long, cream-coloured; **St** 2.3 mm; **Anth** minute; **Ov** with 4 ovules per locule; **Sty** 1.5 mm, with short spreading **Sti**; **Fr** unknown. — [E. Van Jaarsveld]

**A. densiflorus** (Kunth) Jessop (Bothalia 9(1): 65, 1966). — **Distr:** RSA (Eastern Cape, KwaZulu-Natal, Limpopo, Mpumalanga), Swaziland, Moçambique; mainly along the coast of the Indian Ocean, on dunes and rocks, spring- to autumn-flowering.

**Incl.** *Asparagopsis densiflora* Kunth (1850) ≡ *Asparagus sarmentosus* var. *densiflorus* (Kunth) Baker (1875) ≡ *Protasparagus densiflorus* (Kunth) Obermeyer (1992); **incl.** *Asparagus meyersii* hort. (s.a.) (*nom. inval.*, Art. 29.1); **incl.**

*Asparagus aethiopicus* var. *ternifolius* Baker (1871) ≡ *Asparagus ternifolius* (Baker) Hooker fil. (1900); **incl.** *Asparagus sarmentosus* var. *comatus* Baker (1875); **incl.** *Asparagus myriocladus* Baker (1889); **incl.** *Asparagus sprengeri* Regel (1890).

[2] Many-stemmed spreading shrublets, sometimes scrambling and ascending; tubers on the rhizome or laterally on the roots; stems spreading or ascending, to 60 cm, usually straight or slightly tortuous, finely ridged, glabrous; branchlets numerous, to 10 cm, grooved, spreading or ascending; phylloclades flattened or rarely 3-angled, slightly arcuate, 5–15 mm, mucronate, sometimes ternate or numerous, with distinct midrib when flattened; **Sp** well-developed but often not pungent; **Inf** peduncles shorter than the branchlets, sometimes not differentiated; **Fl** solitary; **Ped** articulated near the middle; **Tep** oblong-obovate, obtuse, spreading, white or pale pink, 2–5 mm; **St** ¾ as long as the tepals; **Sty** divided for ± ½ of the length; **Fr** globose, red, ± 5–10 mm Ø, 1-seeded.

Very variable with several local forms. Popular in cultivation, esp. in coastal gardens. Commonly encountered cultivars in Europe are:

‘Sprengeri’: Medley-Wood sent seeds to Sprenger who became its main distributor in Europe at that time (Obermeyer et al. 1992).

‘Meyersii’: A very distinct form with ascending compact cylindrical branches and decorative red berries within the “cylinder”. This form was recently discovered in the wild by the present author along the lower Kei River (S of Gaika Ford), and this seems to be its main distribution range. — [E. Van Jaarsveld]

**A. juniperoides** Engler (Bot. Jahrb. Syst. 10: 3, 1889). **Type:** Namibia (*Marloth* 1538 [B]). — **Distr:** Namibia, RSA (Northern Cape, Western Cape); winter-rainfall regions, in Succulent Karoo and Fynbos, autumn- to mid-winter-flowering.

≡ *Myrsiphyllum juniperoides* (Engler) Obermeyer (1984).

[3] Ascending shrublets, 60–100 cm tall, from a tuberous horizontally creeping rootstock; tubers sessile to shortly stalked, fusiform; stems erect,

annual, glabrous, grooved; branchlets narrow, numerous, to 3 cm, borne directly on the stems; branchlets and phylloclades together forming a cylindrical tapering outline almost like a juniper tree; phylloclades solitary, to 1 cm, flattened, linear, with ciliate margins; **Sp** absent; **Inf** axillary, 1-flowered; **Ped**  $\pm$  2 mm, distally articulated; **Tep** oblong, to 6 mm, white with a green streak and ciliate margins; **St** almost as long as tepals; **Fil** not spurred; **Anth** minute, yellow; **Ov** globose, 1–1.5 mm; **Fr** globose, 1- to 3-seeded,  $\pm$  5 mm  $\varnothing$ , red. — [E. Van Jaarsveld].

**A. mucronatus** Jessop (Bothalia 9(1): 56, 1966). **Type:** RSA, Northern Cape (*Theron* 551 [PRE]). — **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape); in Nama Karoo, Succulent Karoo and Albany Thicket vegetations, usually in brackish soil, mid-summer-flowering.

$\equiv$  *Protasparagus mucronatus* (Jessop) Obermeyer (1992).

[2] Many-stemmed shrubs to  $\pm$  1 m (rarely 2 m) tall, from a distinct tuberous **R**stock; tubers horizontally spreading, often exposed, greyish-brown, to 2 cm  $\varnothing$ ; stems erect, biennial, straight, becoming zigzag higher up, grey to brown, branches acute, to 2 cm; branchlets fascicled and up to 6-nate, pubescent or scabrid, to 6 cm with **Bra** to 5 mm; phylloclades to 10-nate, straight to arcuate, 3–8 mm, terete with non-pungent mucro; **Inf** axillary, 1- or 2-flowered, 4–7 mm; **Ped** articulated below the middle; **Tep** oblong-obovate, 3–4 mm; **St** slightly shorter than the tepals; **Anth** globose; **Ov**  $\pm$  1 mm; **Sty** shortly divided, slightly  $<$  1 mm; **Fr** globose, fleshy, red and wrinkled when ripe,  $\pm$  5 mm  $\varnothing$ , 1- to 2-seeded. — [E. Van Jaarsveld]

**A. multituberosus** R. A. Dyer (Bothalia 6: 442, 1954). **Type:** RSA, Western Cape (*Marloth* 9006 [PRE, STE]). — **Distr:** RSA (Northern Cape, Western Cape); Renosterveld and Fynbos vegetations, flowers winter and spring. **I:** Obermeyer & al. (1992: 72, fig. 14: 1, as *Myrsiphyllum*).

$\equiv$  *Myrsiphyllum multituberosum* (R. A. Dyer) Obermeyer (1984).

[3] Scandent much-branched perennials to 40 cm tall; rhizome thin, horizontal, to 50 cm, with densely overlapping small fusiform tubers 10  $\times$  3 mm; phylloclades ovate to cordate, to 2.5 cm, many-veined, tip apiculate, margin papillate; **Fl** 1–3, axillary from membranous scale-leaves; **Ped** 5 mm, curved, articulated below the flower; **Tep**  $\pm$  7 mm, forming a wide tube below, spreading above; **St** as long as the tepals; **Fil** basally broadened, flat; **Ov** ovoid, with up to 12 ovules per locule; **Sty** 3, curved outwards; **Sti** apical, papillate; **Fr** not seen. — [E. Van Jaarsveld]

**A. ovatus** Salter (J. South Afr. Bot. 6: 167, 1940). **Type:** RSA, Western Cape (*Salter* 8214 [BOL, NBG, PRE]). — **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape); mainly along the coast in Fynbos, Succulent Karoo and thickets. **I:** Obermeyer & al. (1992: 72, fig. 14: 3, 5, as *Myrsiphyllum*).

$\equiv$  *Myrsiphyllum ovatum* (Salter) Obermeyer (1984).

[3] Scandent deciduous twiners to 1.5 m tall; rhizome compact, scaly, woody, with long spreading **R**, tubers numerous, hard, swollen, fusiform, 5–10  $\times$  2–4 mm, developing at some distance from the rhizome; phylloclades deciduous, ovate, 3  $\times$  1.5 cm, many-veined, shiny; **Fl** 2–3, behind the base of the phylloclades; **Ped** 10 mm, articulated near the base of the flower; **Tep**  $\pm$  6 mm, reflexed; **Fil** flattened, erect, with small basal spur on each side; **Ov** oblong, with up to 10 ovules per locule; **Sty** and **Sti** just exerted from the staminal column; **Fr** 10 mm  $\varnothing$ , globose, red when ripe. — [E. Van Jaarsveld]

**A. oxyacanthus** Baker (J. Linn. Soc., Bot. 14: 625, 1875). **Type:** RSA, Eastern Cape (*Bowker* s.n. [K, PRE [photo]]). — **Distr:** RSA (Eastern Cape); in Albany Thicket vegetation; flowering spring to summer.

$\equiv$  *Protasparagus oxyacanthus* (Baker) Obermeyer (1983).

[2] Tufted with tuberous **R**, tubers distant,  $\pm$  6 cm long; stems unbranched, ascending to spreading, 50 cm, pubescent, with numerous narrow, softly spine-like leaf spurs; **Br** solitary,

lacking branchlets; phylloclades solitary, oblong, to 4 cm, with a median vein and thickened margin, mucronate; **Fl** solitary from the axils of the phylloclades; **Ped** 2 mm, articulated distally; **Tep** obovate, obtuse, white, 2–3 mm long, spreading to ascending; **Anth** large, to 0.7 mm; **Ov** globose; **Sty** branches free, short; **Fr** fleshy and red when ripe. — [E. Van Jaarsveld]

**A. striatus** (Linné *fil.*) Thunberg (Prodr. Fl. Cap., 65, 1794). **Type:** RSA, “Cape Prov.” (*Thunberg* s.n. [UPS]). — **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape, Free State); Nama Karoo, Succulent Karoo, Albany Thicket vegetation, on dry stony outcrops, flowering spring to summer.

≡ *Dracaena striata* Linné *fil.* (1781) ≡ *Myrsiphyllum striatum* (Linné *fil.*) Kunth (1850) ≡ *Protasparagus striatus* (Linné *fil.*) Obermeyer (1983); **incl.** *Dracaena erecta* Linné *fil.* (1782) ≡ *Asparagus erectus* (Linné *fil.*) Thunberg (1794); **incl.** *Dracaena stricta* Schultes (1828) (*nom. inval.*, Art. 61.1).

[2] Rhizomes with laterally placed **R** tubers; stems erect, glabrous to minutely pubescent, woody, grooved, branches ascending, similar to the stem, often zig-zag, not further branched; phylloclades terminal and 2- to 3-nate, variable, linear to lanceolate 10–40 × 1–5 mm, rarely almost terete; **Sp** not well developed, small, reflexed; **Fl** in terminal fascicles of 1–2 to up to 15 or more; **Ped** ± 5 mm, articulated below the middle; **Tep** 3–4 mm long, oblong-obovate with a serrate apex; **St** not spurred, almost as long as the tepals; **Anth** ± 0.5 mm; **Sty** ± 1 mm; **Fr** fleshy, red when ripe, ± 5 mm Ø, 1- to 2-seeded. — [E. Van Jaarsveld]

**A. undulatus** (Linné *fil.*) Thunberg (Prodr. Fl. Cap., 66, 1794). **Type:** RSA, Western Cape (*Thunberg* s.n. [UPS 8446]). — **Distr:** S Namibia, RSA (Northern Cape, Western Cape); sandy flats in Fynbos or Succulent Karoo, flowers mid-winter to spring.

≡ *Dracaena undulata* Linné *fil.* (1781) ≡ *Myrsiphyllum undulatum* (Linné *fil.*) Kunth (1850); **incl.** *Asparagus klinghardtianus* Dinter (1931).

[3] Ascending shrublets to 60 cm tall, from a tuberous base; tubers 2.5–5 × 0.8–1.5 cm; stems erect, annual, angled, the edes often winged in the upper parts, green, branches ascending; phylloclades 8–40 mm, solitary, sessile, ovate to lanceolate, undulate, tips sometimes folded, veins prominent; **L** deltoid, not forming a spine; **Fl** 1–3 per node; **Ped** 5–10 mm, articulated in the distal part; **Tep** linear oblong, spreading to reflexed, 6 mm, purplish to greenish; **St** as long as the tepals; **Fil** spurred; **Ov** 2 mm; **Sty** 2.5 mm; **Fr** fleshy and red when ripe, 5–6 mm Ø, 1- to 3-seeded. — [E. Van Jaarsveld]

## References

- Dahlgren, R. M. T. [ & al. 1985], Clifford, H. T. & Yeo, P. F. (1985) The families of the Monocotyledons. Structure, evolution, and taxonomy. Berlin, Heidelberg (DE) etc.: Springer-Verlag. <https://doi.org/10.1007/978-3-642-61663-1>
- Jessop, J. P. (1966) The genus *Asparagus* in Southern Africa. *Bothalia* 9(1): 31–96, *ills.*, key. <https://doi.org/10.4102/abc.v9i1.1576>
- Kubitzki, K. & Rudall, P. J. (1998) *Asparagaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 125–129, *ills.*, key. Berlin (DE) etc.: Springer. [https://doi.org/10.1007/978-3-662-03533-7\\_15](https://doi.org/10.1007/978-3-662-03533-7_15)
- Kubota, S. [ & al. 2012], Konno, I. & Kanno, A. (2012) Molecular phylogeny of the genus *Asparagus* (*Asparagaceae*) explains interspecific crossability between the garden asparagus (*A. officinalis*) and other *Asparagus* species. *Theor. Appl. Genet.* 124(2): 345–354, *map.* <https://doi.org/10.1007/s00122-011-1709-2>
- Malcomber, S. T. & Sebsebe Demissew (1993) The status of *Protasparagus* and *Myrsiphyllum* in the *Asparagaceae*. *Kew Bull.* 48(1): 63–78. <http://www.jstor.org/stable/4115749>
- Nakayama, H. [ & al. 2012a], Yamaguchi, T. & Tsukaya, H. (2012a) Acquisition and diversification of cladodes: Leaf-like organs in the genus *Asparagus*. *Pl. Cell* 24: 929–940, *ills.* <https://doi.org/10.1105/tpc.111.092924>
- Nakayama, H. [ & al. 2012b], Yamaguchi, T. & Tsukaya, H. (2012b) Cladodes, leaf-like organs in asparagus, show the significance of co-option of pre-existing genetic regulatory circuit for morphological diversity of plants. *Pl. Signaling & Behav.* 7(8): 961–964, *ills.* <https://doi.org/10.4161/psb.20913>
- Norup, M. F. [ & al. 2015], Petersen, G., Burrows, S., Bouchenak-Khelladi, Y., Leebens-Mack, J., Pires, J. C., Linder, H. P. & Seberg, O. (2015) Evolution of *Asparagus* L. (*Asparagaceae*): Out-of-South-Africa and multiple origins of sexual dimorphism. *Molec.*

- Phylogen. Evol. 92: 25–44, ills. <https://doi.org/10.1016/j.ympev.2015.06.002>
- Obermeyer, A. A. (1984) Revision of the genus *Myrsiphyllum* Willd. *Bothalia* 15(1–2): 77–88, ills., maps, key. <https://doi.org/10.4102/abc.v15i1/2.1106>
- Obermeyer, A. A. [ & al. 1992], Immelman, K. L. & Bos, J. J. (1992) *Dracaenaceae, Asparagaceae, Luzuriagaceae* and *Smilacaceae*. In: Leistner, O. A. (ed.): *Flora of Southern Africa*, Vol. 5, part 3. Pretoria (ZA): National Botanic Institute.

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**Part VI**

**The Family Asphodelaceae**







# Asphodelaceae

G. F. Smith and E. Figueiredo

## *Including Aloiaceae* Batsch.

Perennial, rarely annual, small, rhizomatous mesophytic to xerophytic herbs, acaulescent geophytes or small herbaceous to rarely erect subshrubs, shrubs, herbaceous, shrubby or pachycaul arborescent, succulent-leaved **Ros** plants, sometimes with a bulbous base; **R** often yellowish inside, sometimes inflated and fusiform or with multi-layered velamen, fibrous, usually terete, sometimes tuberously thickened, fleshy or fusiform; basal stem parts rarely swollen (caudiciform); stem stout or slender, simple or branched, erect, decumbent or pendulous, short to several m tall, sometimes so short that the plants are described as acaulescent; **L** simple, usually spirally set, occasionally distichous, alternate, linear, deltoid, falcate, lanceolate, oblong, triangular, subulate to thickly conical or elliptic, crowded in dense **Ros** at tips of stems and **Br** higher up or at ground-level, sometimes widely spaced along stem, generally dorsiventral, with sheathing base, usually persistent for several years, usually distinctly succulent and mottled with whitish spots or striations,

sometimes terete, often prickly along the margins and sometimes on both faces, apical tip usually ending in a weak to fairly strong **Sp**, surfaces smooth or rough, **L** tissue usually with coloured exudate when broken, amplexicaul, veins longitudinal but indistinct when leaves are succulent; **Inf** terminal or axillary, simple racemes, panicles or rarely spikes on scape-like peduncle, peduncle massive or slender, leafless or with bracteal leaves, nodes unibracteate; **Fl** bisexual, hypogynous, 3-merous throughout, actinomorphic to conspicuously zygomorphic, sometimes stellate, pedicels without articulation (except in the non-succulent *Asphodelus* and *Asphodeline*), red, orange, yellow, white, pinkish or mauve, never blue-violet, rarely green; **Tep** in 2 whorls of 3, petaloid, oblong to oblong-elongated, often fleshy, free or fused or nearly free and connate into a straight or curved sometimes ventricose tube, limb  $\pm$  regular or sometimes bilabiate; **St** 6, free, arising at or near the base of ovary; **Fil** free, linear, smooth or occasionally hairy; **Anth** with 2 thecae, dorsifixed-epipeltate, introrse, opening by longitudinal slits, included or exserted, microsporogenesis simultaneous; **Ov** compound, superior, 3-locular, sometimes with septal **Nec**; placentation axile; ovules 2-many per locule; **Sty** distinct, filiform, terminal; **Sti** small, punctate or discoid, apical; **Fr** 3-locular, loculicidally dehiscent capsules, rarely fleshy, indehiscent berries; **Se** arillate, elongated to angular-ovoid, usually flattened or winged, sometimes prominently so. — **Cytology**: The subfamily *Aloioideae* has a distinctive basic, bimodal

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karyotype of 4 long and 3 short chromosomes, with  $x = 7$ . Most species are diploid, but some polyploidy and aneuploidy occur, especially in *Aloe* and *Haworthia*, as summarized by Riley & Majumdar (1979), Brandham (1983) and Smith (1991). In the *Asphodeloideae*, *Kniphofia* has a basic set of 6 chromosomes ( $2n = 12$ ), while some genera (*Bulbinella*, *Eremurus* [both non-succulent, except *Bulbinella calcicola*] and *Trachyandra* [some spp. weakly succulent]) share a basic chromosome number of  $x = 7$  with the *Aloioideae*, but  $x = 14$  in the case of *Asphodelus* and *Asphodeline*.

**Order:** Asparagales.

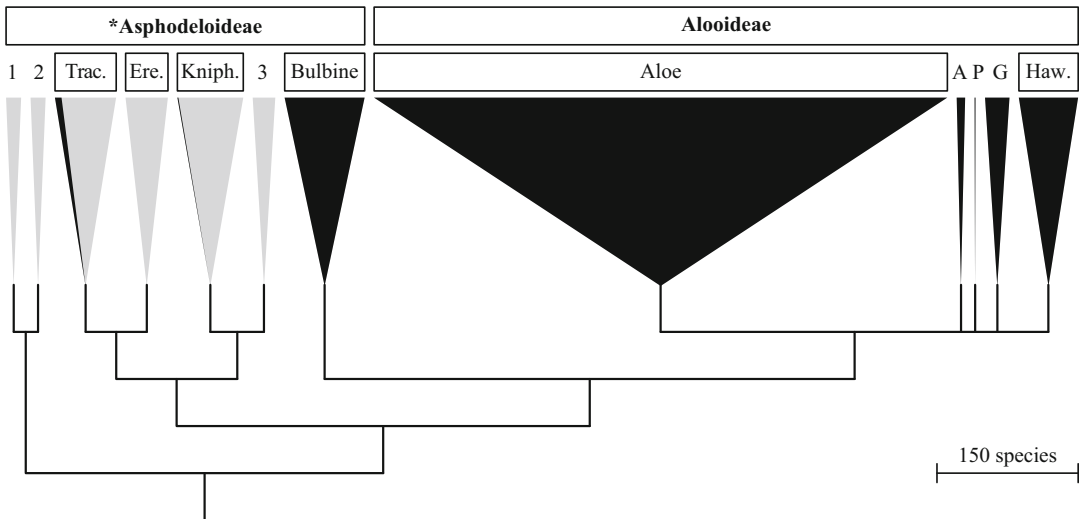
**Important Literature:** Dahlgren & al. (1985: synopsis), Smith & Wyk (1991: systematics); Smith & Wyk (1998: synopsis); Jaarsveld (2001: synopsis, as *Asphodelaceae* s.s.); Smith & Newton (2001: synopsis, as *Aloaceae*); Smith & Steyn (2004: systematics, as *Aloaceae*); Klopper & al. (2010: synopsis phylogeny); Grace & al. (2013: generic classification); Daru & al. (2013: molecular phylogeny).

**Distribution:** Africa, Madagascar, Arabian Peninsula, Mascarene Islands, Socotra, Europe, Asia, Australia, New Zealand.

**Classification and History:** The *Asphodelaceae*, here treated as consisting of two subfamilies, *Aloioideae* and *Asphodeloideae*, is a monophyletic monocot family in the order Asparagales (Smith & Wyk 1998; Klopper & al. 2010). To support the monophyly of the family, the presence of hemitropous ovules and arillate seeds has been used as evidence (Dahlgren & al. 1985; Smith & Wyk 1998; Steyn & Smith 1998; Steyn & Smith 2001; Treutlein & al. 2003).

The *Asphodelaceae* consists of 12 genera (but see below) and  $\pm 1050$  species and is widespread in dry and climatically mild parts of the tropical, subtropical and temperate Old World. Southern Africa is the main present-day centre of diversity of the family, at both genus and species ranks. The subfamily *Aloioideae*, which is widely considered monophyletic, has fairly uniform vegetative and

reproductive morphologies, is a virtually exclusively leaf-succulent group, and has definite present-day centres of diversity in southern African and Madagascar. The *Aloioideae* (as *Aloaceae*, see Cronquist (1981) and Smith & Newton (2001)) is sometimes retained as distinct from the *Asphodelaceae* s.s., from which it differs inconsistently by having succulent leaves, tubular flowers, a basic bimodal chromosome complement of 4 long and 3 short chromosomes and the presence of a parenchymatous cap at the phloem pole. In contrast, the subfamily *Asphodeloideae* is often regarded as paraphyletic, is morphologically varied, leaf succulence is inconsistently found across generic boundaries, and has a wide distribution in continental Europe, W Asia, and S and tropical Africa. Dahlgren & Clifford (1982) proposed a circumscription of the *Asphodelaceae* that included the *Aloaceae* as a subfamily, along with the families *Asteliaceae* and *Anthericaceae*, also as subfamilies. A subsequent refinement of their 1982 work (Dahlgren & al. 1985) recognised the *Asphodelaceae* as a family with only two subfamilies: *Asphodeloideae* and *Aloioideae*, i.e. the classification followed here and also supported by Chase & al. (2000: 949) (Fig. 1). Over the past 15 years APG (2003) has proposed that the *Asphodelaceae* (and *Hemerocallidaceae*) be included in the *Xanthorrhoeaceae*—this name has priority over the older *Asphodelaceae* by virtue of conservation, and must therefore be used, but Klopper & al. (2013) proposed the conservation of the name *Asphodelaceae* to rectify the nomenclatural situation. The proposal was debated by the Nomenclature Committee for Vascular Plants (NCVP), and they strongly recommended the name *Asphodelaceae* for conservation (Applequist 2014: 1362). Recently the General Committee (GC) voted to accept the report of the NCVP (Wilson 2016: 1150), and this was duly accepted by the 19. International Botanical Congress in July 2017 (Turland & al. 2017: 5). The strictly phylogenetic classificatory approach of the APG at that time expanded the *Xanthorrhoeaceae* to about 27 genera and  $\pm 1,500$  species. We here prefer to maintain the *Asphodelaceae* as a separate family (Klopper & al. 2010), a view also advocated by Nyffeler &



**Fig. 1** Summary phylogeny of *Asphodelaceae* based on Devey & al. (2006) (1050 species total, data from Mabberley (2009) and own counts). 1 = *Asphodelus*, 2 = *Asphodeline*, 3 = *Bulbinella*; A = *Astroloba*, Ere =

*Eremurus*, G = *Gasteria*, Haw. = *Haworthia*, Kniph. = *Kniphofia*, P = *Poellnitzia*, Trac. = *Trachyandra*. (Copyright: U. Eggli)

Eggli (2010) and supported by the data of Seberg & al. (2012).

While the *Asphodelaceae* have no obvious gross morphological synapomorphies, it is distinguished from other lilioid monocots by the following combination of characters: A general presence of anthraquinones, the presence of chrysophanol in the roots, a general lack of steroidal saponins, presence of parenchymatous (often secretory) cells in the inner bundle sheath adjacent to the phloem, simultaneous microsporogenesis, predominantly hemitropous ovules and the presence of an appendage (aril) on the seed (Smith & Wyk 1998; Chase & al. 2000).

**Subfamily Alooideae:** Succulent rosette plants to small pachycaul trees: *Aloe* (including *Chortolirion* and *Lomatophyllum*), *Astroloba*, *Gasteria*, *Haworthia* and *Poellnitzia*.

The subfamily *Alooideae* has in the past been treated as tribe *Aloaeae* (often erroneously as ‘*Aloineae*’) of the family *Liliaceae* (Hutchinson 1959), or as a separate family, the *Aloaceae*, by some authors (Cronquist 1981 and Brummitt 1992; see Smith (1993) for clarification on the correct spelling of the family name as *Aloaceae*

rather than *Aloaceae*). *Alooideae* numbers  $\pm$  730 species in 5 genera, all of which occur in or are restricted to southern Africa. While the circumscription of the *Alooideae* is non-contentious, exact genus boundaries in the subfamily remain a topic of much discussion, as the status of genera like *Astroloba*, *Chortolirion*, *Lomatophyllum* and *Poellnitzia* and the monophyly of *Aloe* and *Haworthia* are questioned. Essentially, the current classification system for the subfamily weakly reflects phylogenetic affinities, being rather more indicative of evolutionary diversification. In this respect the likely presence of reticulate evolution caused by frequent historical and recent hybridization is a complicating factor. Subfamily *Alooideae* has a pronounced southern African centre of generic and species diversity, with outliers of *Aloe* in the Arabian Peninsula, Madagascar and the Mascarene Islands (Smith & Wyk 1998; Treutlein & al. 2003).

Based on extensive molecular phylogenetic studies, it has become amply clear that *Aloe* in its current circumscription is paraphyletic relative to *Astroloba*, *Chortolirion*, *Gasteria*, *Haworthia* and *Poellnitzia*, and that *Haworthia* itself is not

monophyletic. Grace & al. (2013) started to formalize a revised classification by recognizing several early-diverging clades of *Aloe* as segregate genera (*Aloidendron*, *Aloiampelos*, *Kumara*) and included *Chortolirion* within the concept of *Aloe* s.s. Manning & al. (2014) went one step further and erected the genera *Aristaloe* and *Gonialoe* for a couple of anomalous taxa in the clade that embraces the part of *Haworthia* that was segregated as *Haworthiopsis* and *Tulista* by Rowley (2013), and *Gasteria*. For the present handbook the conventional circumscriptions of *Aloe* (but with *Chortolirion* included) and *Haworthia* are maintained, partly because the backbone topology of the Alooids still suffers from inadequate statistical support in a number of cases, and partly because the full diversity of *Aloe* has still not been sampled. The only exception is *Chortolirion*, which is now included in *Aloe*. Another option to arrive at a fully phylogenetic classification would be to enlarge *Aloe* to cover all traditionally accepted segregate genera of the subfamily, but this option is at least for the time being considered as impractical and not helpful.

Members of this subfamily share several apomorphies: Consistently hemitropous ovules, a distinctly bimodal basic karyotype consisting of 4 long and 3 short chromosomes, the presence of a parenchymatous, cap-like inner bundle sheath at the phloem poles (Smith & Wyk 1992), the presence of anthrone-C-glycosides in the leaves, and 1-methyl-8-hydroxyanthraquinones in the roots. Steroidal saponins are generally absent. To this may be added the succulent leaf consistency and the widespread occurrence of secondary growth via a secondary thickening meristem, although not all members of the subfamily exhibit the latter character (Smith & Wyk 1998; Chase & al. 2000; Treutlein & al. 2003; Klopper & al. 2010). In gross morphological terms it differs from subfamily *Asphodeloideae*, though not entirely consistently, by invariably having succulent leaves and tubular flowers.

Numerous taxa of *Aloe*, *Gasteria* and *Haworthia* are cultivated by succulent plant enthusiasts, and *Aloe* species are also often planted as conspicuous garden plants in warmer

climates. Apart from limited medicinal and other traditional uses of several taxa of *Haworthia* and *Gasteria*, *Aloe vera* and *A. ferox* are widely used medicinally as purgatives, as ingredients in cosmetic and health products, and to treat skin irritations and burns. The industries based on these two taxa are worth millions of dollars per year alone in RSA.

Numerous bigeneric and some trigenic hybrids have been created and formally named (see Rowley (2006) for a list of accepted and synonymous nothogeneric names; and Rowley (2014) for an updated list reflecting the re-classification of *Aloe* and *Haworthia*). However, Smith & al. (2017) and Smith & al. (2018) do not follow the expanded interpretation of *Tulista* and have published the nothogenus names  $\times$ *Astrolista* Molteno & Figueiredo and  $\times$ *Gonimara* Gideon F.Sm. & Molteno.

**Subfamily *Asphodeloideae*:** Perennial, rarely annual herbs to subshrubs: *Asphodeline* (non-succulent), *Asphodelus* (non-succulent), *Eremurus* (non-succulent), *Bulbine* (including *Jodrellia*), *Bulbinella* (1 species succulent), *Kniphofia* (1 succulent species), *Trachyandra*.

The subfamily *Asphodeloideae* comprises about 320 species. The group has a broad Old World distribution and is found from S and tropical Africa, through, especially Mediterranean Europe to W Asia. The Mediterranean region and the winter rainfall region of the Cape Provinces of South Africa in particular are present-day centres of diversity. In this regard, 2 genera, *Bulbine* and *Bulbinella*, occur predominantly in southern Africa, but with outliers in Australia and New Zealand, respectively.

In both reproductive and vegetative morphology, members of the *Asphodeloideae* vary greatly, with some taxa (e.g. *Trachyandra*) having the general appearance of members of the *Anthericaceae*, and others (e.g. *Kniphofia*) of members of the subfamily *Alooideae*. In the absence of convincing macro- and micro-morphological, and other synapomorphies, this subfamily is generally regarded as being para- or even polyphyletic (Smith & Wyk 1998; Chase



## Key to genera with succulents

1a	<b>Per</b> stellate to campanulate, segments free	2
1b	<b>Per</b> tubular, usually with short, erect or erecto-patent lobes, segments at least partly fused towards the base	4
2a	<b>Fil</b> densely and softly bearded, also in the case of the species formerly included in <i>Jodrellia</i>	<i>Bulbine</i>
2b	<b>Fil</b> glabrous or scabrid	3
3a	<b>Fl</b> white, rarely yellow, pink, or mauve, segments usually dark-keeled; <b>L</b> thickly leathery to succulent	<i>Trachyandra</i>
3b	<b>Fl</b> yellow, orange, white or cream, segments lacking dark keel; <b>L</b> mesophytic to softly succulent ( <i>Bulbinella calcicola</i> )	<i>Bulbinella</i>
4a	<b>L</b> distinctly V-shaped in cross section, soft (mesophytic), not succulent (except <i>Kniphofia typhoides</i> ), in basal rosettes, lacking spines, immaculate; <b>Inf</b> usually a simple, dense raceme or spike	<i>Kniphofia</i>
4b	<b>L</b> cymbi- or crescentiform in cross section, ± succulent, in basal or apical rosettes or cauline, hard, often spiny and/or distinctly to indistinctly maculate with spots or tubercles	5
5a	<b>Fr</b> capsules apically acute; <b>L</b> narrowly linear, margin with dense, small, retrorse teeth; underground parts bulbous; <b>Fl</b> usually <15 mm long, irregular	<i>Aloe</i> sect. <i>Chortolirion</i>
5b	<b>Fr</b> capsules apically rounded or obtuse; <b>L</b> usually thickly succulent, deltoid to lanceolate, margin mostly variously armed with soft or pungent spines; underground parts rhizomatous or stoloniferous (if rarely bulbous then <b>Fl</b> >15 mm long, regular)	6
6a	<b>Fl</b> pendulous at anthesis, <b>Per</b> tube curved upwards at apex	<i>Gasteria</i>
6b	<b>Fl</b> erect, suberect or spreading at anthesis; <b>Per</b> tube straight or curved downwards at apex	7
7a	<b>Per</b> bilabiate, <15 mm long, mouth declined	<i>Haworthia</i>
7b	<b>Per</b> regular (if rarely weakly bilabiate then flowers >15 mm long), mouth upturned	8
8a	<b>Fl</b> usually brightly coloured, fleshy	9
8b	<b>Fl</b> white or dull-coloured, flimsy	<i>Astroloba</i>
9a	<b>Tep</b> spreading; <b>St</b> as long as or longer than the perianth	<i>Aloe</i>
9b	<b>Tep</b> apically connivent; <b>St</b> shorter than the perianth	<i>Poellnitzia</i>

& al. 2000; Klopper & al. 2010). Most taxa in this subfamily are non-succulent, an obvious exception being the genus *Bulbine*, some species of *Trachyandra*, one species of *Bulbinella*, *B. calcicola*, and one species of *Kniphofia*, *K. typhoides*. Although species of *Asphodelus* are generally regarded as bulbous or tuberous rather than succulent, data presented by Sawidis & al. (2005) indicate that the perennial geophyte *A. aestivus* from the European Mediterranean basin behaves like a real succulent, based on the morphology of its subterranean storage organs and the efficiency with which water is stored. It is not unlikely that succulence occurs more widely in the genus.

The subfamily *Asphodeloideae* has no recognized economic importance except that many species are of horticultural interest, and some are locally used in various ways. Amongst the succulents, a small number of species of

*Bulbine* and *Trachyandra* have local importance as food items or for their medicinal properties.

## References

- APG (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436. <https://doi.org/10.1046/j.1095-8339.2003.t01-1-00158.x>
- Applequist, W. L. (2014) Report of the Nomenclature Committee for Vascular Plants: 66. Taxon 63(6): 1358–1371. <https://doi.org/10.12705/636.20>
- Brandham, P. E. (1983) Evolution in a stable chromosome system. In: Brandham, P. E. & Bennett, M. D. (eds.): Kew Chromosome Conference II; pp. 251–260. London (GB): George Allen & Unwin.
- Brummitt, R. K. (Ed.) (1992) Vascular plant families and genera. Richmond (GB): Royal Botanic Gardens Kew.
- Chase, M. W. [et al. 2000], de Bruijn, A. Y., Cox, A. V., Reeves, G., Rudall, P. J., Johnson, M. A. T. & Eguiarte,

- L. E. (2000) Phylogenetics of *Asphodelaceae* (Asparagales): An analysis of plastid rbcL and trnL-F DNA sequences. *Ann. Bot. (Oxford)*, n.s. 86: 935–951. <https://doi.org/10.1006/anbo.2000.1262>
- Cronquist, A. (1981) An integrated system of classification of Flowering Plants. New York (US): Columbia University Press.
- Dahlgren, R. M. T. & Clifford, H. T. (1982) The monocotyledons: A comparative study. London (GB): Academic.
- Dahlgren, R. M. T. [et al. 1985], Clifford, H. T. & Yeo, P. F. (1985) The families of the Monocotyledons. Structure, evolution, and taxonomy. Berlin/Heidelberg (DE) etc.: Springer. <https://doi.org/10.1007/978-3-642-61663-1>
- Daru, B. H. [et al. 2013], Manning, J. C., Boatwright, J. S., Maurin, O., Mclean, N., Schaefer, H., Kuzmina, M. & Bank, M. van der (2013) Molecular and morphological analysis of subfamily *Aloioideae* (*Asphodelaceae*) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62(1): 62–76, ills. <http://www.jstor.org/stable/24389313>
- Grace, O. M. [et al. 2013], Klopper, R. R., Smith, G. F., Crouch, N. R., Figueiredo, E., Rønsted, N. & van Wyk, A. E. (B.) (2013) A revised generic classification for *Aloe* (*Xanthorrhoeaceae* subfam. *Asphodeloideae*). *Phytotaxa* 76(1): 7–14, key. <https://doi.org/10.11646/phytotaxa.76.1.2>
- Hutchinson, J. (1959) The families of flowering plants. Volume 2, Monocotyledons. Oxford (GB): Clarendon Press.
- Jaarsveld, E. J. van (2001) *Asphodelaceae*. In: Eggl, U. (ed.): *Illustrated Handbook of Succulent Plants: Monocotyledons*; p. 232. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-642-56715-5\\_8](https://doi.org/10.1007/978-3-642-56715-5_8)
- Klopper, R. R. [et al. 2010], Wyk, A. E. (B.) van & Smith, G. F. (2010) Phylogenetic relationships in the family *Asphodelaceae* (Asparagales). *Phylogenetische Verwandtschaften in der Familie Asphodelaceae* (Asparagales). *Schumannia* 6: 9–36, ills.
- Klopper, R. R. [et al. 2013], Smith, G. F. & Wyk, A. E. (B.) van (2013) Proposal to conserve the family name *Asphodelaceae* (Spermatophyta: Magnoliidae: Asparagales). *Taxon* 62(2): 402–403. <https://doi.org/10.12705/622.17>
- Manning, J. C. [et al. 2014], Boatwright, J. S., Daru, B. H., Maurin, O. & Bank, M. van der (2014) A molecular phylogeny and generic classification of *Asphodelaceae* subfamily *Aloioideae*: A final resolution of the prickly issue of polyphyly in the Alooids. *Syst. Bot.* 39(1): 55–74, key. <https://doi.org/10.1600/036364414X678044>
- Nyffeler, R. & Eggl, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>
- Riley, H. P. & Majumdar, S. K. (1979) *The Aloineae*. A biosystematic survey. Lexington (US): University Press of Kentucky.
- Rowley, G. D. (2006) Intergeneric hybrids in the *Asphodelaceae* subfamily *Aloioideae*. *Alsterworthia Int.* 6(2): 8–11, ills.
- Rowley, G. D. (2013) Generic concepts in the *Aloioideae*—part 4. *Haworthiopsis* and *Tulista*—old wine in new bottles. *Alsterworthia Int.* 13(3): 6–13, ills., keys.
- Rowley, G. D. (2014) Intergeneric hybrids in the *Asphodelaceae* subfamily *Aloioideae*—2014 update. *Alsterworthia Int.* 14(2): 16–23, ills.
- Sawidis, T. [et al. 2005], Kalyva, S. & Delivopoulos, S. (2005) The root-tuber anatomy of *Asphodelus aestivus*. *Flora (Jena)* 200: 332–338, ills. <https://doi.org/10.1016/j.flora.2004.10.002>
- Seberg, O. [et al. 2012], Petersen, G., Davis, J. L., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99 (5): 875–889, ills. <https://doi.org/10.3732/ajb.1100468>
- Smith, G. F. (1991) The chromosomes of *Chortolirion* and *Poellnitzia* (*Asphodelaceae: Aloioideae*). *Bothalia* 21(2): 171–175, ills. <http://abcjournal.org/index.php/ABC/article/view/884>
- Smith, G. F. (1993) Familial orthography: *Aloaceae* vs. *Aloaceae*. *Taxon* 42(1): 87–90. <http://www.jstor.org/stable/1223308>
- Smith, G. F. & Newton, L. E. (2001) *Aloaceae*. In: Eggl, U. (ed.): *Illustrated Handbook of Succulent Plants: Monocotyledons*; pp. 102–103. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-642-56715-5\\_3](https://doi.org/10.1007/978-3-642-56715-5_3)
- Smith, G. F. & Steyn, E. M. A. (2004) The taxonomy of *Aloaceae*. In: Reynolds, T. & al. (eds.): *Aloes: The genus Aloe*; pp. 15–36. Boca Raton (US): CRC Press.
- Smith, G. F. & Wyk, A. E. (B.) van (1992) Systematic leaf anatomy of selected genera of southern African *Aloioideae* (*Asphodelaceae*). *South Afr. J. Bot.* 58(5): 349–357, ills.; (6): 543 [erratum]. <http://www.jstor.org/stable/1222765>
- Smith, G. F. & Wyk, B-E. van (1991) Generic relationships in the *Aloioideae* (*Asphodelaceae*). *Taxon* 40(4): 557–581, ills., maps. <http://www.jstor.org/stable/1222765>
- Smith, G. F. & Wyk, B-E. van (1998) *Asphodelaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 130–140, ills., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_16](https://doi.org/10.1007/978-3-662-03533-7_16)
- Smith, G. F., Figueiredo, E. & Molteno, S. (2017) ×*Astrolista* Molteno & Figueiredo (*Asphodelaceae*): A new name for the South African endemic nothogenus ×*Astroworthia*. *Bradleya* 35: 195–200. <https://doi.org/10.25223/brad.n35.2017.a22>
- Smith, G. F., Figueiredo, E. & Molteno, S. (2018) ×*Gonimara* Gideon F.Sm. & Molteno (*Asphodelaceae*): A new nothogenus name for the artificial hybrid, ×*Gonimara corderoyi* (A. Berger) Gideon F.Sm. & Molteno, between the alooid species *Gonialoe variegata* and *Kumara plicatilis*, two southern African endemics. *Bradleya* 36: 53–60. <https://doi.org/10.25223/brad.n36.2018.a7>
- Steyn, E. M. A. & Smith, G. F. (1998) Ovule orientation, curvature and internal structure in the *Aloaceae*. *South*

- Afr. J. Bot. 64(3): 192–197, ills. [https://doi.org/10.1016/S0254-6299\(15\)30866-8](https://doi.org/10.1016/S0254-6299(15)30866-8)
- Steyn, E. M. A. & Smith, G. F. (2001) Miscellaneous notes. *Aloaceae*. Are ovules and seeds in *Lomatophyllum* Willd. (*Aloe* sect. *Lomatophyllum* sensu auct.) anatropous and exarillate? *Bothalia* 31(2): 237–240, ills. [https://doi.org/10.1016/S0254-6299\(15\)30866-8](https://doi.org/10.1016/S0254-6299(15)30866-8)
- Treutlein, J. [et al. 2003], Smith, G. F., Wyk, B-E. van & Wink, M. (2003) Phylogenetic relationships in *Asphodelaceae* (subfamily *Alooideae*) inferred from chloroplast DNA sequences (rbcL, matK) and from genomic fingerprinting (ISSR). *Taxon* 52(2): 193–207, ills. <http://www.jstor.org/stable/3647389>
- Turland, N. J. [et al. 2017], Wiersema, J. H., Monro, A. M., Deng, Y.-F. & Zhang, L. (2017) XIX International Botanical Congress: Report of Congress action on nomenclature proposals. *Taxon* 66(5): 1234–1245. <https://doi.org/10.12705/665.16>
- Wilson, K. L. (2016) Report of the General Committee: 15. *Taxon* 65(5): 1150–1151. <https://doi.org/10.12705/655.14>





## × *Algastoloba* ASPHODELACEAE

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× **Algastoloba** D. M. Cumming (Haworthiad 13 (1): 20, 1999). — *Alooiidae* — **Lit:** Cumming (1999). **Etym:** Intergeneric hybrid name that combines the names of the involved genera *Aloe*, *Gasteria* and *Astroloba*.

**Incl.** × *Altulisteria* G. D. Rowley (2014).

= *Aloe* × *Astroloba* × *Gasteria*. The two known combinations have not been formally named.

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### References

Cumming, D. M. (1999) New nothogenera proposed for four trigeneric hybrids within *Aloaceae*. *Haworthiad* 13(1): 20–21.

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## Aloe ASPHODELACEAE

L. E. Newton

**Aloe** Linné (Spec. Pl. [ed. 1], 1: 319, 1753). **Type:** *Aloe perfoliata* Linné [lectotype, designated by Britton & Millspaugh, Bahama Flora, 69, 1920, repeated by Hitchcock, Prop. Brit. Botanists Bot. Congr. Cambridge, 146–147, 1929 (both pre-dating the designation of *Aloe disticha* Linné by P. V. Heath (Calyx 2(4): 142, 1992)]. — **Aloideae** — **Lit:** Reynolds (1950: monograph RSA); Reynolds (1958: monograph Madagascar); Reynolds (1966: monograph tropical Africa & Madagascar); Wood (1983: monograph Yemen); Carter (1994: flora tropical E Africa); Lavranos (1995: flora Somalia); Sebsebe Demissew & Gilbert (1997: flora Eritrea & Ethiopia); Glen & Hardy (2000: flora RSA); Carter (2001: Flora Zambesiaca area); Chaudhary (2001: flora Saudi Arabia); Williamson (2003a: synopsis Zambia); Reynolds (2004: chemistry, medicinal uses); Lane (2004: synopsis Malawi); Rothmann (2004: synopsis Namibia); Craib (2006: grass Aloes RSA); Jaarsveld & Wyk (2006: key to cliff-dwelling taxa RSA); Klopper & Smith (2008: synopsis Namaqualand RSA); Klopper & al. (2009a: synopsis Angola); Klopper & al. (2009b: synopsis Free State RSA); Mays (2009: partial cultivar synopsis); Castillon & Castillon (2010: synopsis Madagascar); Sebsebe Demissew & Nordal (2010: synopsis Ethiopia/Eritrea);

Klopper & Smith (2010b: synopsis Eastern Cape RSA); Figueiredo & Smith (2010: etymology); Grace & al. (2011: etymology); Carter & al. (2011: definitive guide); Klopper & al. (2012: synopsis Malawi); Cousins & Witkowski (2012: synopsis ecology Africa); Hargreaves & al. (2012: synopsis pollination ecology); Daru & al. (2013: molecular phylogeny); Manning & al. (2014a: molecular phylogeny); Wyk & Smith (2014: synopsis RSA); Grace & al. (2015: molecular phylogeny); Bjorå & al. (2015: ethnobotany Kenya); Jaarsveld & Judd (2015: synopsis tree aloes, as *Aloidendron* and *Kumara*); Dee & al. (2018: phylogeny Madagascar & Mascarenes). **Distr:** Africa (esp. S and E), Madagascar, Mascarene Islands, SW Arabia; mainly drier areas, a few in dry forests. **Etym:** From the Gr. ('aloe'), Arabian ('aloch') and Hebrew ('ahalim') names for the plants. [In some earlier literature the name appears as *Aloë*, but as every vowel should be pronounced separately in Latin (Stearn 1992), the diaeresis is not necessary.]

**Incl.** *Kumara* Medikus (1786). **Type:** *Kumara disticha* Medikus [*nom. illeg.*, = *Aloe plicatilis* Linné].

**Incl.** *Lomatophyllum* Willdenow (1811). **Type:** *Lomatophyllum borbonicum* Willdenow [automatic type and only species included; = *Aloe purpurea* Lamarck].

**Incl.** *Rhipidodendrum* Willdenow (1811). **Type:** *Kumara disticha* Medikus [*nom. illeg.*, = *Aloe*

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- plicatilis* Linné, lectotype, designated by Boatwright & J. C. Manning, Syst. Bot. 39: 67, 2014].
- Incl.** *Phylloma* Ker Gawler (1813). **Type:** *Phylloma aloiflorum* Ker Gawler.
- Incl.** *Rhipidodendron* Sprengel (1817) (*nom. inval.*, Art. 61.1). **Type:** *Kumara disticha* Medikus [*nom. illeg.*, = *Aloe plicatilis* Linné, lectotype, designated by Boatwright & J. C. Manning, Syst. Bot. 39: 67, 2014].
- Incl.** *Pachidendron* Haworth (1821). **Type:** not typified.
- Incl.** *Bowiea* Haworth (1824) (*nomen rejiciendum*, Art. 56.1). **Type:** *Aloe bowiea* Schultes & Schultes *fil.* [lectotype designated by G. F. Smith, South Afr. J. Bot. 56(3): 303–308, 1990].
- Incl.** *Pachydendron* Dumortier (1829) (*nom. inval.*, Art. 61.1). **Type:** not typified.
- Incl.** *Agriodendron* Endlicher (1836). **Type:** *Aloe ferox* Miller.
- Incl.** *Succosaria* Rafinesque (1840). **Type:** *Aloe spicata* Linné *fil.*
- Incl.** *Ariodendron* Meisner (1842). **Type:** *Aloe ferox* Miller.
- Incl.** *Busipho* Salisbury (1866). **Type:** not typified.
- Incl.** *Ptyas* Salisbury (1866). **Type:** *Kumara disticha* Medikus [*nom. illeg.*, = *Aloe plicatilis* Linné].
- Incl.** *Chamaealoe* A. Berger (1905). **Type:** *Bowiea africana* Haworth 1824.
- Incl.** *Chortolirion* A. Berger (1908). **Type:** *Haworthia angolensis* Baker.
- Incl.** ×*Lomataloe* Guillaumin (1931).
- Incl.** *Leptaloe* Stapf (1933). **Type:** *Leptaloe albida* Stapf [type according to E. Phillips, Gen. South Afr. Pl., ed. 2, 186, 1951].
- Incl.** *Guillauminia* Bertrand (1956). **Type:** *Aloe albiflora* Guillaumin.
- Incl.** ×*Alolirion* G. D. Rowley (1973).
- Incl.** ×*Allemptauminia* D. M. Cumming (1974) (*nom. inval.*, Art. H6.4).
- Incl.** ×*Alleptauminia* Heath (1993).
- Incl.** *Lemeea* P. V. Heath (1993). **Type:** *Aloe haworthioides* Baker.
- Incl.** *Aloiampelos* Klopper & G. F. Smith (2013). **Type:** *Aloe ciliaris* Haworth.
- Incl.** *Aloidendron* (A. Berger) Klopper & G. F. Smith (2013). **Type:** *Aloe barberae* Dyer.
- Incl.** ×*Aloiampaloe* G. D. Rowley (2014).
- Incl.** ×*Altulista* G. D. Rowley (2014).
- Incl.** *Aristaloe* Boatwright & J. C. Manning (2014). **Type:** *Aloe aristata* Haworth.
- Incl.** *Gonialoe* Boatwright & J. C. Manning (2014). **Type:** *Aloe variegata* Linné.
- Incl.** ×*Kumalista* G. D. Rowley (2014).
- Incl.** ×*Gonimara* Gideon F. Smith & Molteno (2018).
- Incl.** *Aloestrela* Molteno & Gideon F. Smith (2019). **Type:** *Aloe suzannae* Decary.

Perennial leaf succulents, acaulescent, shrubby, or arborescent, simple or branching; **L** rosulate, distichous or scattered along the stem, usually ± triangular, lanceolate or falcate, sometimes linear, amplexicaul, the margins usually armed with soft or pungent deltoid teeth, the teeth usually more crowded near the leaf base, glabrous, sometimes with short prickles on the surface, uniformly coloured or with whitish or pale green spots, surface smooth or rough, usually with a bitter tasting yellow or brown exudate when broken, rarely containing fibres; **Inf** lateral, usually ± erect, simple or branching, with cylindrical or capitate racemes, sometimes with flowers secund; **Fl** bracteate, pedicellate or rarely sessile, protandrous, usually erect in bud and pendulous at anthesis; **Ped** often lengthening in fruit; **Per** base rounded, truncate or attenuate, zygomorphic, cylindrical at the base, usually becoming trigonous and slightly compressed laterally above, usually curved, usually red or yellow, rarely white, usually glabrous, rarely puberulent; **OTep** 3, usually marginally fused at the base, tips free; **ITep** 3, usually with margins free but dorsally adnate to the tube formed by the outer tepals, tips free; **St** 6, usually with **Anth** exerted partly or just clear of the perianth (1–6 mm), each group of 3 elongating and exerted, and then retracted in turn during anthesis; **Sty** simple with small capitate **Sti**; **Fr** usually capsules, sometimes berries; **Se** angular or flattened, black or brown, usually with narrow membranous wings. — **Cytology:** The majority of species investigated are diploid, with a somatic number of  $2n = 14$ . One hexaploid

and several tetraploids are also known. Known chromosome counts were summarised by Riley & Majumdar (1979), and some later authors have provided chromosome numbers when describing new taxa.

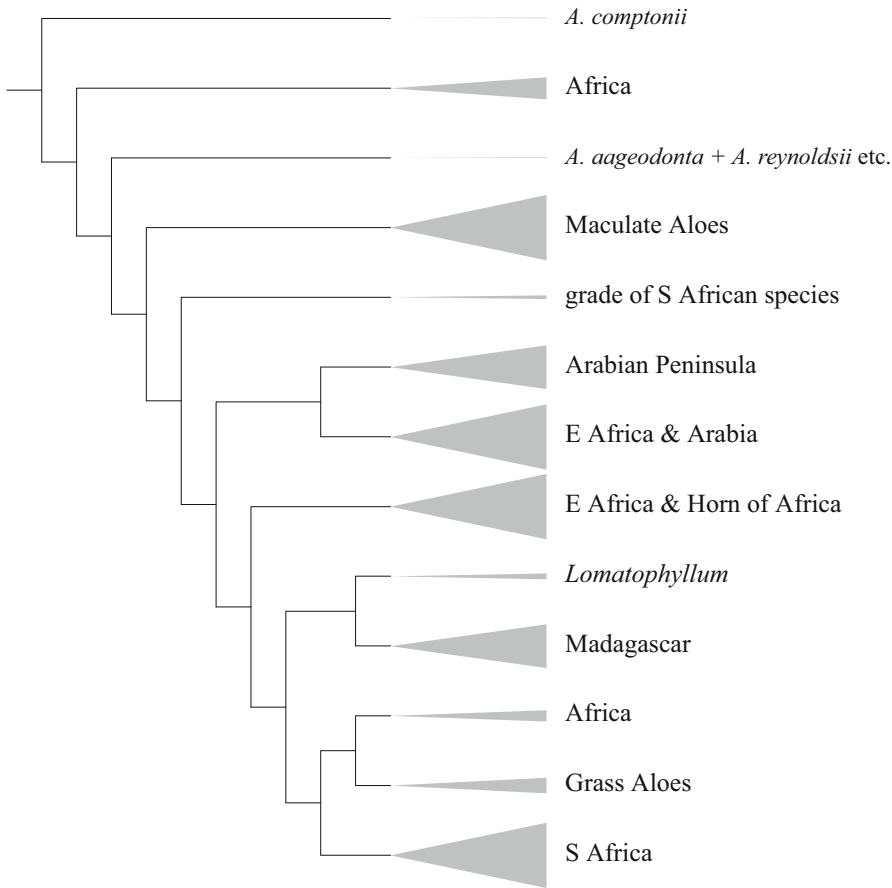
**Classification and History:** In 1753, at the nomenclatural starting point for flowering plants, Linnaeus included the genus *Aloe* with 9 species, some of which had varieties listed, totalling 35 taxa. Only 5 of these taxa are still in the genus *Aloe* today, the rest having been transferred later to the genera *Astroloba* (1947), *Gasteria* (1809), *Haworthia* (1809), *Kniphofia* (1794) and *Sansevieria* (1794).

Many segregate genera have been proposed, as seen in the generic synonymy above, but few have been generally accepted. The genus *Lomatophyllum* was proposed in 1811 for a species with fleshy fruits, later added to by several other species, and was recognised for 185 years until the species were transferred to *Aloe* by Rowley (1996). Early in the twentieth century, Berger described the genus *Chamaealoe* (1905) and later Stapf described the genus *Leptaloe* (1933), but their species are now included in *Aloe*. Much later the monotypic genus *Guillauminia* was proposed for *Aloe albiflora* in 1956, but this was not recognised by Reynolds (1966). Heath (1994) later recognised *Guillauminia* and added 5 other species, but without any explanatory text to justify his action. In the same paper Heath added 2 more species to his genus *Lemeea*, proposed in 1993 for *Aloe* sect. *Aloinella* A. Berger, again without explanatory text.

More recent proposals for taxonomic change are based on molecular taxonomy, which aims to elucidate phylogeny. Grace & al. (2013) proposed the reinstatement of the genus *Kumara*, and the establishment of two new segregate genera, *Aloidendron* and *Aloiampelos*, and the sinking of *Chortolirion* into *Aloe*. However, mostly South African species were mentioned and included in the new combinations, and it is not entirely clear how the rest of the genus might be affected. Rowley (2013a) supported recognition of the segregate genera proposed by Grace & al. (2013), and

goes further by proposing two new genera, one of which, *Tulista*, includes a species of *Aloe* (*A. aristata*) (Rowley 2013b). Daru & al. (2013) also proposed a re-circumscription of the genus, but their findings are not completely congruent with those of Grace & al. (2013). Manning & al. (2014a) (summarized by Manning & al. (2014b)) went further, proposing two other new segregate genera, *Aristaloe* and *Gonialoe*. Manning & al. (2014a) recognised 6 clades, 5 of which were to be considered as separate genera. These are: Sect. *Aloidendron* + sect. *Dracoaloe* (= genus *Aloidendron*), sect. *Aristatae* (= genus *Aristaloe*), sect. *Kumara* + sect. *Haemanthifoliae* (= genus *Kumara*), sect. *Macrifoliae* (= genus *Aloiampelos*), and sect. *Serrulatae* (= genus *Gonialoe*); and the rest of the genus remaining as *Aloe*. As the whole situation is still in a state of flux (as witnessed by the recent paper of Rowley (2014b), where these plus *Astroloba* are treated as subgenera of *Tulista*), the new names are included here as synonyms until consensus has been reached. The same option, i.e. continuing to recognize *Aloe* in its traditional circumscription, was also chosen by Wyk & Smith (2014). An exception is made regarding the synonymization of *Chortolirion*, which is now included into *Aloe* in all recent studies. Grace & al. (2013) and Daru & al. (2013) independently transferred its species to *Aloe*, and the correct names to be used when treated as *Aloe* were explained by Klopper & al. (2013), where 4 species were recognised, and again by Manning & al. (2014a). As we go to press a new paper has appeared (Meer 2019) with many proposed nothogeneric names for various hybrids between the new genera suggested by recent molecular studies, together with new combinations. As there is not yet a generally accepted consensus on these new genera the new nothogeneric names are not listed here.

**Infrageneric relationships as shown in recent molecular studies:** Even though the recent study of Grace & al. (2015) includes a good number (197 species) of the diversity of the genus, and covers all major groups, not even the backbone of their cladogram is statistically well-supported.



**Fig. 1** Approximate phylogeny of *Aloe* s.s. derived from the molecular phylogeny of Grace & al. (2015), based on DNA sequencing of 197 species. Minor clades and grades

are collapsed into single items; triangle widths are arbitrary and only give a very rough indication of the number of species per clade. (Copyright: U. Eggli)

Based on the main topology and major clades (Fig. 1), the following conclusions are emerging:

- The placement of several species raises pronounced doubt, either concerning the correctness of the identification of the studied material, or concerning possible statistical artefacts in the interpretation of the sequence data. For instance, the Madagascan *A. acutissima* and *A. bakeri* occupy a position deeply embedded in a clade of species from the Arabian Peninsula. Another such example is the Madagascan *A. propagulifera*, shown as sister to the Somalian *A. eminens* and a clade made up of the South African *A. albida* and *A. chortolirioides*. Similar suspected mis-placings (e.g. *A. propagulifera* or *A. anivoranoensis* next to South African taxa) are also evident in the cladogram of Manning & al. (2014a).
- All basal clades are of African origin. Grace & al. (2015) show *A. comptonii* as basal sister to the rest of *Aloe* s.s. (i.e. excluding *Aloidendron*, *Aloiampelos*, *Kumara*), and as next higher clade a rather well-supported group embracing *A. melanacantha*, *A. pearsonii*, *A. arenicola*, *A. distans* and *A. perfoliata*. Most of these species are also shown as relatively basal in the cladogram of Manning & al. (2014a).
- The “Maculate Aloes” of S and E Africa, i.e. ser. *Saponariae*, form a coherent species group.



- Species from the Arabian Peninsula also form a coherent group (that includes *A. vera*), in sister-position to a similarly supported clade of E African and Arabian species.
- A further reasonably well-supported clade is formed by a group of species from E Africa and the Horn of Africa (esp. Ethiopia).
- The analysed species of the former genus *Lomatophyllum* form the sister group to a reasonably well-supported clade of Madagascan species, which is, however, morphologically very heterogeneous and includes, inter alia, *A. haworthioides* in close proximity to *A. vaombe*.
- A phylogenetic study of species of Madagascar and other Indian Ocean islands (Dee & al. 2018) suggests that they are not a phylogenetic unit. Some are more closely related to species on the African continent, suggesting that there were several dispersal events in the development of the Madagascan *Aloe* flora.
- The so-called “Grass Aloes” also form a reasonably well-supported clade (also shown in the phylogeny of Manning & al. (2014a)) which includes the former genus *Chortolirion*. “Grass Aloes” are thus a relatively highly derived group that diversified in a special habitat.
- The final clade, and sister to the “Grass Aloes”, is made up entirely by South African species. It is another morphologically disparate clade, including a diversity of growth forms as exhibited, e.g., by *A. arborescens*, *A. ferox*, *A. humilis* and *A. bowiea*.
- If the placement of species in the phylogeny is correct, neither the E African/Arabian Aloes nor the Madagascan Aloes form single clades, so multiple migrations to these regions have to be assumed. There is also the likelihood of neoendemic groups, such as the species with hairy flowers and the *A. archeri* group (Newton 1980).
- With the exception of the “Maculate Aloes” and the “Grass Aloes”, the molecularly defined clades appear to lack diagnostic characters, and many are (as indicated above) morphologically highly diverse. If the relationships shown in the cladogram of Grace & al. (2015) are correct,

growth form is a highly plastic character that changes rapidly during evolution.

- Only about 33% of all *Aloe* species have so far been analyzed molecularly. With the inclusion of more species, the relative relationships even in the reasonably supported sections of the cladogram are likely to change. The present state of knowledge is thus still to be considered as very provisional.

**Pollination:** Typically, aloes are ornithophilous, with nectar-feeding sunbirds (*Nectariniidae*) as the principal pollen vectors. Bees also visit the flowers but are not efficient pollinators, except in some species with short flowers (Hargreaves & al. 2012). One species, *A. inconspicua*, has been shown to be exclusively pollinated by bees (Hargreaves & al. 2008). Those bees collecting pollen for their own use are regarded as “nectar thieves”, and those seeking nectar only may contribute to pollination. The nectar of a few species, including *A. vryheidensis*, contains phenolic compounds, giving it a dark colour and bitter taste. Experiments suggest that this deters visits by bees (Johnson & al. 2006). Detailed field studies of pollination showed that nocturnal visits by some small mammals also contributed to seed production in *A. peglerae* (Payne & al. 2016) and *A. reitzii* (Symes 2017), though not as efficiently as birds. Arena (2018) reports visits by Elephant Shrews to the flowers of *A. claviflora*.

**Ethnobotany:** *Aloe vera* has been used as a medicinal plant for centuries, having featured in early herbals, and today it is the basis of a thriving industry in the production and world-wide marketing of skin creams, “health drinks”, and many cosmetic products (Upton & al. 2012). *A. ferox* has also become an important commercial plant in South Africa (Newton & Vaughan 1996). Apart from this large-scale commercial use of aloes, many species are used locally throughout the range of the genus (Grace & al. 2009, Grace 2011, Wyk 2013, BJORÅ & al. 2015). Whilst medicinal uses predominate, for both humans and domestic animals, other local uses for aloes range from hedging around farms to using the

roots in brewing beer. Chinchilla & al. (2013) provide a full review of chemistry studies and biological activities, and report baked clay tablets from Sumeria from 2100 BCE as first account of the use of *Aloe*.

**Hybrids:** Some intergeneric hybrids are known, especially between *Aloe* and *Gasteria* (=  $\times$ *Gasteraloe*). Many early intergeneric hybrids were documented by Rowley (1982), and Rowley (2014a) presents an update reflecting the proposed re-classification of *Aloe* and *Haworthia*. This reclassification has led to a number of new nothogeneric names, summarized by Rowley (2017: 192).

Interspecific hybrids have occurred spontaneously in the wild, and many were recorded by Reynolds (1950), Reynolds (1966), and Newton (1998a). There has also been some artificial hybridization with the aim of producing worthwhile cultivars, the greatest number of named ones being in southern Africa (described in *Aloe*, Journal of the South African Succulent Society, between 1971 and 1978), and in the USA (Riley 1993), with a few in England (Brandham 1973). Naturally occurring named hybrids are treated in their appropriate alphabetical sequence.

The following names refer to intrageneric hybrids obtained in cultivation: *A. \times antoninii*, *A. \times heteracantha*, *A. \times jacobseniana*, *A. \times pallancae*, *A. \times panormitana*, and *A. \times principis* (incl. *A. \times salm-dyckiana*).

**Infrageneric Classification:** No satisfactory infrageneric classification has been proposed since that of Berger (1908), since which time numerous new species have been described. The diversity of character combinations in the genus has, so far, obscured the phylogenetic relationships. For species of southern Africa Reynolds (1950) enlarged Berger's scheme somewhat, but when dealing with tropical species, he (Reynolds 1966) created new groups without formal names or ranks, some of them clearly artificial. These groups were mainly based on growth habit, starting with smaller plants and leading to trees.

This system was followed, with modification, in several later publications (Wyk & Smith 2004, Carter & al. 2011). The development of a new infrageneric classification for the genus is a long way off and so for the present a completely artificial synopsis is presented below, based on growth habit and inflorescence form. Some very variable species appear in more than one group:

#### Artificial Groups:

**A.** Plants acaulescent or with stems shorter than the  $\emptyset$  of the rosette; **L** broad (>2 cm) unless otherwise stated:

- [1] Plants with linear or very narrow **L** (usually <2 cm wide), solitary or forming groups.
- [2] Plants always solitary; **Inf** usually unbranched or with 1 **Br**.
- [3] Plants always solitary; **Inf** usually with 2 or more **Br**.
- [4] Plants solitary or forming small groups; **Inf** usually unbranched or with 1 **Br**.
- [5] Plants solitary or forming small groups; **Inf** usually with 2 or more **Br**.
- [6] Plants suckering to form groups; **Inf** unbranched or with 1 **Br**.
- [7] Plants suckering to form groups; **Inf** with 2 or more **Br**.

**B.** Plants with obvious stems; **L** broad (>2 cm) unless otherwise stated:

- [8] **Ros** on unbranched stems to 2 m tall.
- [9] Trees with usually unbranched trunks to >2 m tall; in some taxa suckering or branching at the base to produce 2 or more trunks.
- [10] Plants with linear or very narrow **L**, solitary or branching, sometimes pendulous.
- [11] Plants forming low clumps, often dense.
- [12] Plants forming large clumps (at least 1 m tall).
- [13] Plants with decumbent, sprawling or pendulous stems.
- [14] Plants with stems scrambling in or supported by surrounding vegetation.
- [15] Plants forming shrubs to 1 m tall.
- [16] Plants forming shrubs >1 m tall.

[17] Trees with basal trunks and branching above.

C. [18] Plants of unknown or uncertain growth habit.

In the descriptions below, width of leaf or bract is width at the widest point, at or near the base; details of marginal teeth refer to the middle of the leaf; and diameter of flowers is as seen from the side. Character states that are common to the majority of taxa are not stated, only the exceptions being given. For example, unless otherwise stated, leaves are erect or slightly spreading, flat or slightly canalicate above and convex below, inflorescences are erect, floral bracts are scarious, whitish with darker veins, flowers are glabrous, with cylindrical base and laterally compressed with trigonous shape above, and fruits are capsules.

The following names are of unresolved application but are referred to this genus: *Agave armata* Anonymous (1878); *Aloe abyssinica* Lamarck (1783); *Aloe agavefolia* Todaro (1878); *Aloe albispina* Haworth (1804)  $\equiv$  *Aloe mitriformis* var. *albispina* (Haworth) A. Berger (1908); *Aloe ankabeensis* Hort. W. Sterk (1988) (*nom. inval.*, ICN Art. 36.1b, 39.1); *Aloe arabica* Salm-Dyck (1817) (*nom. illeg.*, ICN Art. 53.1); *Aloe arborea* Forsskål (1775); *Aloe chloroleuca* Baker (1877); *Aloe cinnabarina* Diels & A. Berger (1905); *Aloe commelinii* Willdenow (1811)  $\equiv$  *Aloe mitriformis* var. *commelinii* (Willdenow) Baker (1880); *Aloe congolensis* De Wildeman & T. Durand (1899); *Aloe consobrina* Salm-Dyck (1863); *Aloe defalcata* Chiovenda (1932); *Aloe deflexidens* Pillans (1935); *Aloe dorsalis* Haworth (1821); *Aloe drepanophylla* Baker (1875); *Aloe elizae* A. Berger (1910); *Aloe flavispina* Haworth (1804)  $\equiv$  *Aloe mitriformis* var. *flavispina* (Haworth) Baker (1880); *Aloe fraskii* Croucher (1874); *Aloe gasterioides* Baker (1880); *Aloe grahamii* Schönland (1903); *Aloe greenii* Green ex Robinson (1875); *Aloe hexapetala* Salm-Dyck (1817); *Aloe horrida* Haworth (1804); *Aloe humilis* var. *macilentata* Baker (1880); *Aloe leucantha* A.

Berger (1905); *Aloe longiflora* Baker (1888); *Aloe macracantha* Baker (1880); *Aloe mitis* A. Berger (1908); *Aloe mitriformis* var. *humiliior* Willdenow (1811); *Aloe mitriformis* var. *pachyphylla* Baker (1880); *Aloe nobilis* Baker (1880) (*nom. illeg.*, ICN Art. 53.1); *Aloe nobilis* var. *densifolia* Baker (1880); *Aloe obscura* A. Berger ex Schönland (1905) (*nom. illeg.*, ICN Art. 53.1); *Aloe pallescens* Haworth (1821)  $\equiv$  *Aloe serrulata* var. *pallescens* (Haworth) Baker (1880); *Aloe perfoliata* var. *obscura* Aiton (1789); *Aloe perfoliata* var. *serrulata* Aiton (1789)  $\equiv$  *Aloe serrulata* (Aiton) Haworth (1804); *Aloe platylepis* Baker (1877); *Aloe pungens* A. Berger (1908); *Aloe rossii* Todaro (1891); *Aloe rubescens* De Candolle (1799); *Aloe runcinata* A. Berger (1908); *Aloe saponaria* var. *obscura* Haworth (1804); *Aloe sororia* A. Berger (1908); *Aloe spinulosa* Salm-Dyck (1822)  $\equiv$  *Aloe mitriformis* var. *spinulosa* (Salm-Dyck) Baker (1880); *Aloe spuria* A. Berger (1908); *Aloe stans* A. Berger (1908); *Aloe straussii* A. Berger (1912); *Aloe tenuifolia* Lamarck (1783); *Aloe xucraiae* A. Terraciano (1897)  $\equiv$  *Aloe arborescens* var. *ucraiae* (A. Terraciano) A. Berger (1908); *Aloe venenosa* Engler (1893); *Aloe virens* Haworth (1804); *Aloe virens* var. *macilentata* Baker (1880); *Aloe xanthacantha* Willdenow (1811)  $\equiv$  *Aloe mitriformis* var. *xanthacantha* (Willdenow) Baker (1880).

**A. aaata** T. A. McCoy & Lavranos (Cact. Succ. J. (US) 86(6): 259–260, ill. (pp. 258–260), 2014). **Type:** Saudi Arabia, Asir Prov. (McCoy 3861 [FT]). — **Distr:** Saudi Arabia (Asir Prov.); granite outcrops, 2000 m.

[6,7] Acaulescent, suckering to form large groups; **L** 12–18, rosulate, lanceolate, 20–25  $\times$  8–12 cm, light green with a few elongated white spots near the base, glaucous, pruinose, lower surface more grey-green, exudate clear, drying light yellow, **marginal teeth** 1–2 mm, brown, 15–22 mm apart; **Inf** 60–80 cm, erect, with 1–2 **Br**; racemes cylindrical, dense; **Bra** lanceolate-acute, 12–15  $\times$  4–8 mm, scarious, white, 3- to 5-veined; **Ped** 6–9 mm, light green, slightly

pubescent; **Fl** bright yellow, lobes white-edged, finely white-hirsute, 27–36 mm, 6 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for 8–10 mm; **St** exerted 2 mm; **Sty** exerted 2 mm; **Fr** yellow-green, white-pubescent.

**A. aageodonta** L. E. Newton (Cact. Succ. J. (US) 65(3): 138–140, ills., 1993). **Type:** Kenya, Eastern Prov. (Newton 3643 [K, EA]). — **Distr:** Kenya (Eastern Prov.: Muvaroa Hill); rocky hills, forest clearing and edge of thickets, in soil pockets, 960–1250 m; known only from the region of the type locality. **I:** Carter & al. (2011: 619). — Fig. 2.

[13] Caulescent, branching at the base; stem erect for 1 m, then becoming decumbent and sprawling to 2 m, 3 cm  $\varnothing$ ; **L** 12–20, laxly rosulate and persistent for 20–30 cm below, triangular, 50  $\times$  8 cm, dull green, spotted on young shoots, surface smooth, exudate yellow, drying brown, **marginal teeth** 4 mm, pungent, uncinatate, tips brown; **Inf** 70 cm, erect, with 6–10 **Br**; racemes with 20–40 secund flowers, lax at the base but most flowers crowded near the tip; **Bra** 4–6 mm; **Ped** 10–13 mm; **Fl** yellow or dark red, 30 mm, base attenuate, 7–8 mm  $\varnothing$  across the ovary, narrowed to 5–6 mm above, scarcely widening towards the apex; **OTep** free for 5–7 mm, tips spreading to 10–12 mm; **St** exerted 7 mm; **Sty** exerted 4–5 mm.

Red- and yellow-flowered plants occur together in one population.

**A.  $\times$ abhaica** Lavranos & Colletette (Cact. Succ. J. (US) 72(2): 87, ills. (p. 85), 2000). **Type:** Saudi Arabia, Asir Prov. (Colletette 7165 [K]). — **Distr:** Saudi Arabia (Asir Prov.); rocky slopes, 1400 m. **I:** Colletette (1999: 18).

[13] Only incompletely described; **L** 10–12, rosulate, lanceolate, 70 cm, dark green, margins regularly toothed; **Inf** erect, with up to 11 **Br**; racemes cylindrical.

= *A. pseudorubroviolacea*  $\times$  *A. edentata*.

**A. abyssicola** Lavranos & Bilaidi (Cact. Succ. J. (US) 43(5): 204–208, ills., 1971). **Type:** Yemen (Lavranos & Bilaidi 7490 [FI]). — **Lit:** Favell (2001). **Distr:** S Yemen (Jabal Al Arays); cliff faces, 900 m; known only from the type locality. **I:** Carter & al. (2011: 347).

[3] Acaulescent or with very short stems, simple, pendulous; **L** up to 50, rosulate, pointing downwards, 50  $\times$  12 cm, grey-green, upper surface flat becoming canaliculate towards the tip, **marginal teeth** obtuse, hard, dark, 1 mm, 35–40 mm apart; **Inf** to 60 cm, growing downwards with only the tips of the racemes curved upwards, with 5–6 short spreading **Br**; peduncle yellow-green; racemes lax; **Bra** ovate-lanceolate, 7–8  $\times$  3 mm; **Ped** 8–9 mm, green; **Fl** yellow-green, 25 mm, base rounded, 7 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, enlarging to 8 mm at the mouth; **OTep** free for 7 mm; **St** exerted 3 mm; **Sty** not exerted.

**Fig. 2** *Aloe aageodonta*.  
(Copyright: L. E. Newton)





**A. aculeata** Pole-Evans (Trans. Roy. Soc. South Africa 5: 34, 1915). **Type:** RSA, Limpopo (*Pole-Evans* s.n. in Govt. Herb. PRE 55 [PRE]). — **Distr:** Botswana, S Zimbabwe, RSA (Limpopo, N Mpumalanga); rocky or stony mountain slopes, in hot semi-arid areas, grassland or open bushveld, 500–1765 m. **I:** Reynolds (1950: 448–449); Carter & al. (2011: 368); Wyk & Smith (2014: 140–141).

[5] Acaulescent or with procumbent stem to 80 cm, usually simple; **L**  $\pm 30$ , densely rosulate, lanceolate-attenuate, to  $60 \times 8$ – $12$  cm, arcuate-erectly incurved, dull green to glaucous with scattered reddish-brown prickles, **marginal teeth** 5–6 mm, pungent, reddish-brown, 10–20 mm apart; **Inf** 1 m, with 2–4 **Br**; peduncle deep brown; racemes cylindrical,  $40$ – $60 \times 7$  cm, dense; **Bra** deltoid-acuminate, reflexed,  $10 \times 7$  mm; **Ped** 2–3 mm; **Fl** lemon-yellow with green-orange veins on the lobes, 25–40 mm, base rounded; **OTep** free for 14 mm; **St** exerted 15 mm; **Sty** exerted 18 mm. — **Cytology:**  $2n = 14$  (Müller 1941).

Leaf marginal teeth and surface prickles sometimes arise from white tuberculate bases, and racemes vary in length. Natural hybrids with other species have been reported (Reynolds 1950). Hargreaves (2009) reports the species also for SE Botswana near the border with Zimbabwe.

**A. acutissima** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 17, 1926). **Type** [syn]: Madagascar, Fianarantsoa (*Perrier* 1107 [P?]). — **Lit:** Carter & al. (2011: 559–561, with ills.). **Distr:** Madagascar (Fianarantsoa, Toliara).

**A. acutissima** var. **acutissima** — **Distr:** S & SW Madagascar (Fianarantsoa, Toliara); thin soil on rocks, 240–1200 m. **I:** Reynolds (1966: 495–497); Castillon & Castillon (2010: 164–167). — Fig. 3.

[15] Caulescent, much branched; stem to 1 m, 2–3 cm  $\varnothing$ , erect, divergent or decumbent; **L**  $\pm 20$ , subdensely rosulate and persistent for 20–30 cm below, lanceolate, long-attenuate,  $30 \times 4$  cm, grey-green tinged reddish, **marginal teeth** 3 mm, pungent, pale brown, 10 mm apart, leaf



**Fig. 3** *Aloe acutissima* var. *acutissima*. (Copyright: D. J. Supthut)

sheath green-striate; **Inf** 50 cm, with 2–3 **Br**; racemes cylindrical-acuminate,  $10$ – $15 \times 5$ – $6$  cm, subdense; **Bra** deltoid, clasping the pedicels, 10–15 mm; **Ped** 15 mm, reddish-scarlet; **Fl** 30 mm, reddish-scarlet, base attenuate, 5.5 mm  $\varnothing$  across the ovary, slightly narrowed above and enlarging towards the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

Variable in the size of stems, leaves and flowers. Plants at higher altitudes are more robust.

**A. acutissima** var. **antanimorensis** Reynolds (J. South Afr. Bot. 22(1): 27–29, ills., 1956). **Type:** Madagascar, Toliara (*Reynolds* 7792 [TAN, K, P, PRE]). — **Distr:** S Madagascar (Toliara: hills N of Antanimora); flat rock surfaces among thorn bushes. **I:** Reynolds (1966: 498); Castillon & Castillon (2010: 203–205).

[15] Differs from var. *acutissima*: Stems shorter, thinner; **L**  $10$ – $15 \times 1.5$ – $2$  cm; **Inf** mostly



simple; racemes shorter; **Ped** 10 mm; **Fl** 20–25 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

**A. acutissima** var. **fiherenensis** J.-B. Castillon (Succulent 2007(4): 3, 6, ill. (pp. 6–7), 2007). **Type**: Madagascar, Toliara (*Castillon* 31 [HBG]). — **Distr**: S Madagascar (Toliara); limestone outcrops, 100 m. **I**: Castillon & Castillon (2010: 282–283).

[15] Differs from var. *acutissima*: Stems 30–80 cm, 0.7–1 cm  $\varnothing$ ; **L** 20  $\times$  3 cm, lineolate, **marginal teeth** short, whitish, 2–4 mm apart; **Inf** shorter, few-flowered.

**A. acutissima** var. **isaloana** J.-B. Castillon (Succulent 2007(4): 6–7, ill. (p. 5), 2007). **Type**: Madagascar, Toliara (*Castillon* 32 [HBG]). — **Distr**: S Madagascar (Toliara); degraded forest, on bare sandstone. **I**: Castillon & Castillon (2010: 168–169).

[15] Differs from var. *acutissima*: Stems longer and more robust; **L** longer and broader, lineolate; marginal teeth >8 mm apart; **Inf** usually with 2 branches.

**A. acutissima** var. **itampoloana** J.-B. Castillon (Cact.-Avent. Int. 83: 30, ill. (p. 29), 2009). **Type**: Madagascar, Toliara (*Castillon* 43 [TAN]). — **Distr**: S Madagascar (Toliara: Mahafaly Plateau); limestone cliffs, 20–80 m. **I**: Castillon & Castillon (2010: 284).

**Incl.** *Aloe acutissima* ssp. *itampolensis* Rebmann (2008).

[15] Differs from var. *acutissima*: **L** 18–20  $\times$  2.8–3.3 cm; **Inf** 80–85 cm; racemes 20 cm, sub-lax; **Ped** 8–10 mm; **Fl** 20 mm.

**A. adigratana** Reynolds (J. South Afr. Bot. 23 (1): 1–3, ill., 1957). **Type**: Ethiopia, Tigray (*Reynolds* 8076 [PRE, K]). — **Distr**: Ethiopia (Tigray: W of Adigrat); rocky hills, 1800–2700 m; known only from the region of the type locality. **I**: Reynolds (1966: 215–216); Sebsebe Demissew & Nordal (2010: 91–92); Carter & al. (2011: 625).

$\equiv$  *Aloe camperi* ssp. *adigratana* (Reynolds) Fikre (2006) (*nom. inval.*, ICN Art. 29.1); **incl.** *Aloe abyssinica* Hooker fil. (1900) (*nom. illeg.*,

ICN Art. 53.1); **incl.** *Aloe eru* var. *hookeri* A. Berger (1908).

[15] Caulescent, branching; stem erect to 1 m, 12 cm  $\varnothing$ , decumbent to 2 m; **L** 16–20, rosulate, spreading and slightly recurved, ensiform, 60–80  $\times$  15 cm, dull green with pale green spots, exudate drying deep brown, **marginal teeth** 10 mm, 25–35 mm apart, pungent; **Inf** 90 cm with 3–5 **Br**; racemes cylindrical-conical, 15–20  $\times$  8–9 cm, dense; **Bra** deltoid, 8  $\times$  3 mm; **Ped** 18 mm; **Fl** orange or yellow, 28–33 mm, clavate, base attenuate, 6 mm  $\varnothing$  across the ovary; **OTep** free for 14–16 mm; **St** and **Sty** exerted 5–6 mm. — **Cytology**:  $2n = 14$  (Fentaw & al. 2013).

On the 2 possible synonyms, Reynolds (1966) states “The following almost certainly belong here”.

**A. affinis** A. Berger (in Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 206, 1908). **Type**: RSA, Mpumalanga (*Wilms* 1490 [not located]). — **Lit**: Smith & al. (2005). **Distr**: RSA (Mpumalanga, NW Gauteng?); on sandstone or quartzite in mountainous rocky grassland, 1220–2000 m. **I**: Reynolds (1950: 243–244); Carter & al. (2011: 186); Wyk & Smith (2014: 210–211).

[3] Acaulescent, simple; **L**  $\pm$ 20, densely rosulate, arcuate-erect, 30–45  $\times$  9–11 cm, green with longitudinal dark lines, with prominent horny reddish-brown margin, exudate drying pale yellow, **marginal teeth** 5–8 mm, pungent, 10–15 mm apart; **Inf** to 1 m with 5–10 **Br**; racemes cylindrical, to 25 cm, rather dense; **Bra** narrowly deltoid, 15 mm; **Ped** 15 mm; **Fl** dull brick-red, 45 mm, base rounded, 9–10 mm  $\varnothing$  across the ovary, abruptly narrowed to 5–6 mm above, then slightly decurved and enlarging towards the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 0–1 mm.

Reynolds (1950) reports some variants with leaves obscurely spotted on the upper surface. Natural hybrids with other species have been reported by the same author.

**A. africana** Miller (Gard. Dict., Ed. 8, [no. 4], 1768). **Type** [neo]: RSA, Western Cape (*Pole-Evans* 225 [PRE, BM]). — **Distr**: RSA (Western Cape, Eastern Cape); mostly bush and scrub



**Fig. 4** *Aloe africana*. (Copyright: G. F. Smith)

country, to 300 m. **I**: Reynolds (1950: 457–458); Carter & al. (2011: 672); Wyk & Smith (2014: 52–53). – Fig. 4.

≡ *Pachidendron africanum* (Miller) Haworth (1821); **incl.** *Aloe perfoliata* var. *β* Linné (1753); **incl.** *Aloe perfoliata* var. *africana* Aiton (1789); **incl.** *Aloe pseudoafricana* Salm-Dyck (1817); **incl.** *Aloe africana* var. *angustior* Haworth (1819); **incl.** *Aloe africana* var. *latifolia* Haworth (1819); **incl.** *Aloe angustifolia* Haworth (1819) ≡ *Pachidendron angustifolium* (Haworth) Haworth (1821); **incl.** *Pachidendron africanum* var. *angustum* Haworth (1821); **incl.** *Pachidendron africanum* var. *latum* Haworth (1821); **incl.** *Aloe bolusii* Baker (1880).

[9] Caulescent, usually simple; stem erect, to 4 m, dead leaves persistent; **L** ±30, densely rosulate, spreading to recurved, 65 × 12 cm, dull green to glaucous, upper face glabrous or with few reddish prickles near the tip, lower face with median reddish prickles near the tip, **marginal**

**teeth** 4–5 mm, pungent, 15 mm apart; **Inf** 60–80 cm with 2–4 **Br**; racemes cylindrical-acuminate, 40–60 × 10–12 cm, dense; **Bra** ovate-lanceolate, 11 × 7–8 mm; **Ped** 5–6 mm; **Fl** yellow to yellow-orange, 55 mm, base rounded, 5–6 mm Ø across the ovary, enlarging to 8 mm at the mouth, upper ½ markedly upcurved; **OTep** free for 19 mm; **St** and **Sty** exerted 15–20 mm.

Natural hybrids with other species have been reported (Reynolds 1950).

**A. ahmarensis** Favell & al. (Cact. Succ. J. (US) 71(5): 257–259, ills., 1999). **Type**: Yemen (*al-Gifri* 3776 [Herb. Univ. Aden]). — **Lit**: Favell (2001). **Distr**: Yemen; valley bottoms and basalt lava flows in sparsely vegetated sandy plains, ±500 m. **I**: Carter & al. (2011: 441).

[7] Caulescent or usually acaulescent, solitary or usually suckering with to up to 25 **Ros**; stem procumbent, to 50 cm; **L** ±12, densely rosulate, deltoid-arcuate, ascending, ±30 × 9 cm, upper face pale pinkish-grey with waxy bloom, lower face greenish-grey with a bloom, exudate honey-coloured, **marginal teeth** 2–3 mm, dark brown, 18–30 mm apart; **Inf** 65 cm, ascending, with many **Br**, lower ones rebranched; racemes cylindrical, subdense, **Bra** ovate-deltoid, 6 × 2 mm; **Ped** 7–8 mm, pink; **Fl** bright coral-pink, yellowish at the tip, 33 mm, base rounded, 8 mm Ø across the ovary, narrowing above to 6 mm, widening to 7 mm at the tip; **OTep** free for 10 mm; **St** exerted 1.5 mm; **Sty** exerted 5 mm.

**A. alaotrensis** J.-P. Castillon (Adansonia, sér. 3, 39(1): 10–12, ills., 2017). **Type**: Madagascar, Toamasina (*Humbert* 17572 [P, P]). — **Distr**: E Madagascar (Toamasina); forest, 800 m.

[8] Caulescent; stem to 40 cm; **L** rosulate, narrowly lanceolate, 60 × 2.5 cm, maroon-green, exudate yellow-green, drying brown, **marginal teeth** 5 mm, with white base, green above, 12–18 mm apart; **Inf** to 50 cm, ascending, simple, rarely with 1 **Br**, producing bulbils; racemes capitate or conical, 4–8 cm, dense; **Bra** deltoid, 2 × 2 mm, white, scarious, with 1 maroon nerve; **Ped** 9 mm; **Fl** red, pale green towards the mouth, 23 mm, 4 mm Ø across the ovary, narrowed to 3 mm above, then enlarging to 5 mm at the mouth;



**Fig. 5** *Aloe albida*. (Copyright: U. Eggli)

**OTep** free for 7.6 mm; **St** not exerted; **Sty** exerted 4 mm; **Fr** berries.

*A. albida* (Stapf) Reynolds (J. South Afr. Bot. 13(2): 101, 103, 1947). **Type:** RSA, Mpumalanga (*Galpin* 873 [PRE]). — **Lit:** Craib (2006: 30–32, with ills.); Lüthy (2006: 19–20, conservation, with ills.). **Distr:** RSA (Mpumalanga: Barberton area), adjacent Swaziland; mountain grassland in the mist belt, stony ground or on rocks, 1450–1800 m. **I:** Reynolds (1950: 112–113, t. 2); Glen & Hardy (1990: t. 2010); Carter & al. (2011: 111); Wyk & Smith (2014: 344–345). — Fig. 5.

≡ *Leptaloe albida* Stapf (1933); **incl.** *Aloe kraussii* var. *minor* Baker (1896) ≡ *Aloe myriacantha* var. *minor* (Baker) A. Berger (1908); **incl.** *Aloe kraussii* Schönland (1903) (*nom. illeg.*, ICN Art. 53.1).

[1] Acaulescent, usually simple; **R** fusiform; **L** 6–12, rosulate, linear, 10–15 × 0.4–0.5 cm, dull

green, **marginal teeth** 0.5 mm, 1 mm apart; **Inf** 9–15 cm, simple; raceme capitate, 2–5 × 5 cm with 8–16 flowers; **Bra** ovate-acuminate, 10–15 mm; **Ped** 10–15 mm; **Fl** dull creamy-white, green-tipped, 18 mm, base attenuate, narrowed slightly above the ovary to the bilabiate mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Müller 1945: as *Leptaloe*).

Dependent on regular fires for reproduction, and destroyed by afforestations (Craib 2006).

*A. albiflora* Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 12: 353, 1940). **Type:** Madagascar, Toliara (*Boiteau* 227 p.p. [P]). — **Lit:** Lüthy (2006: 21–22, conservation, with ills.). **Distr:** SW Madagascar (Toliara); known from the type collection only. **I:** Reynolds (1966: 406–407); Castillon & Castillon (2010: 206); Carter & al. (2011: 216).

≡ *Guillauminia albiflora* (Guillaumin) A. Bertrand (1956).

[1] Acaulescent, suckering to form small clumps; **R** fusiform; **L** 10, rosulate, linear-attenuate, 15 × 1.5 cm, grey-green with many small dull-white spots, with narrow dull-white cartilaginous margin, **marginal teeth** 0.5–1 mm, soft to firm; **Inf** 30–36 cm, simple; raceme 9 cm, lax, with ±18 flowers; **Bra** ovate-long acuminate, 5–6 × 2 mm; **Ped** 8 mm; **Fl** white, 10 mm, base rounded, campanulate, 14 mm Ø across the mouth; **OTep** free to the base; **St** exerted 8 mm; **Sty** exerted 9 mm.

*A. albobstriata* T. A. McCoy & al. (Kakt. and Sukk. 59(2): 43–45, ills., 2008). **Type:** Madagascar, Antananarivo (*Pronk* s.n. in *Lavranos* 32229 [Herb. Univ. Antananarivo, FT]). — **Distr:** C Madagascar (Antananarivo: Ibity Range); mountainous country. **I:** Castillon & Castillon (2010: 99); Carter & al. (2011: 551).

[11] Low shrub, branching from the base to form small groups; stems to 30 cm; **L** 10–15 on the upper 10–12 cm of the stem, ascending, lanceolate, 20–25 × 2 cm, pale green, with many longitudinal whitish stripes, exudate drying clear, **marginal teeth** 0.75–1 mm, 5–15 mm apart, often obsolete; **Inf** to 70 cm, erect, simple or with 1–2 **Bra**; racemes cylindrical-acute, to 25 cm, lax; **Bra**

acute, 10 × 2 mm; **Ped** 12–15 mm, pink; **Fl** orange-red, yellow towards the mouth, 22–24 mm, 3.5–4 mm Ø across the ovary; **OTep** free for 12–13 mm; **St** and **Sty** exerted 1 mm.

**A. albovestita** S. Carter & Brandham (Bradleya 1: 20–21, ills., 1983). **Type:** Somalia, Sanaag Region (*Bailes* 214 [K]). — **Distr:** NE Somalia (Sanaag Region: Al Madu Range), Djibouti; rocky ground and rock crevices, juniper forest on limestone, often in deep shade, ±1450 m. **I:** Carter & al. (2011: 161).

[7] Acaulescent, suckering to form small clumps; **L** rosulate, lanceolate, 20–30 × 12 cm, glaucous, distinctly longitudinally striate, upper face with few paler spots, with narrow cartilaginous margin, **marginal teeth** 1.5 mm, red-brown, 5–10 mm apart; **Inf** 75 cm, with 2–3 **Br**; racemes cylindrical to subcapitate, 10–20 × 5 cm; **Bra** lanceolate, 15 × 3 mm; **Ped** 18 mm; **Fl** dull pink with greyish tip, finely white-flecked and densely covered with white bloom, 25–33 mm, base rounded, 7 mm Ø across the ovary, narrowed to 4.5 mm above; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (protologue).

**A. aldabrensis** (Marais) L. E. Newton & G. D. Rowley (Excelsa 17: 59, 1997). **Type:** Seychelles, Aldabra Archipelago (*Stoddart* 920 [K]). — **Distr:** Seychelles (Aldabra Archipelago: Aldabra, Assumption, Astove); limestone in mixed scrub or thickets, almost sea-level. **I:** Castillon & Castillon (2010: 388, 390); Carter & al. (2011: 465).

≡ *Lomatophyllum aldabrense* Marais (1975).

[8] Acaulescent or caulescent; stem erect or decumbent, to 2 m; **L** densely rosulate, linear-lanceolate to ensiform, long-attenuate, 60–100 × 4–10 cm, green, often tinged orange or red, with horny margin, **marginal teeth** small; **Inf** 15–35 cm, with 3–5 **Br**, rarely rebranched; racemes cylindrical, subdense; **Bra** ovate to deltoid, 2.5–4.5 mm; **Ped** 12–20 mm; **Fl** bright orange-red, 18–25 mm, base shortly attenuate; **OTep** free for slightly more than ½; **St** and **Sty** slightly exerted; **Fr** berries, 15 × 12 mm.

**A. alexandrei** Ellert (Cact. Succ. J. (US) 78(1): 11, ills. (pp. 10–14), 2006). **Type:** Comoros, Grande Comore (*Ellert* 1175 [ARIZ, MO, NY, P]). — **Distr:** Comoro Islands (Grande Comore); soil pockets on basalt lava. **I:** Castillon & Castillon (2010: 388–389); Carter & al. (2011: 664).

[9] Caulescent, usually simple; stem >3 m, 16 cm Ø; **L** 19–30, rosulate, 60–100 × 12 cm, pale green to greenish-yellow, with obscure lineation, surface smooth, exudate greenish-yellow, margin reddish, **marginal teeth** 0.5–2 (–4) mm, whitish, 5–10 mm apart; **Inf** 55–100 cm, erect, with 2–4 **Br**; racemes cylindrical-acuminate, 30 × 12.5 cm, dense; **Bra** minute; **Ped** 14–25 mm; **Fl** red, orange or yellow, 30 mm, 5–8 mm Ø across the ovary; **OTep** free for 10 mm; **St** and **Sty** exerted 3–5 mm; **Fr** berries, 12 × 14 mm.

Similar to *A. peyrierasii* according to Castillon & Castillon (2010: 388–389).

**A. alfredii** Rauh (Cact. Succ. J. (US) 62(5): 232–233, ills., 1990). **Type:** Madagascar, Antananarivo (*Rauh* 68690 [HEID]). — **Lit:** Lüthy (2006: 23–24, conservation, with ills.). **Distr:** C Madagascar (Antananarivo: Ibity Range); quartz fields, 1400 m; not found again after the original collection. **I:** Castillon & Castillon (2010: 95); Carter & al. (2011: 556).

[11] Caulescent, branching at the base; stem 25 × 1.5 cm; **L** scattered along the stem, linear, 30 × 1.5 cm, dark dull green, **marginal teeth** 1 mm, white, leaf sheath 15 mm, red-brown with darker veins; **Inf** 60 cm, simple; raceme cylindrical, 8–10 × 5–6 cm, many-flowered; **Bra** triangular, 5 mm; **Ped** 5 mm; **Fl** lemon-yellow with green mid-stripe, 20 mm, base rounded; **St** and **Sty** exerted 4–5 mm.

**A. allochroa** L. E. Newton & Mwadime (CactusWorld 37(2): 139–140, ills. 2019). **Type:** Kenya, Rift Valley Prov. (*Mwadime & Luke* 1979 [EA, K]). — **Distr:** W Kenya; dry scrub on rocky ground, and on steep cliffs, 1975–2445 m.

[14] Caulescent, branching at the base, stem to 2 m, erect for 1 m, then mostly becoming decumbent unless supported by rocks or surrounding vegetation; **L** numerous, persistent along the



stems, somewhat falcate, apex acute,  $50 \times 5$  cm, mid-green, surface smooth, exudate pale yellow, quickly becoming dark purple, **marginal teeth** pointing forwards, 3 mm, green, whitish at the apex, 10–13 mm apart, leaf sheaths 10 cm long, green; **Inf** 65 cm, erect, with 5 **Br**; racemes cylindrical, to 12 cm, dense; **Bra** ovate-attenuate, apex acute,  $3 \times 2$  mm, hyaline with 1 brown vein; **Ped** 15 mm, orange; **Fl** tube scarlet, fading to orange at anthesis, lobes orange-yellow, 32 mm, base shortly attenuate, terete across the ovary, becoming trigonous above, 6 mm  $\varnothing$  across the ovary, narrowing to 5 mm above, widening to 7 mm just below the mouth; **OTep** free for 12–15 mm; **St** exserted 7 mm; **Sty** exserted 5 mm.

**A. alooides** (Bolus) van Druten (*Bothalia* 6(3): 544–545, 1956). **Type:** RSA, Mpumalanga (*MacLea* s.n. in *BOL* 3011 [BOL, SAM]). — **Distr:** RSA (Mpumalanga); dolomite outcrops in mountains, (1200–) 1700–2000 m. **I:** Reynolds (1950: 437–438, t. 58, as *A. recurvifolia*); Carter & al. (2011: 657); Wyk & Smith (2014: 54–55). — Fig. 6.

≡ *Urginea alooides* Bolus (1881) ≡ *Noto-sceptrum alooides* (Bolus) Bentham (1883); **incl.** *Aloe recurvifolia* Groenewald (1935).

[8] Caulescent; stem usually simple, rarely branched low down, erect, stout, 2 m, covered with remains of dead leaves; **L** densely rosulate, lanceolate-ensiform, long-attenuate, deeply canaliculate, arcuate-recurved,  $130 \times 18$  cm, green, sometimes slightly reddish, usually with distinct reddish margin, **marginal teeth** 2–3 mm, usually curved towards the leaf tip, 10 mm apart, brownish-tipped; **Inf** 1.3 m, erect, simple; raceme narrowly cylindrical, slightly acuminate,  $80 \times 4.5$  cm, dense; **Bra** ovate-acute,  $5-7 \times 4-5$  mm; **Ped** none; **Fl** sessile, lemon-yellow, 9 mm, base rounded, campanulate, 8 mm  $\varnothing$  across the mouth; **OTep** free to the base; **St** and **Sty** exserted 7–8 mm.

**A. ambigens** Chiovenda (Pl. Nov. Min. Not. Ethiop. 1: 6, 1928). **Type:** Somalia (*Puccioni & Stefanini* 447 [FI]). — **Distr:** Somalia (Mudug Region); bushland on steep limestone rock faces,  $\pm 250$  m; known only from the type locality. **I:** Carter & al. (2011: 483).



**Fig. 6** *Aloe alooides*. (Copyright: G. F. Smith)

[15] Caulescent, branching; stem to 40 cm; **L** 5–15, laxly rosulate, to  $20 \times 2-3$  cm, glaucous green, sometimes with a few paler spots, **marginal teeth** to 1 mm, white, 10–20 mm apart; **Inf** to 1 m, with up to 8 **Br**; racemes cylindrical, 4–12 cm, lax; **Bra**  $5 \times 3$  mm; **Ped** 4 mm; **Fl** red or yellow, 20–25 mm, 7 mm  $\varnothing$  across the ovary; **OTep** free for 6 mm; **St** and **Sty** scarcely exserted.

**A. ambositrae** J.-P. Castillon (*CactusWorld* 26 (1): 32–33, ills., 2008). **Type:** Madagascar, Fianarantsoa (*Castillon* 36 [TAN, HBG]). — **Distr:** W Madagascar (Fianarantsoa: Betsileo Region); loam overlying rocks on granitic inselbergs, 1650 m; known only from the type locality. **I:** Castillon & Castillon (2010: 144–145); Carter & al. (2011: 617).

[15] Caulescent, suckering; stem prostrate to 20 cm, then erect to 1 m, with persistent dried leaves; **L** 18–25, rosulate,  $30-45 \times 3-4$  cm, dark green, **marginal teeth** 3 mm, greenish-white, 8–25 mm apart; **Inf** 1 m, erect, with 2–5 **Br**;



racemes cylindrical, 15–23 cm, semi-dense; **Bra** 5 × 3 mm, red; **Ped** 14–20 mm; **Fl** yellow, red in bud, 25 mm; **OTep** free to the base; **St** and **Sty** not exerted.

**A. ambrensis** J.-B. Castillon (CactusWorld 25 (1): 12, ills. (pp. 12–14), 2007). **Type:** Madagascar, Antsiranana (*Castillon* 28 [HBG]). — **Distr:** N Madagascar (Antsiranana: Cap d’Ambre); forest, among basaltic and limestone boulders. **I:** Castillon & Castillon (2010: 350–351); Carter & al. (2011: 290).

[2] Acaulescent, solitary; **L** 11–15, rosulate, spreading, lanceolate-attenuate, deeply channelled, 70 × 3.5–6 cm, green or tinged red, **marginal teeth** 1.5 mm, white, 15–20 mm apart; **Inf** 30–40 cm, erect, simple or with 1 **Br**; racemes cylindrical, 12–20 cm, lax; **Bra** papery, 5 × 2 mm; **Ped** 5 mm; **Fl** red, 32 mm, 5 mm Ø across the ovary, narrowing above to 3 mm, then widening to 5 mm; **OTep** free for 3–4 mm; **St** and **Sty** scarcely exerted; **Fr** berries, 2 cm Ø.

**A. amicorum** L. E. Newton (Cact. Succ. J. (US) 63(2): 80–81, ills., 1991). **Type:** Kenya, Eastern Prov. (*Newton* 3217 [K, EA]). — **Distr:** Kenya (Eastern Prov.: Marsabit Distr., Mt. Kulal); ledges on steep rock face, 1450 m; known only from the type locality. **I:** Carter & al. (2011: 507).

[13] Caulescent, branching sparsely near the base; stem pendulous, 112 × 2.5 cm Ø, covered with dead sheathing leaf bases; **L** laxly rosulate but curving to give an almost distichous appearance, falcate, 46 × 5.5 cm, bluish-green, tinged purplish-red in sun, sometimes with few scattered whitish spots on the upper face, surface slightly rough, with narrow white cartilaginous margin, exudate yellow, drying brownish-yellow, **marginal teeth** 1 mm, 8–10 mm apart, red-tipped, leaf apex obtuse with 1–2 minute teeth; **Inf** 76 cm, slightly ascending, almost horizontal, with 6 **Br**, lightly covered with white bloom; racemes with secund flowers, 8–27 cm, lax; **Bra** triangular, 3.5 × 2.5 mm; **Ped** 8 mm; **Fl** crimson with a light cover of white bloom, margins of the lobes creamy-white, 28 mm, base truncate, 11–12 mm Ø across the ovary, narrowed to 7 mm above,

lobes spreading to 10 mm; **OTep** free for 10–11 mm; **St** and **Sty** exerted 3–5 mm.

**A. ammophila** Reynolds (J. South Afr. Bot. 2: 116, 1936). **Type:** RSA, Limpopo (*Reynolds* 1345 [PRE]). — **Lit:** Smith & al. (2012c). **Distr:** RSA (Limpopo); sandy soil in grassland or woodland clearings. **I:** Reynolds (1950: 270–271); Wyk & Smith (2014: 212–213).

[7] Acaulescent, suckering to form dense groups; **L** 10–14, densely rosulate, lanceolate-attenuate, to 22 × 5–6 cm, dull green with numerous oval white spots in irregular transverse bands, **marginal teeth** 4–5 mm, light brown, 8–12 mm apart; **Inf** 66 cm, erect, with 5–7 **Br**, the lowermost sometimes rebranched; racemes cylindrical, slightly acuminate, 20–25 × 7 cm, lax; **Bra** deltoid-acuminate, 15 mm or slightly longer; **Ped** 15 mm; **Fl** coral-red, 30–33 mm, 9–10 mm Ø across the ovary, constricted above to 5–6 mm, enlarged to the mouth; **OTep** free for 10–11 mm; **St** exerted 3–4 mm; **Sty** exerted 2–4 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Included by some authors in *A. zebrina* Baker, e.g. by Carter & al. (2011: 166).

**A. ampefyana** J.-B. Castillon (Haseltonia 13: 26–27, ills., 2008). **Type:** Madagascar, Antananarivo (*Castillon* 30 [HBG]). — **Distr:** C Madagascar (Antananarivo); exposed precipitous granite slopes, 1360 m; known only from the area of the type locality. **I:** Castillon & Castillon (2010: 54–55); Carter & al. (2011: 248).

[5] Acaulescent or with stems to 30 cm (to 100 cm when pendulous on cliffs), solitary or branching to form clumps of up to 6 rosettes; **L** 25–30, rosulate, lanceolate, 25–30 × 3–6 cm, green, with green pustules when juvenile, **marginal teeth** 4 mm, pale green, 10–15 mm apart; **Inf** 70 cm, erect, simple or with 1–2 **Br**; racemes cylindrical, 10–15 cm, subdense; **Bra** ovate-acuminate, 10 mm; **Ped** 17 mm; **Fl** pale yellow, red in bud, 17 mm, 4 mm Ø across the ovary; **OTep** free to the base; **St** and **Sty** exerted 4–10 mm.

Probably a hybrid *A. capitata* × *A. arborescens* according to Castillon & Castillon (2010), though its natural spread by fertile seeds

suggests not. Also, *A. arborescens* is an African species, and Castillon & Castillon (2010) do not mention its occurrence in Madagascar.

**A. amudatensis** Reynolds (J. South Afr. Bot. 22(3): 136–137, ills., 1956). **Type:** Uganda, Karamoja (Reynolds 7996 [PRE, EA, K]). — **Distr:** NW Kenya, NE Uganda; dry bushland, sandy soils, 915–1340 m. **I:** Reynolds (1966: 77); Carter & al. (2011: 162); Cole & Forrest (2017: 24–29).

[6] Acaulescent, suckering to form small to large dense clumps; **L** ±12, densely rosulate, lanceolate-attenuate, 22 × 5 cm, dull green with oval white spots in irregular transverse bands, with white-cartilaginous margin, **marginal teeth** 2 mm; **Inf** 50–65 cm, mostly simple, sometimes with 1–2 **Br**; racemes cylindrical, slightly conical, 8 × 6–7 cm, sublax; **Bra** ovate-deltoid, 10 × 3 mm; **Ped** 17 mm; **Fl** rose-pink to coral-red, 23 mm, base truncate, 9 mm Ø across the ovary, abruptly narrowed to 6 mm above, then enlarging towards the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

A natural hybrid with *A. tweediae* has been reported (Reynolds 1966). Wabuyele & al. (2006) treat the species as a synonym of *A. ellenbeckii*, which has wider leaves with larger marginal teeth, and slightly shorter flowers.

**A. analavelonensis** Letsara & al. (Malagasy Nat. 6: 47, ills. (pp. 48, 50), 2012). **Type:** Madagascar, Toliara (Letsara & al. 938 [TAN, CAS, K]). — **Distr:** S Madagascar (Toliara); humid forest on rocky substrate, 1035 m.

[6] Acaulescent, suckering to form dense clumps; **L** 9–12, rosulate, narrowly linear, 12–15 × 2–2.5 cm, green with 6–8 faint parallel veins, surface smooth, exudate colourless, **marginal teeth** deltoid, 1.6 mm, green or light brown, 3–5 mm apart; **Inf** 18 cm, erect, simple; racemes cylindrical, 8.5 cm, lax; **Bra** deltoid, 2–3 mm wide at the base, scarious, pale brown; **Ped** 14 mm, reddish-orange; **Fl** orange or reddish-orange, with yellow-green and dark green nerves towards the mouth, 26 mm, 6 mm Ø across the ovary, narrowed above, widening to the mouth; **OTep**

free to the base (?); **St** exerted 2–5 mm; **Sty** scarcely exerted.

The protologue states “outer tepals free”, but the illustrations suggest that they are free for slightly less than ½ the length of the perianth.

**A. andersonii** Van Jaarsveld & P. Nel (Bradleya 32: 112–114, ills., 2014). **Type:** RSA, Mpumalanga (Van Jaarsveld & Nel 24278 [PRE]). — **Distr:** RSA (Mpumalanga: N Drakensberg; Mt. Anderson); E-facing quartzitic sandstone cliffs, 1700–2200 m.

[1] Shortly caulescent from fleshy roots, suckering to form dense groups to 30 cm Ø; stem 5–10 cm, spreading to pendent, bases covered with old leaf remains; **L** 7–11, rosulate, pendent, linear-lanceolate, 15–25.4 × 0.8–1.4 cm, green, white-spotted at the base, lower face purplish-green towards the base, surface smooth, **marginal teeth** cartilaginous, 0.5 mm, white, semi-translucent, 1–1.5 mm apart; **Inf** 9–15 cm, decumbent, simple; racemes subcapitate, 6.5–7 cm, dense; **Bra** deltoid, acuminate, 14 × 5 mm, scarious; **Ped** 22–25 mm, orange; **Fl** bright orange-red, lobes green-tipped, 30 mm, 4 mm Ø across the ovary, widening to 6 mm above, narrowing to the mouth; **OTep** free for 10 mm; **St** and **Sty** not exerted.

**A. andongensis** Baker (Trans. Linn. Soc. London, Bot. 1: 263, 1878). **Type:** Angola, Cuanza Sul (Welwitsch 3729 [BM, K, LISC, LISU]). — **Lit:** Klopper & al. (2009a: 23). **Distr:** Angola.

**A. andongensis** var. **andongensis** — **Distr:** W Angola (Cuanza Sul, Huambo, Malange); exposed rocks, 1050–1525 m. **I:** Reynolds (1966: 347); Carter & al. (2011: 550).

[15] Caulescent, branching; stem ascending, sometimes becoming decumbent, 30–60 cm; **L** ±14, rosulate, persistent for 30 cm below, lanceolate-attenuate, 20–25 × 6–7 cm, dull grey-green, upper face mostly without spots, sometimes sparingly spotted, lower face usually with many crowded white spots near the base, with slight cartilaginous margin, **marginal teeth** 2–3 mm, 5–7 mm apart; **Inf** 30–40 cm, with 2–3 **Br**;

racemes subcapitate to cylindrical-acuminate, 6–12 × 6–8 cm; **Bra** lanceolate-acute, 5–8 × 3 mm; **Ped** 14–18 mm; **Fl** pale orange-scarlet, paler at the mouth, 25 mm, base shortly attenuate, 5–6 mm  $\varnothing$  across the ovary, narrowed to 4–5 mm above, enlarging to 6–7 mm at the mouth; **OTep** free for 8 mm; **St** and **Sty** slightly exerted. — **Cytology**: 2n = 14 (Brandham 1971).

A natural hybrid with *A. gossweileri* has been reported (Reynolds 1966).

**A. andongensis** var. **repens** L. C. Leach (J. South Afr. Bot. 40(2): 115–116, ill., 1974). **Type**: Angola, Cuanza Sul (*Leach & Cannell* 13950 [LISC, BM, BR, K, PRE, SRGH]). — **Distr**: W Angola (Cuanza Sul); slopes of rounded granite hills.

[13] Differs from var. *andongensis*: Stem prostrate, forming large spreading clumps; **L** smaller, proportionately narrower, more copiously white-spotted, the spots tending to be in wavy transverse bands, **marginal teeth** more crowded.

**A. andringitrensis** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 41, 1926). **Type**: Madagascar, Fianarantsoa (*Perrier* 13637 [P]). — **Distr**: Madagascar (Fianarantsoa: Andringitra Range); gravelly places, (1800–) 2000–2600 m. **I**: Reynolds (1966: 452–453); Castillon & Castillon (2010: 152–153); Carter & al. (2011: 342).

[3] Acaulescent, simple; **R** fusiform; **L** 15–20, rosulate, triangular, 50 × 7 cm, grey-green, surface very slightly asperulous, **marginal teeth** 1 mm, pinkish, 5–10 mm apart; **Inf** 80–90 cm, with 6–8 **Br**; racemes subcapitate, 6–10 cm, dense; **Bra** ovate-acute, 8 × 3 mm; **Ped** 25 mm; **Fl** dull orange to yellowish, 22 mm, base rounded, 4 mm  $\varnothing$  across the ovary, enlarging upwards to 9 mm at the mouth; **OTep** free for 17 mm; **St** not exerted; **Sty** scarcely exerted. — **Cytology**: 2n = 14 (Resende 1937).

**A. angelica** Pole-Evans (Flow. Pl. South Afr. 14: t. 554 + text, 1934). **Type**: RSA, Limpopo (*Pole-Evans* s.n. [PRE 13040]). — **Distr**: RSA (Limpopo: Soutpansberg Mts.); rocky slopes, 500–1700 m. **I**: Reynolds (1950: 471–472); Carter & al. (2011: 673); Wyk & Smith (2014: 56–57).

[9] Caulescent, simple or branched; stem 3–4 m, upper ½ covered with dead leaf remains; **L** densely rosulate, ensiform, youngest spreading, oldest much recurved, 80 × 10–12 cm, green, with brownish-red margin, **marginal teeth** 2–3 mm, brownish-red, pungent, 10 mm apart; **Inf** with up to 20 **Br**; racemes densely capitate, 8–10 × 8–10 cm; **Bra** ovate-acute, 8–10 × 8–10 mm; **Ped** 25 mm; **Fl** greenish-yellow to yellow, 25 mm, ventricose with the mouth slightly upturned, base rounded; **OTep** free for 18 mm; **St** and **Sty** exerted 15 mm. — **Cytology**: 2n = 14 (Riley 1959: 241).

Natural hybrids with other species have been reported (Reynolds 1950).

**A. angolensis** Baker (Trans. Linn. Soc. London, Bot. 1: 236, 1878). **Type**: Angola, Bengo (*Welwitsch* 3728 [BM, LISU]). — **Distr**: NW Angola (Bengo), adjacent Botswana and Namibia; wooded hills, 1000–1400 m. **I**: Reynolds (1966: 311).

[18] Very shortly caulescent; **L** densely rosulate, lanceolate-ensiform, very fleshy, 60 × 4–5 cm, glaucous, **marginal teeth** 2 mm, 15–20 mm apart; **Inf** 90 cm, simple or with 1–3 arcuate-erect **Br**; racemes cylindrical, slightly acuminate, ±10 cm, dense; **Bra** ovate-acute, 10 mm; **Ped** 3–6 mm; **Fl** sulphur-yellow, 20–24 mm, base rounded; **OTep** free for <10 mm.

A little-known species, whose identity is in doubt. Reynolds (1966) suggested that it might belong to the *A. littoralis*-complex, while Carter (2001) reduced it to synonymy under that species. It is still included in *A. littoralis* in Carter & al. (2011), but Klopper & al. (2009a) argue for its acceptance as a distinct species.

**A. anivoranoensis** (Rauh & Hebding) L. E. Newton & G. D. Rowley (Bradleya 16: 114, 1998). **Type**: Madagascar, Antsiranana (*Rauh* 22864 [HEID]). — **Distr**: NE Madagascar (Antsiranana: Ankarana massif); limestone rocks in deciduous forest. **I**: Rauh (1998: 99, as *Lomatophyllum*); Castillon & Castillon (2010: 346–347); Carter & al. (2011: 557).

≡ *Lomatophyllum anivoranoense* Rauh & Hebding (1998).

[11] Caulescent; stems 1 or branching at the base, to 30 cm, thin at the base, thicker towards the tip, up to 2 cm  $\varnothing$ ; **L** 8–10, scattered along the stem, erect when young, curved downwards when older, linear, up to 30  $\times$  2 cm, canaliculate, tip long attenuate and often spirally coiled, blue-green, **marginal teeth** deltoid, 2 mm, 1–1.5 mm apart, leaf sheath 1–2 cm, white tinged reddish; **Inf** simple, erect or ascending; raceme up to 10 cm, lax, 15- to 30-flowered; **Bra** triangular, long-attenuate, to 15 mm; **Fl** bright cinnabar-red, whitish with green midstripe at the tip, 25–30 mm, scarcely constricted above the ovary, slightly curved; **OTep** free almost to the base (?); **St** and **Sty** exerted 10 mm; **Fr** berries, 15  $\times$  12 mm.

The description of the protologue states that the outer tepals are united for 3–5 mm, but in the accompanying Fig. 17 they seem to be united almost to the tip.

**A. ankoberensis** M. G. Gilbert & Sebsebe (Kew Bull. 52(1): 146–147, 1997). **Type:** Ethiopia, Shewa Region (*Ash* 2353 [K]). — **Distr:** C Ethiopia (Shewa Region); steep basalt rocky slopes and cliffs of the escarpment, 3000–3500 m. **I:** Sebsebe Demissew & Nordal (2010: 81–82); Carter & al. (2011: 505); Starha (2014a).

[13] Caulescent, usually simple; stem pendulous, to 6 m; **L** densely rosulate, 20–30  $\times$  7–17.5 cm, dull greyish- to bluish-green, **marginal teeth** 2–3 mm, pale, usually with minute dark reddish-brown tip, 0.7–1.9 mm apart; **Inf** descending at the base and curving upwards again with U-bend, with 1–6 **Br**; racemes cylindrical, 6–8 cm, dense; **Bra** ovate-lanceolate, acute, 14–25  $\times$  5–6.5 mm; **Ped** (6–) 10–25 mm; **Fl** bright orange-red, 35–40 mm, 6–10 mm  $\varnothing$  when pressed; **OTep** free for 12–22 mm; **St** and **Sty** shortly exerted. — *Cytology:* 2n = 14 (Fentaw & al. 2013).

**A. anodonta** T. A. McCoy & Lavranos (CactusWorld 33(3): 180, ill. (pp. 179–181), 2015). **Type:** Somalia, Bari Region (*McCoy* 3420 [FT]). — **Distr:** NE Somalia (Puntland: Bari Region); limestone hill, 550 m.

[7] Acaulescent, suckering to form groups of up to 10 **Ros**; **L** densely rosulate, narrowly lanceolate-acuminate, often slightly falcate,

35–40  $\times$  5–7 cm, grey-green, exudate dark yellow, drying greenish-yellow, margin entire, with pink-white cartilaginous edge; **Inf** 60–65 cm, erect, with 3–6 **Br**; racemes conical-cylindrical, 35–50 cm; **Bra** deltoid-acuminate, 12 mm, scarious, white, with 3–5 brown nerves; **Ped** 5 mm, dark pink, pruinose; **Fl** dull reddish to pink, with yellow to white mouth, papillose-tomentose, 35 mm, 6 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for 10 mm; **St** exerted 4 mm; **Sty** exerted 5 mm.

**A.  $\times$  anosyana** J.-P. Castillon (Adansonia, sér. 3, 34(1): 20, fig. 5, 2012). **Type:** Madagascar, Toliara (*Decary* 10778 [P]). — **Distr:** S Madagascar (Toliara: Tolanaro).

[9] Caulescent, suckering at the base; stem erect, to 3 m, 5–10 cm  $\varnothing$ , with dead leaves persistent; **L** 40–60, in the terminal 50–70 cm of the stem, 50–70  $\times$  8–12 cm, blue-green; **Inf** erect, with 4–10 **Br**; racemes conical, 20–30 cm, dense; **Fl** yellow.

= *A. helenae*  $\times$  *A. divaricata* ssp. *vaotsohy*.

**A. ansoultae** Rebmann (Cact. Succ. 8(2): 36, ill. (pp. 36–37), 2016). **Type:** Madagascar, Toliara (*Rebmann* 830 [TAN]). — **Distr:** Madagascar (Toliara: Anosy), shaded granite rocks in dry forest, 550 m, known only from the type locality.

[6] Acaulescent, suckering to form clumps to 80 cm  $\varnothing$ ; **L** 12–15, rosulate, lanceolate, 8–12  $\times$  3 cm, brownish-green with many white spots, margin red-brown, **marginal teeth** deltoid, whitish; **Inf** 28 cm, simple; raceme cylindrical, 8 cm; **Bra** deltoid, 8–12 mm, whitish; **Ped** 8–12 mm; **Fl** orange, greenish towards the mouth, 22–25 mm, 4–5 mm  $\varnothing$  across the ovary.

**A. antandroi** (Decary) H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 19, 1926). **Type:** Madagascar (*Decary* s.n. [P]). — **Distr:** S & SW Madagascar (Toliara); dry limestone rocks or rubble, 50–200 m. **I:** Reynolds (1966: 491–492); Castillon & Castillon (2010: 537).

= *Gasteria antandroi* Decary (1921); **incl.** *Aloe leptocaulon* Bojer (1837) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Aloe antandroi* ssp. *toliarana* J.-B. Castillon (2009).

[14] Caulescent, branching at or near the base; **R** woody; stem usually partly supported by surrounding vegetation, 60–100 × 0.5–0.7 cm; **L** 12–20, laxly rosulate, triangular, 10–15 × 0.6–1 cm, grey-green, upper face sometimes with a few scattered small white spots, lower face with many dull white spots, apex obtusely rounded with ±3 small soft white teeth, **marginal teeth** 0.5–1 mm, white to very pale brown, 7–10 mm apart, leaf sheaths green-striate, 10 mm apart; **Inf** 16 cm, simple or with 1 **Br**; racemes subcapitate, 3 × 5 cm, lax, ±10-flowered; **Bra** ovate-acute, 4 × 3 mm; **Ped** 8 mm; **Fl** scarlet, 22 mm, base truncate, 6 mm Ø across the ovary, slightly narrowed above and enlarging towards the mouth; **OTep** free for 15–16 mm. — **Cytology**: 2n = 14 (Brandham 1971).

Features said to distinguish ssp. *toliarana* occur throughout this widespread species.

**A. antoetrana** J.-B. Castillon (CactusWorld 29(1): 53–54, ill. (pp. 51–53), 2011). **Type**: Madagascar, Fianarantsoa (*Castillon* 48 [TAN]). — **Distr**: Madagascar (Fianarantsoa); in grass on quartzitic mountain.

[1] Caulescent, suckering to form dense clumps of 15–30 shoots; stem 20–40 cm, 0.8 cm Ø; **L** 7–15, laxly rosulate, lorate-attenuate, both sides convex, 24–35 × 0.8 cm, green, reddish in full sun, exudate colourless, **marginal teeth** 2–4 mm, green or red, 10 mm apart; **Inf** 50 cm, erect, simple; racemes subcapitate, 2–3 cm, dense; **Bra** 4 × 6 mm, base orange, apex white; **Ped** 28 mm, yellowish-orange; **Fl** yellowish-green, 28 mm, narrowed above the ovary, then widening to the mouth; **OTep** free to the base.

**A. antonii** J.-B. Castillon (CactusWorld 24(3): 130, ill. (pp. 129–132), 2006). **Type**: Madagascar, Mahajanga (*Castillon* 25 [HBG, P]). — **Distr**: W Madagascar (Mahajanga: Bemaraha National Park); karstic limestone (“tsingy”). **I**: Castillon & Castillon (2010: 300–301); Carter & al. (2011: 666).

[9] Caulescent; stem simple, erect or decumbent, to 3 m, 3–5 cm Ø, with bulbils; **L** 20–25, spreading, becoming deflexed, 30–50 × 4–8 cm, green, **marginal teeth** 1–2 mm, 10 mm apart; **Inf**

80–100 cm, with 7–11 **Br**; racemes 15–20 × 5 cm, lax; **Bra** 5 × 3 mm, red at the base, scarious above; **Ped** 7 mm, red; **Fl** crimson, apically yellowish, 30 mm, base obconical, 5 mm Ø across the ovary, narrowing above, then to 7 mm at the mouth; **OTep** free for 20 mm; **St** exerted to 1–3 mm; **Sty** not exerted.

**A. antsingyensis** (Leandri) L. E. Newton & G. D. Rowley (Excelsa 17: 59, 1997). **Type** [syn]: Madagascar, Antsiranana (*Decary* 7936 [K]). — **Distr**: W Madagascar (Antsiranana); limestone, in the shade of forests. **I**: Rauh (1995: 79, 329); Castillon & Castillon (2010: 304); Carter & al. (2011: 574).

≡ *Lomatophyllum antsingyense* Leandri (1935).

[13] Caulescent; stem decumbent, to 1 m, 1 cm Ø; **L** scattered along the stem, linear, 20–50 × 2 cm, dull green, **marginal teeth** to 1 mm, 10 mm apart, leaf sheath 2–3 cm, striate, with white spots; **Inf** 10–12 cm, simple; racemes cylindrical, lax, with 15–30 flowers; **Bra** acute, ±8–10 mm; **Ped** 8–10 mm; **Fl** red, green-tipped, ±20 mm, base rounded, ±8 mm Ø across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for 3–4 mm; **St** and **Sty** exerted to 1 mm; **Fr** berries.

**A. arborescens** Miller (Gard. Dict., Ed. 8, [Aloe no. 3], 1768). **Type** [neo]: RSA, Eastern Cape (*Galpin* 2463 [PRE, GRA]). — **Lit**: Smith & al. (2012b); Thiede & al. (2015). **Distr**: C-S to S Malawi, Moçambique, E Zimbabwe, Botswana (cult. only?), RSA (Limpopo, North-West Province, Gauteng, Mpumalanga, KwaZulu-Natal, Western Cape, Eastern Cape, E Free State), Swaziland; rocky slopes, sometimes in dense bush, sea-level to 2150 m; neophyte in Spain, Portugal and Australia. **I**: Reynolds (1966: 383); Carter & al. (2011: 660); Klopper & al. (2012: 69–70, 76, with distribution map); Wyk & Smith (2014: 86–87).

≡ *Aloe perfoliata* var. *arborescens* (Miller) Aiton (1789) ≡ *Catevala arborescens* (Miller) Medikus (1789); **incl.** *Aloe perfoliata* var. *η* Linné (1753); **incl.** *Aloe fruticosa* Lamarck (1783); **incl.** *Aloe arborea* Medikus (1783)



(*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe frutescens* Salm-Dyck (1817)  $\equiv$  *Aloe arborescens* var. *frutescens* (Salm-Dyck) Link (1821); **incl.** *Aloe sigmoidea* Baker (1880); **incl.** *Aloe*  $\times$  *fulgens* Todaro *pro sp.* (1889)  $\equiv$  *Aloe salmdyckiana* var. *fulgens* (Todaro) A. Berger (1908); **incl.** *Aloe natalensis* J. M. Wood & M. S. Evans (1901)  $\equiv$  *Aloe arborescens* var. *natalensis* (J. M. Wood & M. S. Evans) A. Berger (1908); **incl.** *Aloe arborescens* var. *milleri* A. Berger (1908); **incl.** *Aloe arborescens* var. *pachythyrsa* A. Berger (1908); **incl.** *Aloe arborescens* var. *viridifolia* A. Berger (1908); **incl.** *Aloe arborescens* ssp. *mzimnyati* Van Jaarsveld & A. E. van Wyk (2005).

[16] Caulescent, much branched; stem to 2–3 m, 30 cm  $\varnothing$  at the base, with dead leaves persistent for 30–60 cm; **L** densely rosulate, triangular, 50–60  $\times$  5–7 cm, dull green to grey-green, **marginal teeth** 3–5 mm, usually curved towards the leaf apex, firm, 5–20 mm apart; **Inf** 60–80 cm, usually simple, sometimes with 1 **Br**; racemes conical to elongate-conical, 20–30  $\times$  10–12 cm, dense; **Bra** ovate-acute to obtuse, 15–20  $\times$  10–12 mm; **Ped** 35–40 mm; **Fl** scarlet, 40 mm, base rounded, 7 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging towards the mouth; **OTep** free to the base; **St** and **Sty** exerted 5 mm. — **Cytology**: 2n = 14 (Taylor 1925).

In spite of the specific epithet, this species is usually a large shrub, rarely a tree with a single trunk, though very variable. The population on Mt. Mulanje, Malawi, is largely single-stemmed, mostly with few or no branches, though sometimes with a distinct trunk and large crown (Thiede & al. 2015). It is the most widespread *Aloe* in South Africa, and the third-widest distributed of all *Aloe* species according to Klopper & al. (2012: 75, 77). Although Botswana was included in its distribution by Germishuizen & Meyer (2003), Hargreaves (2007) suggested that the record is doubtful, and no wild population is known. It is also widely cultivated elsewhere, and is reported as neophyte in Spain (Dana Sánchez & Sanz Elorza 2008), Portugal (Smith & Figueiredo 2009, Silva & al. 2015), and Australia (Lebrun & Stork 2012). Natural hybrids with other species have been reported (Reynolds 1950), and a full list of known hybrids, with a list

of those named, was presented by Smith & al. (2012b).

**A. archeri** Lavranos (Cact. Succ. J. (US) 49 (2): 74–75, 1977). **Type** [neo]: Kenya, Rift Valley Prov. (*Powys & Archer* s.n. in Newton 3118 [K, EA]). — **Lit**: Newton (1992). **Distr**: Kenya (Rift Valley Prov.: Laikipia Plateau); dry *Acacia* scrub, shade of trees, 1250–1800 m. **I**: Carter & al. (2011: 614).

[13] Caulescent, branching from the base; stem erect, to 70  $\times$  3.5 cm, then becoming decumbent to 4 m; **L** laxly rosulate and persisting for  $\pm$ 60 cm below, triangular, 40  $\times$  10 cm, dark green (on young shoots and seedlings with scattered whitish spots), surface rough, exudate yellow, drying brownish-yellow, **marginal teeth** 5 mm, firm, uncinat, 6–15 mm apart; **Inf** 70–140 cm, with 6–12 **Br**, lower ones sometimes rebranched; racemes cylindrical, 10–22 cm, subdense; **Bra** ovate-lanceolate, 12–15  $\times$  4 mm, closely imbricate in bud stage; **Ped** 10 mm; **Fl** red, with yellow margin on the lobes, 22–25 mm, base shortly attenuate, 5 mm  $\varnothing$  across the ovary, narrowed slightly to 4.5 mm above, then enlarging to 7 mm at the mouth; **OTep** free for 12–15 mm; **St** and **Sty** exerted 5 mm.

The original description of *A. archeri* included characters from 2 different taxa, the type (holotype) specimen illustrated in the protologue, and plants from another locality that were later named *A. murina* L. E. Newton. The holotype was deposited at EA but later found to be missing (Newton 1992).

**A. arenicola** Reynolds (J. South Afr. Bot. 4(1): 21–24, ill., 1938). **Type**: RSA, Northern Cape (*Reynolds* 2574 [PRE, BOL]). — **Distr**: RSA (Northern Cape, Western Cape); coastal sandy plains. **I**: Reynolds (1950: 380–381); Carter & al. (2011: 547); Wyk & Smith (2014: 124–125).

[12] Caulescent, simple or branching to form low clumps; stem 1 m, 3–4 cm  $\varnothing$ , decumbent, apical 20–30 cm ascending and leafy; **L**  $\pm$ 20, subdensely rosulate, lanceolate-attenuate, tip usually a whitish spine, 18  $\times$  5.5 cm, bluish-green with many irregularly scattered oblong white spots, with whitish horny margin, **marginal**

**teeth** 0.5 mm, 5–8 mm apart; **Inf** 50 cm, simple or with 1–2 **Br**; racemes densely capitate, 6 × 9 cm; **Bra** 10 × 3–4 mm; **Ped** 35 mm; **Fl** peach-red, paler at the mouth, 40 mm, base rounded; **OTep** free for 20 mm; **St** and **Sty** exerted 3 mm.

A natural hybrid with *A. krapohlana* has been reported (Reynolds 1950).

**A. argenticauda** Merxmüller & Giess (Mitt. Bot. Staatssamml. München 11: 437–444, 1974). **Type:** Namibia, Maltahöhe (*Merxmüller & Giess* 28216 [M, PRE, WIND]). — **Distr:** Namibia (Maltahöhe, Lüderitz, Bethanien); open grassland, usually >1500 m. **I:** Carter & al. (2011: 417).

[6] Acaulescent or with short stems, suckering to form dense clumps of up to 50 rosettes; **L** densely rosulate, 30 × 3–5 cm, grey-green, surface rough, **marginal teeth** 2 mm, dark brown, 8 mm apart; **Inf** 120 cm, simple or rarely with 1 **Br**; peduncle mostly covered with large silvery bracts; racemes 25–30 cm, dense; **Bra** lanceolate-acuminate, 50–70 × 8–12 mm, silvery; **Ped** 5–7 mm; **Fl** pinkish to dark red, greenish towards the mouth, 30–35 mm; **St** exerted 3–4 mm; **Sty** exerted 6 mm.

**A. argentifolia** T. A. McCoy & al. (Cact. Succ. J. (US) 89(5): 214–218, ills., 2017). **Type:** Moçambique, Cabo Delgado (*McCoy* 4024 [FT]). — **Distr:** NE Moçambique (Cabo Delgado); rocky outcrops, 50 m.

[13] Caulescent, solitary or **Ros** dividing dichotomously, stem to 1 m, decumbent; **L** 15–20, densely rosulate, lanceolate-long attenuate, 45–65 × 5–6 cm, silvery-grey with thick pruinose coat, lower surface light grey, often with white spots near the base, exudate yellowish, drying yellow-green; **marginal teeth** deltoid, 1 mm, white, 8–10 mm apart; **Inf** 60–90 cm, oblique, simple or rarely with 1 **Br**; raceme with secund flowers, 30–45 cm, dense; **Bra** deltoid, 2 mm, greenish-white, red towards the apex, with 3–5 brown nerves; **Ped** 2–3 mm; **Fl** mostly red, some orange, 28–30 mm, ventricose, 5.5 mm Ø across the ovary, enlarging above and narrowing to the mouth; **OTep** free for 18 mm; **St** exerted to 10 mm; **Sty** exerted to 15 mm.

The flower is said to be 5.5 mm diameter across the ovary and 4–5 mm above, yet the flower is seen in the photographs to be ventricose, i.e. becoming much wider above the ovary. This is probably the acaulescent variant of *A. mawii* collected at lower altitudes in Moçambique by Leach and regarded as possibly a variety of *A. mawii* (Reynolds 1966).

**A. argyrostachys** Lavranos & al. (Bradleya 25: 18–20, ills., 2007). **Type:** Madagascar, Antananarivo (*Pronk* 111 [Herb. Biol. Dept. Univ. Antananarivo]). — **Distr:** C Madagascar (Antananarivo: Antsirabe region); poor acid soil on quartzite mountains. **I:** Castillon & Castillon (2010: 76); Carter & al. (2011: 644).

[8] Caulescent; stem simple, to 50 cm, 6 cm Ø; **L** to 30, distichous, arcuate-ascending, linear-lanceolate, 36 × 5 cm, bluish-green, surface smooth, exudate clear drying clear to very light green, **marginal teeth** 1–2 mm, white, brown-tipped, 10 mm apart; **Inf** 60–70 cm, erect, simple; racemes cylindrical, 10 cm, dense; **Bra** ovate, 12–20 mm, whitish; **Ped** 0–1 mm; **Fl** white with brown veins, 30 mm, cylindrical, 5 mm Ø; **OTep** free for 17 mm; **St** and **Sty** exerted 5 mm.

**A. aristata** Haworth (Philos. Mag. J. 66: 280, 1825). **Type** [neo]: RSA, Northern Cape (*Reynolds* 1024 [PRE]). — **Distr:** Lesotho, RSA (SE Northern Cape, NE Western Cape, N Eastern Cape, Free State, KwaZulu-Natal); sandy flats to grassy mountain slopes, 200–2200 m. **I:** Reynolds (1950: 169–171); Carter & al. (2011: 435); Wyk & Smith (2014: 286–287); Marx (2014).

≡ *Tulista aristata* (Haworth) G. D. Rowley (2013) ≡ *Aristaloe aristata* (Haworth) Boatwright & J. C. Manning (2014); **incl.** *Aloe longiaristata* Schultes & Schultes fil. (1829); **incl.** *Aloe aristata* var. *leiophylla* Baker (1880); **incl.** *Aloe aristata* var. *parvifolia* Baker (1896); **incl.** *Aloe ellenbergeri* Guillaumin (1934).

[6,7] Acaulescent, rarely simple, usually in dense clumps of up to 12 rosettes; **L** 100–150, lanceolate, tapering to a long dry awn-like bristle, 8–10 × 1–1.5 cm, green with scattered small white spots, spots more numerous and sometimes in ± transverse bands on the lower face, upper

face with several soft white prickles near the tip, lower face with several soft white prickles in 1 or 2 median rows near the tip, **marginal teeth** 1–2 mm, soft, white, 1–2 mm apart; **Inf** 50 cm, occasionally simple, usually with 2–6 **Br**; racemes laxly subcapitate, 15–20 × 12–15 cm, with 20–30 flowers; **Bra** 11–12 mm; **Ped** 35 mm; **Fl** jasper-red on the upper side, paler beneath, 40 mm, base rounded, 7 mm  $\varnothing$  across the ovary, slightly narrowed to 6 mm above, enlarging towards the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology**:  $2n = 14$  (Resende 1937).

**A. armatissima** Lavranos & Collenette (Cact. Succ. J. (US) 72(1): 22–23, ills. (incl. p. 21), 2000). **Type**: Saudi Arabia, Hijaz Prov. (Collenette 3738 [K]). — **Distr**: Saudi Arabia (Hijaz Prov: Escarpment W of Taif); in sparse forest on granite. **I**: Collenette (1999: 19); Carter & al. (2011: 355).

**Incl.** *Aloe vulcanica* Lavranos & Collenette (2000) (*nom. inval.*, ICN Art. 32.1b, 39.1).

[3] Acaulescent or with a short prostrate stem, solitary; **L** 10–14, densely rosulate, lanceolate, 30–50 × 9–17 cm, glaucous green, often with many paler spots, **marginal teeth**  $\pm 5$  mm, brown-tipped, 8–17 mm apart; **Inf** to 170 cm, erect, with 4–8 (–27) **Br**; racemes cylindrical, 25–55 cm, subdense; **Bra** lanceolate, 10–12 × 5–7 mm; **Ped** 6–8 mm; **Fl** yellow or rarely

red,  $\pm 38$  mm, base shortly attenuate, 6–7 mm  $\varnothing$  across the ovary, scarcely constricted above; **OTep** free for 22 mm; **St** and **Sty** exerted 3–4 mm.

**A. arneodoi** N. Rebmann (Cact. Succ. 8(1): 18–20, ills., 2016). **Type**: Madagascar, Toliara (Rebmann 27 [BR]). — **Distr**: SE Madagascar (Toliara); rocky outcrops, 850 m.

[6] Shortly caulescent, rarely suckering at the base; stem 15–20 cm; **L** 23–25, rosulate, lanceolate, 17–22 × 3.8–4.2 cm, blue-grey, glaucous, **marginal teeth** reddish, 4–5 mm apart; **Inf** 72 cm, erect, simple; racemes cylindrical, 35 cm, lax; **Bra** 4–15 × 3 mm, scarious; **Ped** 20–23 mm; **Fl** pale yellow to slightly greenish, 40 mm, 6.5 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for  $\pm 16$  mm; **St** and **Sty** exerted.

**A. asperifolia** A. Berger (Bot. Jahrb. Syst. 36: 63, 1905). **Type**: Namibia (*Stapf* 7 [Z]). — **Distr**: Namibia; very arid places, often dependent on night fog for moisture, to 1250 m. **I**: Reynolds (1950: 312–313); Carter & al. (2011: 413). — Fig. 7.

[7] Acaulescent, forming dense clumps of 20–40 rosettes, or with short creeping rooting stems, simple or branched; **L** lanceolate-acuminate,  $\pm$  falcate, 15–25 × 4–7 cm, glaucous to sometimes almost white, surface very rough,

**Fig. 7** *Aloe asperifolia*.  
(Copyright: L. E. Newton)



**marginal teeth** 2–3 mm, horny, brownish, 5–15 mm apart; **Inf** 50–75 cm, oblique, with 2–3 **Br**; racemes with subsecund flowers, 20–25 cm, sub-lax; **Bra** deltoid-ovate to deltoid-acuminate, 10–15 × 3–4 mm; **Ped** 6–8 mm; **Fl** scarlet, 28 mm, base shortly attenuate, 6–7 mm Ø across the ovary, slightly swollen above, narrowing towards the mouth, mouth distinctly upturned; **OTep** free for 10 mm; **St** exerted 8–10 mm; **Sty** exerted 10 mm.

**A. aufensis** T. A. McCoy (Excelsa 21: 2, ills. (pp. 3–4), 2007). **Type:** Saudi Arabia, Medina (*McCoy* 1119 [MO]). — **Distr:** W Saudi Arabia (Medina: summit of Jabal Auf); rocky area with sparse vegetation, 2000 m; known only from the area of the type locality. **I:** Carter & al. (2011: 351).

[3] Acaulescent, solitary; **L** ±20, rosulate, lanceolate, 50 × 14 cm, light green, exudate orange-yellow, drying yellowish-brown, **marginal teeth** 4 mm, white, 13–22 mm apart; **Inf** to 130 cm, erect, with up to 5 **Br**; racemes cylindrical, 60–70 cm, dense; **Bra** 23 × 5–7 mm, white, scarious; **Ped** 8–9 mm, dark green; **Fl** orange, mouth yellow, clavate, 35–40 mm, 10 mm Ø at the widest point; **OTep** free for 23–27 mm; **St** exerted 12–13 mm; **Sty** exerted 10 mm.

**A. aurelieni** J.-B. Castillon (CactusWorld 26 (2): 109–112, ills., 2008). **Type:** Madagascar, Toamasina (*Castillon* 37 [TAN, HBG]). — **Distr:** C-E Madagascar (Toamasina); humic soil in ancient woodland, 940 m. **I:** Castillon & Castillon (2010: 370–371); Carter & al. (2011: 296).

[5] Acaulescent, solitary or with up to 3 suckers; **L** 15–30, rosulate, erect-spreading, lanceolate-attenuate, 80–110 × 10–12 cm, canalicate, pale bluish-green, sometimes tinged reddish, **marginal teeth** 3 mm, pinkish-white, 15–20 mm apart; **Inf** 60–70 cm, ± erect, with 3 **Br**; racemes cylindrical-conical, 10–15 cm, subdense; **Bra** acute, 3 × 2.5 mm, pink, scarious; **Ped** 10–20 mm; **Fl** pink, cylindrical, 25–30 mm, 5 mm Ø across the ovary, narrowed to 3 mm above, then enlarging to the mouth; **OTep** free for 7 mm; **St** and **Sty** not exerted; **Fr** berries, greyish-green, 18–25 mm Ø.

**A. austroarabica** McCoy & Lavranos (Cact. Succ. J. (US) 75(3): 123–124, ills., 2003). **Type:** Saudi Arabia, Asir Prov. (*McCoy* 969 [MO, P]). — **Distr:** S Saudi Arabia (Asir Prov.), N Yemen; dry rocks, 1100 m. **I:** Carter & al. (2011: 366).

[5] Acaulescent, solitary or rarely with up to 3 rosettes; **L** 20–25, densely rosulate, spreading or ascending, lanceolate-attenuate, 50–60 × 12 cm, green, margin cartilaginous, white, exudate orange, drying yellowish-brown, **marginal teeth** 3 mm, white, 18–25 mm apart; **Inf** 145 cm, with 2–5 **Br**; racemes cylindrical-acuminate, 55 cm, dense; **Bra** ovate, acute, 10–14 × 5–8 mm, puberulous; **Ped** 7–10 mm, green or pink; **Fl** yellow with green longitudinal stripes, rarely dark pink, pubescent, 30–40 mm, 6–8 mm Ø across the ovary; **OTep** free for 20–25 mm; **St** and **Sty** exerted 5 mm.

**A. austrosudanica** T. A. McCoy (Avonia 34 (4): 196–201, ills., 2016). **Type:** South Sudan, Equatoria (*Powys* s.n. in *McCoy* 3722 [FT]). — **Distr:** South Sudan (Equatoria: Namorunyang State); grassy slopes and cliff edges, ±1525 m.

[13] Caulescent, branching at the base to form small groups; stem to 20 cm, procumbent or pendulous; **L** to 10, laxly rosulate, persistent below the shoot apex, lanceolate-attenuate, 10–15 × 1.8–2 cm, dull grey-green, usually heavily white-spotted, sometimes without spots, surface slightly rough, exudate almost clear, drying light yellow, **marginal teeth** uncinat, 2–3 mm, reddish-brown, 4–6 mm apart; **Inf** 30 cm, arcuate-ascending, with up to 2 **Br**; racemes cylindrical-conical, 7 cm, subdense; **Bra** narrowly lanceolate-acute, 10–14 × 2.5 mm, scarious, tan with 3 brown nerves; **Ped** 10–12 mm; **Fl** yellowish-green to bright yellow, 23 mm, base slightly rounded, 5 mm Ø across the ovary, slightly narrowed above, enlarging to 5 mm at the mouth; **OTep** free for 18–20 mm; **St** and **Sty** exerted 3 mm.

**A. babatiensis** Christian & I. Verdoorn (Bothalia 6(2): 440–442, ills., 1954). **Type:** Tanzania, Northern Prov. (*Pole-Evans & Erens* 872 [PRE, SRGH]). — **Distr:** C-N Tanzania (Mbulu Highlands); exposed rocks or grassland,



1700–2100 m. **I:** Reynolds (1966: 358–359); Carter & al. (2011: 627).

[16] Caulescent, branching to form dense shrubs; stem erect or divergent, sometimes decumbent, to >1 m, 5 cm Ø; **L** ±24, densely rosulate, persistent for 30 cm, lanceolate-attenuate, 25 × 8–9 cm, olive-green tinged reddish, surface slightly glossy, **marginal teeth** 4–5 mm, reddish-brown, ±10 mm apart, sheathing leaf base fibrous; **Inf** 65 cm, with 2–4 **Br**; racemes cylindrical-acuminate, 20–25 × 10 cm, subdense; **Bra** ovate-acute, 30 × 15 mm, imbricate in bud stage; **Ped** 20–25 mm; **Fl** salmon-pink, 38–40 mm, base truncate, 7–8 mm Ø across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 8–10 mm; **St** and **Sty** exerted 1–3 mm. — **Cytology:** 2n = 14 (Cutler & al. 1980).

In spite of the specific epithet, this species does not occur near Babati; the nearest population is 54 km W of Babati, at a higher altitude. According to Lebrun & Stork (2012), this species seems to form hybrids with *A. secundiflora*.

**A. bakeri** Scott-Elliot (J. Linn. Soc., Bot. 29: 60, 1891). **Type:** Madagascar, Toliara (*Scott-Elliot* 2937 [K]). — **Lit:** Lüthy (2006: 25–26, conservation, with ills.). **Distr:** S Madagascar (Toliara: Tolanaro); shallow soil and crevices on rocky hills, 40 m. **I:** Reynolds (1966: 414–416);

Castillon & Castillon (2010: 238–239); Carter & al. (2011: 532). – Fig. 8.

≡ *Guillauminia bakeri* (Scott-Elliot) P. V. Heath (1994).

[11] Caulescent, branching and suckering from the base to form dense clumps of up to 100 or more shoots; stem 10–20 × 0.5–0.7 cm; **L** ±12, scattered along the stem for 5–8 cm, triangular, attenuate-acute, 7 × 0.8 cm, green tinged reddish, sometimes with pale green spots (few on the upper face, many on the lower face), **marginal teeth** 1 mm, firm, white, 1–2 mm apart, leaf sheath 0.5–1 cm; **Inf** 25–30 cm, simple; raceme subcapitate, 3–4 cm, lax, 8- to 10-flowered; **Bra** ovate-acuminate, 3 × 1.5 mm; **Ped** 10–12 mm; **Fl** apricot-scarlet at the base, becoming orange then yellow towards the mouth, the lobes greenish-tipped, 23 mm, base shortly attenuate, narrowed slightly above the ovary, then enlarging towards the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Said by Castillon & Castillon (2010: 238) to be extinct at the type and known only locality because of urban and commercial development.

**A. ballii** Reynolds (J. South Afr. Bot. 30(3): 123–125, ills., 1964). **Type:** Zimbabwe, Melsetter Distr. (*Bullock* 37/1 [SRGH]). — **Distr:** Moçambique, Zimbabwe.

**Fig. 8** *Aloe bakeri*.  
(Copyright: U. Eggli)





**A. ballii** var. **ballii** — **Distr:** W Moçambique, E Zimbabwe: SE Chimanimani Mts.; in crevices on rock faces, 380–400 m. **I:** Reynolds (1966: 11–12); Carter & al. (2011: 130).

[10] Caulescent, branching freely with up to 50 **Ros**; stem pendulous on steep rocks, spirally coiled and 1–1.5 m, 0.9 cm Ø; **L** 7–12, distichous, triangular-acute, 20–30 × 1 cm, green with white or pale green elongated spots near the base, **marginal teeth** minute, white, 2–4 mm apart, absent towards the apex; **Inf** 50–60 cm, oblique to horizontal or arching downwards, simple; raceme cylindrical-acuminate, up to 44 × 4 cm, sublax, with 40–50 flowers; **Bra** ovate-acute, 3 × 2 mm; **Ped** 14–20 mm; **Fl** flame-scarlet to pale reddish-orange, 12–16 mm, slightly campanulate, base attenuate, 4 mm Ø across the ovary, enlarging to the wide mouth; **OTep** free to the base; **St** and **Sty** not exerted. — **Cytology:** 2n = 14 (Brandham 1971).

**A. ballii** var. **makurupiniensis** Ellert (Cact. Succ. J. (US) 70(3): 130–131, ills., 1998). **Type:** Zimbabwe/Moçambique (Ellert 525 [SRGH]). — **Distr:** W Moçambique, E Zimbabwe: SE tip of the Chimanimani Mts.; open grassy woodland on quartzite ridges and slopes, 400–900 m. **I:** Carter & al. (2011: 131).

[10] Differs from var. *ballii*: Erect, almost acaulescent, suckering from the base only, with up to 12 **Ros**; **L** up to 48.5 cm; **Inf** up to 73 cm, erect.

**A. ballyi** Reynolds (J. South Afr. Bot. 19(1): 2, 1953). **Type:** Kenya, Coast Prov. (Reynolds 6378 [PRE, EA, K]). — **Distr:** SE Kenya, NE Tanzania; dense bush and riverine thickets, 900–1500 m. **I:** Reynolds (1966: 325–326); Carter & al. (2011: 685). – Fig. 9.

[9] Caulescent, simple; stem erect, 5–6 m, 10–15 cm Ø, without persistent dead leaves; **L** ±25, densely rosulate, spreading when young, becoming greatly recurved, lanceolate long attenuate, 90 × 14 cm, grey-green, surface smooth, exudate colourless, **marginal teeth** 4–5 mm, pungent, sometimes uncinuate, white, 10–15 mm apart; **Inf** 60 cm, suboblique, with ±20 **Br**; terminal raceme cylindrical, lateral racemes with



**Fig. 9** *Aloe ballyi*. (Copyright: L. E. Newton)

±20 subsecund to secund flowers, to 14 cm, lax; **Bra** ovate-acute, 5 × 5 mm; **Ped** 10 mm; **Fl** carmine to reddish-orange, greyish-tipped, 33 mm, base rounded, 9 mm Ø across the ovary, very slightly narrowed above; **OTep** free for 22 mm; **St** and **Sty** exerted 4–5 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Broken leaves give off a strong odour reminiscent of rats or mice, and the sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984.) Some accidental human deaths are reported, when the plants were mistakenly used medicinally as *Aloe vera*.

At the type locality, the taxon has become extinct because of habitat destruction (Newton 2007). Tanzanian populations W of Arusha mentioned by Reynolds (1966) are distinct, and they were later described as *A. elata*.

**A. barbara-jeppeae** T. A. McCoy & Lavranos (Cact. Succ. J. (US) 85(4): 156–158, ills. (pp. 154, 157, 159), 2013). **Type:** RSA, Mpumalanga

(*Lavranos* 26380 [FT]). — **Distr:** RSA (N Mpumalanga: Lydenburg Distr.: Steenkampsberg); grassy sandstone rock outcrop; known only from the type locality. **I:** Wyk & Smith (2014: 142–143).

[4] Acaulescent, or decumbent and stem to 30 cm, solitary or with up to 3 **Ros**; **L** 25–35, densely rosulate, arcuate-erect, lanceolate-attenuate, 70 × 12 cm, green, exudate yellowish, drying brownish-yellow, **marginal teeth** 4 mm, red, 12–15 mm apart; **Inf** 1.3–1.5 m, erect, simple; racemes cylindrical-acuminate, 85 cm, dense; **Bra** obovate-acute, 17–20 × 12–14 mm, yellow; **Ped** 1–2 mm, green; **Fl** yellow to orange, 14–15 mm, 8 mm Ø across the ovary; **OTep** free; **St** and **Sty** exerted 1.4 mm.

**A. barberae** Dyer (Gard. Chron., ser. nov. 1: 568, 1874). **Type:** RSA, KwaZulu-Natal (*Anonymus* s.n. [K]). — **Lit:** Jaarsveld & Judd (2015: 36–39, ills., as *Aloidendron*). **Distr:** S Moçambique, RSA (Eastern Cape, KwaZulu-Natal, Mpumalanga), Swaziland; dense bush and low forest, sandy soil, 20–600 m. **I:** Reynolds (1950: 499–501, t. 58–59, as *A. bainesii*); Carter & al. (2011: 695); Wyk & Smith (2014: 38–39).

≡ *Aloe bainesii* var. *barberae* (Dyer) Baker (1896) ≡ *Aloidendron barberae* (Dyer) Klopper & Gideon F. Smith (2013); **incl.** *Aloe bainesii* Dyer (1874); **incl.** *Aloe zeyheri* hort. ex Baker (1880) (*nom. inval.*, ICN Art. 36.1c).

[17] Caulescent, copiously branching dichotomously; stem erect, to 18 m, 1–3 m Ø at the base; **L** ±20, densely rosulate, ensiform, 60–90 × 7–9 cm, dull green, **marginal teeth** 2–3 mm, dull white, brownish-tipped, firmly horny, 10–25 mm apart; **Inf** 40–60 cm, usually with 2 **Br**; racemes cylindrical, slightly acuminate, 20–30 × 8–10 cm, dense; **Bra** linear-acuminate, 10 × 1 mm; **Ped** 10 mm; **Fl** rose to rose-pink, 33–37 mm, base rounded; **OTep** free for 28–32 mm; **St** and **Sty** exerted 15–20 mm. — **Cytology:** 2n = 14 (Resende 1937: as *A. bainesii*).

In most literature this species appears as *A. bainesii* Dyer, a name published in the same paper as *A. barberae*. A few months later Dyer published a note in which the 2 taxa were united, and he chose *A. barberae* as the name for the

united species. This later note was overlooked until attention was drawn to it by Smith & al. (1994). In accordance with ICN Art. 11.5, Dyer's choice of name must be used.

Wyk & Smith (1996) report a small variant (± 2 m tall at maturity) in Moçambique. Ndhlala & al. (2009) report antimicrobial, antifungal and anti-inflammatory activity in bark, leaf and root extracts, corroborating the effects ascribed to the species in traditional herbalist medicine.

**A. barbertoniae** Pole-Evans (Trans. Roy. Soc. South Africa 5: 705, 1917). **Type:** RSA, Mpumalanga (*Thorncroft* s.n. [BOL]). — **Lit:** Klopper & al. (2014: with ill.). **Distr:** RSA (Mpumalanga, C Limpopo Prov.); coarse sandy soil and fine loam, in open grassland to bushy river valleys in hilly country, altitude not recorded.

[3] Acaulescent or with short stem, usually solitary; **L** 14–20, densely rosulate, lanceolate-attenuate, 30–40 × 10–11 cm, upper face green, reddish brown-tinged, with many elongated white spots, ± confluent in undulating transverse bands, sometimes with few spots, lower face uniformly pale green, exudate clear, drying yellow, **marginal teeth** deltoid, 5–6 mm, brown, 10–15 mm apart; **Inf** to 100 cm, arcuate-erect, with 5–8 **Br**, lower ones rebranched; racemes cylindrical-acuminate, 25–30 cm, sublux; **Bra** narrowly deltoid-acuminate, 15–20 mm; **Ped** 12–14 mm; **Fl** dull reddish-pink, with a bloom, pale pinkish-striped, 36–49 mm, 10–12 mm Ø across the ovary, abruptly constricted above, enlarging to the mouth, strongly decurved; **OTep** free for 10 mm; **St** exerted 1 mm; **Sty** exerted 1–2 mm.

Until recently included in the synonymy of *A. greatheadii* var. *davyana*.

**A. bargalensis** Lavranos (Cact. Succ. J. (US) 45(3): 116–117, ills., 1973). **Type:** Somalia, Bari Region (*Lavranos & Bavazzano* 8459 [FI]). — **Distr:** NE Somalia (Bari Region); shallow soil on limestone, 0–1400 m. **I:** Carter & al. (2011: 287).

[6] Acaulescent or shortly caulescent, suckering at the base; **L** rosulate, lanceolate, somewhat falcate, 30–40 × 6 cm, green with irregular white spots and prominently furrowed, with dark green

striations, **marginal teeth** 1–2 mm, 12–25 mm apart; **Inf** 70–120 cm, simple or rarely with 1–2 **Br**; racemes narrowly cylindrical-acuminate, 30–40 cm, subdense; **Bra** ovate-deltoid, long-acute, to 15 × 5 mm; **Ped** 5–7 mm; **Fl** reddish, yellow towards the mouth, 30 mm, base attenuate, 5 mm Ø across the ovary, narrowed to 4 mm Ø above, then enlarging to 7 mm at the mouth; **OTep** free for 15–16 mm; **St** and **Sty** scarcely exerted.

**A. beankaensis** Letsara & al. (Malagasy Nat. 6: 49, ills. (pp. 50–51), 2012). **Type:** Madagascar, Mahajanga (*Letsara* 937 [TAN, CAS, K]). — **Distr:** Madagascar (Mahajanga: Tsingy de Bemaraha); on limestone in forests. **I:** Castillon & Castillon (2010: 313).

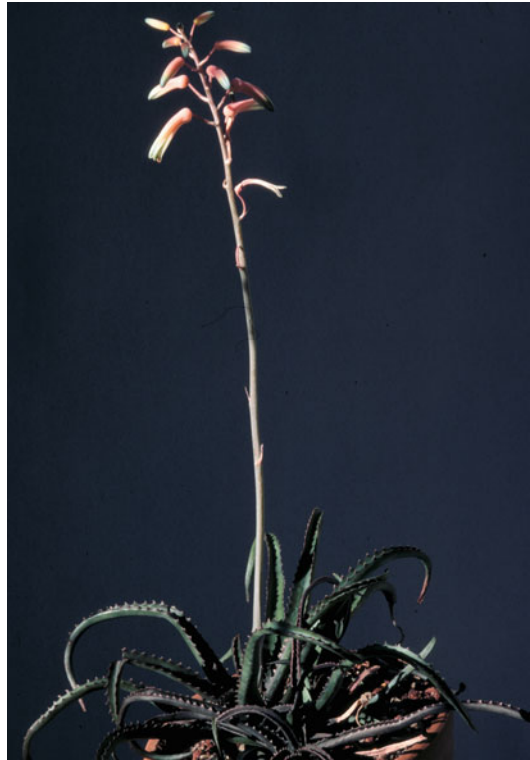
[4] Shortly caulescent, suckering to form groups of up to 5 rosettes; stem decumbent or ascending, 6 × 0.3–0.4 cm; **L** 6–10, rosulate and also dispersed along the stem, narrowly linear, 8.5 × 0.8 cm, green with scattered elliptical white spots and dark green longitudinal veins, exudate colourless, **marginal teeth** deltoid, 1 mm, white, 3–4 mm apart; **Inf** 19.7 cm, erect, simple; racemes capitate, 5–8 cm, lax; **Bra** narrowly lanceolate, 8–10 mm, scarious, pale tan, with 1 nerve; **Ped** 3–4 mm, reddish; **Fl** reddish-orange, yellow at the mouth, 21 mm, 7 mm Ø across the ovary, narrowed above, widening at the mouth; **OTep** free (?); **St** and **Sty** not exerted.

The description in the protologue states “outer tepals free”, but the illustrations suggest that they are free for about 1/3 the length of the perianth.

**A. belavenokensis** (Rauh & Gerold) L. E. Newton & G. D. Rowley (Excelsa 17: 59, 1997). **Type:** Madagascar, Toliara (*Rauh* 73987 [HEID]). — **Distr:** S Madagascar (Toliara: Tolanaro region); coastal forest on sand. **I:** Castillon & Castillon (2010: 237); Carter & al. (2011: 416). – Fig. 10.

≡ *Lomatophyllum belavenokense* Rauh & Gerold (1994).

[1] Very shortly caulescent, stoloniferous and forming groups to 1 m Ø; stem subterranean, to 1.5 × 1–1.5 cm; **L** ±10, densely rosulate, linear-attenuate, 20–30 × 1 cm, green, red-brown to violet at the base, exudate white becoming yellow



**Fig. 10** *Aloe belavenokensis*. (Copyright: U. Eggli)

in air, **marginal teeth** 1 mm, white to pale red; **Inf** 25–40 cm, simple; racemes cylindrical, 10–20 cm, lax, with 10–15 (–20) flowers; **Bra** acute, 3–5 mm; **Ped** 10–15 mm; **Fl** bright cinnabar-red, whitish with green veins in the upper 1/3, 20–25 mm, base rounded, 6–7 mm Ø across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 15–20 mm; **St** and **Sty** not exerted; **Fr** berries.

**A. belitsakensis** Rakotoarisoa (Phytotaxa 328 (3): 277–280, ills., 2017). **Type:** Madagascar, Mahajanga (*Rakotoarisoa* 847 [TAN, K]). — **Distr:** Madagascar (Mahajanga); dry shrubland on white sand, ±225 m.

[4] Acaulescent, solitary or suckering to form small clumps; **L** 20–25, densely rosulate, lanceolate-acuminate, 37–45 × 6.5–8.5 cm, green tinged reddish, **marginal teeth** deltoid, 3 mm, yellow, 15 mm apart; **Inf** 70–115 (–200) cm, erect, simple or rarely with 1 **Br**; racemes capitate, 10 cm, dense; **Bra** 4 × 3 mm, papery; **Ped** 35–38

mm, reddish-orange; **Fl** orange-yellow, 20–22 mm, 5 mm  $\varnothing$  across the ovary, narrowly campanulate; **OTep** free to the base; **St** exerted 10–13 mm; **Sty** exerted 8 mm.

From its position in the description, it is assumed that “petiole” in the protologue refers to the pedicel. Said to be uncommon in the area where it occurs, and conservation status regarded as “Endangered”.

**A. bella** G. D. Rowley (Repert. Pl. Succ. 23: 12, 1974). **Type:** Somalia, Bari Region (*Lavranos & Bavazzano* 8458 [FI]). — **Lit:** Lavranos (1973: as *A. pulchra*). **Distr:** NE Somalia (Bari Region); stony coastal plain and limestone plateau, 0–100 m. **I:** Carter & al. (2011: 453).

≡ *Aloe pulchra* Lavranos (1973) (*nom. illeg.*, ICN Art. 53.1).

[7] Acaulescent or shortly caulescent, suckering to form dense clumps; stem decumbent; **L** rosulate, deltoid, acute, rather falcate, to 50 × 11 cm, pinkish-brown with red cartilaginous margin, **marginal teeth** small, red,  $\pm 20$  mm apart; **Inf** to 1 m, with up to 5 **Br**; racemes conical to subcapitate, 6–11 cm, dense; **Bra** deltoid-acute, 8–10 × 4 mm; **Ped** 6–7 mm; **Fl** bright red, becoming green towards the mouth, 27 mm, base rounded, 8–9 mm  $\varnothing$  across the ovary, slightly narrowed above towards the mouth; **OTep** free for 7–9 mm; **St** and **Sty** exerted 3–6 mm.

**A. bellatula** Reynolds (J. South Afr. Bot. 22 (3): 132–134, *ills.*, 1956). **Type:** Madagascar, Fianarantsoa (*Millot* s.n. in *Reynolds* 6591 [PRE, P, TAN]). — **Lit:** Lüthy (2006: 27–28, conservation, with *ills.*). **Distr:** W Madagascar (Fianarantsoa: S Itremo Mts.; granite outcrops, mountain slopes, 1500–2000 m. **I:** Reynolds (1966: 402–404); Castillon & Castillon (2010: 123); Carter & al. (2011: 403). – Fig. 11.

≡ *Guillauminia bellatula* (Reynolds) P. V. Heath (1994).

[1] Acaulescent, suckering to form dense clumps; **L**  $\pm 16$ , densely rosulate, linear-attenuate, 10–13 × 0.9–1 cm, dark green with many pale green spots, surface rough, **marginal teeth** 1 mm, soft, cartilaginous, smaller or absent towards the apex; **Inf** 60 cm, simple or with 1 **Br**; racemes



**Fig. 11** *Aloe bellatula*. (Copyright: U. Eggli)

cylindrical-acuminate, 12–16 × 4 cm, lax with 35 flowers, denser above; **Bra** deltoid-acuminate, 4–6 × 2 mm; **Ped** 12 mm; **Fl** light coral-red, 13 mm, campanulate, base attenuate, 6 mm  $\varnothing$  across the ovary; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Close to or even conspecific with *A. perrieri*, and not currently known from the wild (Castillon & Castillon 2010: 123).

**A. benishangulana** Sebsebe & Tesfaye (Kew Bull. 66(1): 113, fig. 1 (p. 114), 2011). **Type:** Ethiopia, Benishangul-Gumuz (*Hermann* 157 [ETH, K [photo]]). — **Distr:** W Ethiopia (Benishangul-Gumuz); rock crevices in bamboo thicket, 1490–1500 m. **I:** Sebsebe Demissew & Nordal (2010: 66–67).

[6] Acaulescent, suckering to form groups; **L** laxly rosulate, 20–46 × 1–4.5 cm, dull green, surface smooth, exudate drying yellow, **marginal**



**teeth** 1–1.5 mm, white, 3–8 mm apart; **Inf** 50–60 cm, erect, with up to 2 **Br**; racemes cylindrical, 28 cm, lax; **Bra** ovate-acuminate, 8–10 × 4 mm; **Ped** 8–10 mm; **Fl** bright scarlet, paler to whitish at the mouth, 37–40 mm, base truncate, 8 mm Ø across the ovary; **OTep** free for 10 mm. — **Cytology**: 2n = 14 (Fentaw & al. 2013).

The description in the protologue states “inflorescence simple”, but a photograph clearly shows two branches on an inflorescence in fruit.

**A. berevoana** Lavranos (Kakt. and. Sukk. 49 (7): 161–162, ills., 1998). **Type**: Madagascar, Toliara (Rössli & Hoffmann s.n. [P, MO]). — **Distr**: W Madagascar (Toliara), W coastal plain, sandstone cliffs in dry forests along the Tsiribihina River, to 70 m. **I**: Castillon & Castillon (2010: 292–293); Carter & al. (2011: 558).

≡ *Aloe acutissima* var. *berevoana* (Lavranos) J.-B. Castillon & J.-P. Castillon (2010) (*nom. inval.*, ICN Art. 36.1b, 41.5).

[11] Caulescent, branching at the base to form very large groups; stems ascending, to 60 cm; **L** 8–10, laxly arranged, lanceolate, tip acute, 30 × 3 cm, grass-green, with longitudinal striations, **marginal teeth** 2 mm, dark green with whitish tip, 8–12 mm apart; **Inf** to 60 cm, with 3 **Br**; raceme 10–12 cm, lax, few-flowered; **Bra** 5 mm, triangular; **Ped** 10 mm; **Fl** dark red, 17 mm, 4 mm Ø; **OTep** free for 5 mm; **St** and **Sty** slightly exerted.

**A. bergeriana** (Dinter) Boatwright & J. C. Manning (Syst. Bot. 39(1): 68, 2014). **Type**: Namibia (Dinter 4295 [B]). — **Distr**: SE Namibia, RSA (Gauteng, Mpumalanga, Northern Cape, North-West Prov.); rocky grassland on shallow sandy soil, gravel patches and termite mounds. **I**: Craib (2006: 133, 135, as *Chortolirion angolense*); Zonneveld & Fritz (2010: 28, as *C. tenuifolium*); Wyk & Smith (2014: 356–357).

≡ *Chortolirion bergerianum* Dinter (1914); **incl.** *Haworthia tenuifolia* Engler (1888) ≡ *Chortolirion tenuifolium* (Engler) A. Berger (1908) ≡ *Aloe tenuifolia* (Engler) Boatwright & J. C. Manning (2013) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Haworthia stenophylla* Baker (1891) ≡ *Chortolirion stenophyllum* (Baker) A. Berger

(1908); **incl.** *Haworthia saundersiae* Baker (1891) (*nom. inval.*, ICN Art. 36.1b); **incl.** *Aloe barendii* Klopper & Gideon F. Smith (2013).

[2] Acaulescent, solitary, herbaceous; **L** from a short subterranean butt; bulb always solitary, ovoid-oblong, formed by membranous leaf bases, 3–4 cm, 1.5–3.3 cm Ø; **L** rosulate, slightly succulent, grass-like, flaccid to erect, glaucous green, once twisted, 15–29 cm, 1–3 mm Ø, margins denticulate; **Inf** synanthous, racemose, simple, 20–35 cm, lower sterile parts bracteate; **Ped** short, erect, persistent; **Fl** erect, zygomorphic, bud decurved; **Tep** pinkish-white with greenish keels, base obtuse, basally united, closely adhering to each other for 2/3 of their length, limb bilabiate, tube straight, 14–17 mm.

The invalid name ×*Gastrolirion* E. Walther was proposed in 1933 for hybrids between this species (as *Chortolirion tenuifolium*) and species of *Gasteria*.

**A. bernadettae** J.-B. Castillon (Adansonia, sér. 3, 22(1): 136–138, ills., 2000). **Type**: Madagascar, Toliara (*Castillon 2* [P]). — **Distr**: S Madagascar (Toliara); on gneissic rocks, 100–500 m; known only from the type locality. **I**: Castillon & Castillon (2010: 224–225); Carter & al. (2011: 585).

[13] Caulescent, suckering; stem procumbent, to 1.5 m and 6 cm Ø; **L** 15–20, rosulate, 70 × 3–7 cm, green, **marginal teeth** 2 mm, curved, 7–10 mm apart; **Inf** 80 cm, erect, simple; racemes cylindrical, 15–20 × 5 cm, dense, with 80–100 sessile flowers and a tuft of sterile bracts at the tip; **Bra** 10 × 4 mm; **Fl** lemon-yellow, 16 mm, 6 mm Ø across the ovary, campanulate; **OTep** free for 11–14 mm; **St** and **Sty** exerted 3–5 mm.

**A. bernardii** J.-P. Castillon (Cact.-Avent. Int. 89: 25–27, ills., 2011). **Type**: Madagascar, Fianarantsoa (*Castillon 49* [TAN, P, TAN]). — **Distr**: S-C Madagascar (Fianarantsoa: S Itremo Mts.); rocky hills, 1700–1800 m.

[2] Acaulescent, solitary; **L** 20–30, rosulate, triangular, apex rounded, 17–22 × 7–9 cm, dull reddish-green, exudate colourless to clear yellow, **marginal teeth** 1 mm, yellow with dark red base, 1 mm apart, sometimes absent; **Inf** 78 cm, erect,



simple; racemes cylindrical, to 33 cm, dense; **Bra** ovoid, 15 × 10 mm, brown; **Ped** absent; **Fl** red-brown, 20.8 mm, clavate; **OTep** free; **St** exerted 16 mm; **Sty** exerted 10 mm.

Intermediate between *A. conifera* and *A. macroclada*.

**A. bertemariae** Sebsebe & Dioli (Kew Bull. 55(3): 679–681, ills., 2000). **Type:** Ethiopia, Harerge Region (*Dioli* 4 [ETH, K]). — **Distr:** E Ethiopia (Harerge Region); sandy clay soil in *Acacia* woodland, 300–400 m; known only from the type locality. **I:** Sebsebe Demissew & Nordal (2010: 56–57); Carter & al. (2011: 288).

[4] Acaulescent, suckering to form groups of up to 4 **Ros**; **L** 13–15, rosulate, erect or slightly recurved, triangular to lanceolate, strongly canaliculate, becoming tubular in dry conditions, 50–65 × 8–9 cm, both faces densely spotted with 2 × 0.5–0.9 mm whitish-green blotches, longitudinally striped, lower face of most leaves with 3–5 brown prickles 1–2 mm long, exudate dark yellow, drying brown, **marginal teeth** 1–2 mm, brown, 15–25 mm apart; **Inf** 1–2 m, simple; racemes cylindrical-conical, 50–80 cm, subdense; **Bra** triangular-acuminate, deflexed, 9–12 × 3–4 mm, with many brown veins; **Ped** 4–7 mm; **Fl** dark coral-red, whitish at the mouth, cylindrical-trigonous, 26–28 × 5 mm, slightly constricted above the ovary, minutely pubescent; **OTep** free for 8.7–9.3 mm; **St** and **Sty** not exerted; **Fr** capsules ovoid, 14–17 × 5–6 mm, shortly pubescent, transversely ridged.

Resembling *A. citrina* (Lebrun & Stork 2012).

**A. betsileensis** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 48, 1926). **Type:** Madagascar, Toliara (*Perrier* 13676 [P]). — **Distr:** S-C Madagascar (Toliara); rocky grassland slopes, 800–1400 m. **I:** Reynolds (1966: 482–483); Castillon & Castillon (2010: 162–163); Carter & al. (2011: 323).

[3] Acaulescent, simple; **L** 20–30 (–50), densely rosulate, triangular with the apex slightly twisted, 30–40 × 7–9 cm, dull green tinged reddish, with reddish margin, exudate drying yellow, **marginal teeth** 2–3 mm, reddish, pungent, 8–12 mm apart; **Inf** 60 cm and simple in young plants,

70 cm to >100 cm with 3–5 **Br** in old plants; racemes cylindrical, 30–35 × 4–5 cm, very dense, **Fl** sessile, arranged in 13 spirally twisted rows; **Bra** ovate-obtuse, 8–10 × 6–8 mm, fleshy, reddish; **Fl** yellow with orange tips, 15 mm, slightly campanulate, base rounded, 7 mm Ø across the ovary, enlarging to 9 mm at the mouth; **OTep** free to the base; **St** exerted 3–4 mm; **Sty** exerted 5 mm.

Flowering starts on the sunny side of the raceme, where the flowers are more orange in colour.

**A. bicomitum** L. C. Leach (*Kirkia* 10: 385–386, 1977). **Type:** Tanzania, Western Prov. (*Reynolds* 8948 [PRE, EA, K]). — **Lit:** Reynolds (1959: protologue *A. venusta*). **Distr:** SE Tanzania, N Zambia: shores of Lake Tanganyika; rock outcrops in *Brachystegia* woodland, 780–1400 m. **I:** Reynolds (1966: 174–175, as *A. venusta*); Carter & al. (2011: 346).

≡ *Aloe venusta* Reynolds (1959) (*nom. illeg.*, ICN Art. 53.1).

[5] Acaulescent, simple or in small groups; **L** ±20, densely rosulate, triangular, 50 × 9 cm, dull grey-green with many elliptic pale green spots, more crowded towards the base, smaller and more crowded on the lower face, with continuous pinkish margin, **marginal teeth** 3 mm, uncinat, pinkish, 8–10 mm apart; **Inf** 1–1.2 m, with ±10 **Br**; racemes cylindrical-conical, 15–20 cm, dense; **Bra** ovate-cuspidate, 11 × 10 mm, somewhat fleshy in the middle, imbricate in bud stage; **Ped** 13 mm; **Fl** pale scarlet, minutely pubescent, 32 mm, base very shortly attenuate, 7 mm Ø across the ovary, slightly narrowed above, then enlarging towards the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 3–5 mm.

**A. boiteau** Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 14: 349, 1942). **Type:** Madagascar, Toliara (*Boiteau* s.n. [P]). — **Distr:** S Madagascar (Toliara: near Tolano); known only from the type collection, extinct in the wild. **I:** Reynolds (1966: 420); Castillon & Castillon (2010: 234–235); Carter & al. (2011: 231).

≡ *Lemeea boiteau* (Guillaumin) P. V. Heath (1994).

[1] Acaulescent or with short stem, suckering; **L**  $\pm 10$ , rosulate, triangular, 15–20  $\times$  1.4 cm, olive-green, with narrow pinkish cartilaginous margin, **marginal teeth** 0.5–1 mm, pinkish, 2 mm apart, absent towards the apex; **Inf** 10–15 cm, simple; raceme 5 cm, lax, with  $\pm 10$  flowers; **Bra** deltoid-acute, 5  $\times$  3 mm; **Ped** 10 mm; **Fl** bright scarlet, 25 mm, base shortly attenuate, slightly narrowed above the ovary, then enlarging towards the mouth; **OTep** free for 18 mm; **St** and **Sty** slightly exerted.

**A. boscawenii** Christian (J. South Afr. Bot. 8 (2): 165–167, ills., 1942). **Type:** Tanzania, Tanga Distr. (*Boscawen* 7 in *Christian* 902 [SRGH, EA, K, PRE]). — **Distr:** NE Tanzania (Tanga Distr.); scrub on sandy soil along coast, to 60 m. **I:** Reynolds (1966: 365); Carter & al. (2011: 596).

[14] Caulescent, branching near the base; stems 1–2 m  $\times$  5–7 cm, erect for 20–30 cm, when longer sprawling or supported by surrounding vegetation; **L** scattered along the stem for 20–30 cm, ovate-lanceolate, 44–50  $\times$  8 cm, light green, with narrow cartilaginous margin, surface smooth, exudate yellow, **marginal teeth** 2–3 mm, brown-tipped, pungent, 7–18 mm apart; **Inf**  $\pm 90$  cm, with 3–9 **Br**, lower ones sometimes rebranched; racemes cylindrical, 10–12  $\times$  7 cm, lax below, more dense towards the apex; **Bra** long-acuminate, 7  $\times$  3 mm; **Ped** 18 mm; **Fl** yellow, becoming brownish towards the apex, 30 mm, base attenuate, 9 mm  $\varnothing$  across the ovary, very slightly narrowed above; **OTep** free for 18 mm; **St** and **Sty** scarcely exerted.

**A. bosseri** J.-B. Castillon (Adansonia, sér. 3, 22(1): 135–137, ills., 2000). **Type:** Madagascar, Toliara (*Castillon* 1 [P]). — **Distr:** W Madagascar (Toliara, Mahajanga); steep limestone cliffs along the Manambolo River, and adjacent “tsingy” areas. **I:** Castillon & Castillon (2010: 296–297).

[6, 7] Acaulescent or caulescent to 40 cm, suckering at the base; **L** 10–15, rosulate, tip attenuate, 30–70  $\times$  4 cm, blue-green to yellowish-green, upper face finely lineate, margins a 1 mm wide whitish or rose border, **marginal teeth** absent or 0.1–0.5 mm, 0.5–1 mm apart, leaf sheath

$\pm 1$  cm; **Inf** 70 cm, erect or ascending, simple or with 2–6 **Br**; racemes cylindrical,  $\pm 10$  cm, lax, with 15–20 flowers; **Bra** ovate-acute, 2.5–3.5 mm; **Ped** 12–15 mm; **Fl** red, with green tips, inner lobes whitish, 20–25 mm, 8 mm  $\varnothing$  across the ovary; **OTep** free for 16–21 mm; **St** and **Sty** scarcely exerted.

**A. bowiea** Schultes & Schultes *fil.* (Syst. Veg. 7(1): 704, 1829). **Type:** [neo — icono]: K [unpubl. drawing]. — **Lit:** Smith (1990); Smith (1991a). **Distr:** RSA (Eastern Cape: around Port Elizabeth and Kariega); Valley Bushveld vegetation, dense thickets, 0–100 m. **I:** Carter & al. (2011: 106); Wyk & Smith (2014: 358–359).

**Incl.** *Bowiea africana* Haworth (1824)  $\equiv$  *Chamaealoe africana* (Haworth) A. Berger (1905).

[1] Acaulescent, suckering to form dense groups; **R** fusiform; **L** 18–25, rosulate-multifarious, linear, 10–15  $\times$  1.25 cm, pale glaucous green with scattered white spots, more numerous on the lower face, **marginal teeth** minute, soft, white; **Inf**  $\pm 45$  cm, simple; racemes cylindrical,  $\pm 15$  cm, lax; **Bra** deltoid; **Ped** 1–2 mm; **Fl** greenish-white, 8–15 mm, clavate, base shortly attenuate, enlarging above the ovary to the mouth; **OTep** free to the base; **St** and **Sty** exerted 6–8 mm.

**A. boylei** Baker (Bull. Misc. Inform. Kew 1892: 84, 1892). **Type:** RSA, KwaZulu-Natal (*Allison* s.n. in *Boyle* s.n. [K]). — **Distr:** RSA, Swaziland. **I:** Carter & al. (2011: 147); Wyk & Smith (2014: 298–299).

Included in *A. ecklonis* by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011) and Wyk & Smith (2014).

Flowers are visited by nectar-seeking birds, and also by the bee *Amegilla natalensis*, probing the flowers for nectar, but the bees are less efficient pollinators than the birds (Hargreaves & al. 2012).

**A. boylei** ssp. **boylei** — **Distr:** RSA (Eastern Cape, KwaZulu-Natal, Mpumalanga, Limpopo); grasslands, often in the mist belt. **I:** Craib (2006: 33–35); Wyk & Smith (2014: 298–299).

**Incl.** *Aloe micracantha* Pole-Evans (1923) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe agrophila* Reynolds (1936).

[4] Caulescent, simple or branching; stem short or up to 20 × 6 cm with age, simple or branching at the base to form groups of 6–12 shoots; **L** ±10–14, rosulate, lanceolate to ensiform, 50–60 × 1.5–3 cm, dark green, upper face sometimes lineate and with few scattered elliptic spots near the base, lower face with many white spots from the base to the middle, with soft white margin ±2 mm, **marginal teeth** 1–3 mm, soft, white, 2–5 mm apart, smaller and more crowded towards the leaf tip; **Inf** 40–60 cm, simple; raceme capitate, 10–12 × 10–12 cm, with ±40 flowers; **Bra** ovate-acuminate, ±20–23 mm; **Ped** 40–45 mm; **Fl** salmon-pink, greenish-tipped, 30–35 mm, base attenuate, 11–12 mm Ø across the ovary, narrowing to 8–9 mm at the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Müller 1945).

**A. boylei** ssp. **major** Hilliard & B. L. Burt (Notes Roy. Bot. Gard. Edinburgh 42(2): 252, 1985). **Type**: RSA, KwaZulu-Natal (Hilliard & Burt 8438 [E, NU]). — **Distr**: RSA (Eastern Cape, KwaZulu-Natal, Mpumalanga, Limpopo); dry stony grassland, 680–1800 m. **I**: Reynolds (1950: 154–155, as *A. boylei*); Carter & al. (2011: 147).

[4] Differs from ssp. *boylei*: Plants more robust; **L** 7 cm broad; **Fl** 40 mm.

Plants regarded by Reynolds (1950) as a “weak form” of this species (also described as *A. agrophila*) match Baker’s description of *A. boylei*, and plants regarded by Reynolds as typical are now ssp. *major*. Craib (2006) and Wyk & Smith (2014) do not mention this subspecies and presumably do not accept it.

**A. braamvanwykii** Gideon F. Smith & Figueiredo (Bradleya 30: 162–165, ills., 2012). **Type**: RSA, North-West Prov. (Smith & Figueiredo 1 [PRE]). — **Lit**: Smith & al. (2017: portrait). **Distr**: RSA (C-S North-West Prov.); wooded grassland on red sandy loam or occasionally clay. **I**: Wyk & Smith (2014: 216–217).

[7] Acaulescent, solitary or with up to 70 **Ros**; **L** 12–15, rosulate, linear-attenuate, 17–26 × 3.5–5.5 cm, dull mid-green with elongated white spots in irregular transverse bands, smooth, exudate pale yellowish drying purple, **marginal teeth** 4 mm, with green base and light brown tips, 10–13 mm apart; **Inf** to 75 cm, erect, with 5–7 **Br**; racemes cylindrical, 14–17 cm, semidense; **Bra** narrowly triangular, long attenuate, 5–9 × 4–5 mm, straw-coloured; **Ped** 10–12 mm, pinkish-brown; **Fl** orange-red to bright red, 20–25 mm, base truncate, 6 mm Ø across the ovary, narrowed above to 3 mm, enlarging to 6–7 mm at the mouth; **OTep** free for 7 mm; **St** exerted 2–5 mm; **Sty** exerted 1–2 mm.

Similar to *A. transvaalensis*, which may also be its closest relative (Smith & al. 2017: 18).

**A. brachystachys** Baker (Curtis’s Bot. Mag. 121: t. 7399 + text, 1895). **Type**: “Zanzibar” (Kirk s.n. [K]). — **Distr**: SE Tanzania; rock outcrops in montane bushland and at the edge of mist forest, 1450–2100 m. **I**: Lavranos & Newton (1976: 279–280, as *A. schliebenii*).

**Incl.** *Aloe lastii* Baker (1901); **incl.** *Aloe schliebenii* Lavranos (1970).

[4] Acaulescent, or with short procumbent stem with age, simple or suckering to form small groups; **L** 20–30, rosulate, lanceolate-attenuate, 30–60 × 4–8 cm, yellowish-green, red-brown in sun, longitudinally lineate, **marginal teeth** 1–3 mm, brown-tipped, curved, 10 mm apart; **Inf** 40–100 cm, simple or occasionally with 1 short **Br**; raceme cylindrical, 15–20 cm, dense; **Bra** ovate, 12–14 × 5–10 mm, fleshy, red, becoming scarious with age, imbricate in bud stage; **Ped** 16–22 mm; **Fl** pale orange-red, yellow-green at the mouth, 25–32 mm, clavate, base attenuate, 4–5 mm Ø across the ovary, not narrowed above, enlarging to 7–8 mm at the mouth; **OTep** free for 8–10 mm; **St** and **Sty** exerted 2–4 mm.

One of many plants sent to Kew from Zanzibar by the governor, Sir John Kirk, without locality information. Most of these plants had been collected on the African mainland, in parts of Kenya and Tanzania.

**A. branddraaiensis** Groenewald (Flow. Pl. South Afr. 20: t. 761 + text, 1940). **Type:** RSA, Mpumalanga (*van der Merwe* s.n. [PRE 24208]). — **Distr:** RSA (Mpumalanga, Limpopo); Bushveld vegetation in frost-free areas, 850–1000 m. **I:** Reynolds (1950: 219–220); Carter & al. (2011: 183); Wyk & Smith (2014: 218–219).

[5] Acaulescent, usually simple; **L** 20–25, rosulate, sometimes subdistichous or somewhat spirally twisted, lanceolate-attenuate,  $\pm 35 \times 8$ –10 cm, green with many longitudinal dull whitish striations and many irregular, somewhat H-shaped, whitish spots, **marginal teeth** 2–3 mm, pale brown, deflexed, 10–15 mm apart; **Inf** 1–1.5 m, with many **Br**, lower ones rebranched; racemes capitate, 3–6  $\times$  7 cm, with  $\pm 15$  flowers; **Bra** deltoid-acuminate, 8 mm; **Ped** 20 mm, shorter on lateral racemes; **Fl** dull scarlet at the base, paler at the mouth, 27 mm, base rounded, 5.5 mm  $\varnothing$  across the ovary, narrowed to 3.5 mm above, then enlarging to 6 mm at the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 1 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

A natural hybrid with *A. burgersfortensis* has been reported (Reynolds 1950).

**A. brandhamii** S. Carter (Fl. Trop. East Afr., Aloaceae, 32–33, ills., 1994). **Type:** Tanzania, Iringa Distr. (Carter & al. 2600 [K, DAR, EA, NHT]). — **Distr:** C Tanzania; riverine deciduous forest, light shade on rocky slopes, 750–1200 m. **I:** Carter & al. (2011: 382).

[7] Acaulescent or shortly caulescent, suckering to form small groups; stem to 1 m on old plants, ascending; **L** densely rosulate, lanceolate, 50–80  $\times$  10–20 cm, dull dark green, often bronzed, surface smooth, exudate drying yellow, **marginal teeth** 2–3 mm, pungent, brown-tipped, 10–20 mm apart; **Inf** 1.5–2 m, with up to 25 **Br**, lower ones sometimes rebranched; racemes with flowers secund, 15–30 cm, lax; **Bra** ovate, 12–15  $\times$  5–7 mm; **Ped** 5–9 mm; **Fl** coral-pink, paler at the mouth, minutely white-flecked, 30–40 mm, base rounded, 7–8 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for  $\pm 10$ –13 mm; **St** and **Sty** exerted 3–4 mm.

**A. brevifolia** Miller (Gard. Dict. Abr. ed. 6, [no. 8], 1771). **Type:** [proposed lecto — icono] Commelin, Praeludia Bot., 73, t. 22, 1703. — **Distr:** RSA. **I:** Carter & al. (2011: 398–399); Wyk & Smith (2014: 288–289).

**Incl.** *Aloe perfoliata* var.  $\delta$  Linné (1753).

**A. brevifolia** var. **brevifolia** — **Distr:** RSA (S Western Cape); open bushland, clay soil in rocky places, to 150 m; neophyte in Spain (Valencia). **I:** Reynolds (1950: 184–186); Carter & al. (2011: 398); Wyk & Smith (2014: 288–289).

**Incl.** *Aloe proliferata* Haworth (1804); **incl.** *Aloe proliferata* var. *major* Salm-Dyck (1817); **incl.** *Aloe postgenita* Schultes & Schultes fil. (1830)  $\equiv$  *Aloe brevifolia* var. *postgenita* (Schultes & Schultes fil.) Baker (1880).

[6] Acaulescent, suckering to form dense clumps; **L** 30–40, densely rosulate, lanceolate-deltoid, 6  $\times$  2 cm, glaucous, lower face with a few soft prickles in a median line or irregular in the upper  $\frac{1}{3}$ , tip a firm spine, **marginal teeth** 2–3 mm, whitish, 10 mm apart; **Inf** 40 cm, simple; raceme conical, 15  $\times$  7 cm, subdense; **Bra** ovate-lanceolate, 15 mm; **Ped** 15 mm; **Fl** pale scarlet, 38 mm, base truncate, very slightly narrowed above the ovary, slightly enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 5 mm. — **Cytology:**  $2n = 14$  (Resende 1937).

*A. postgenita* and *A. proliferata* var. *major* are said to be intermediate between this and var. *depressa* (Wyk & Smith 2014). The taxon was recently recorded as neophyte from Spain (Guillot 2013). A natural hybrid with *A. mitriformis* has been reported (Reynolds 1950), referred to as “*A.  $\times$  nobilis*” without authorship by Zonneveld (2003), though with reference to Jacobsen’s Lexicon, which includes *A.  $\times$  nobilis* Haworth (see entry under this name).

**A. brevifolia** var. **depressa** (Haworth) Baker (J. Linn. Soc., Bot. 18(108): 160, 1880). **Type:** not typified. — **Distr:** RSA (S Western Cape: near Caledon only); shale cliffs, to 100 m. **I:** Reynolds (1950: 189); Carter & al. (2011: 399).

$\equiv$  *Aloe depressa* Haworth (1804); **incl.** *Aloe perfoliata* var.  $\zeta$  Linné (1753); **incl.** *Aloe serra* De

Candolle (1799)  $\equiv$  *Aloe brevifolia* var. *serra* (De Candolle) A. Berger (1908).

[6] Differs from var. *brevifolia*: **L**  $\pm$ 60, 12–15  $\times$  6 cm, surface smooth or with white sub-tuberculate spots in the upper  $\frac{1}{2}$ , **marginal teeth** 2–4 mm; **Inf** 60 cm; **Bra**  $\pm$ 15 mm; **Ped** to 20 mm; **Fl** 40 mm, flame-scarlet. — **Cytology**:  $2n = 14$  (Resende 1937).

Larger than the typical variety.

**A. breviscapa** Reynolds & P. R. O. Bally (J. South Afr. Bot. 24(4): 176–177, t. 19, 1958). **Type**: Somalia, Northern Region (Reynolds 8542 [PRE, EA, K]). — **Distr**: N Somalia; arid gypsum plains,  $\pm$ 1400 m. **I**: Reynolds (1966: 267–268); Carter & al. (2011: 443).

[7] Caulescent, suckering to form small to large dense clumps, with almost horizontal **Ros**; stem short or to 50 cm, decumbent, to 1 m with age; **L**  $\pm$ 24, densely rosulate, lanceolate-attenuate, 30–35  $\times$  8–10 cm, bluish-grey tinged reddish, exudate drying yellow, **marginal teeth** absent or few in the basal  $\frac{1}{4}$ , 1–2 mm, blunt, 10 mm apart; **Inf**  $\pm$ 50 cm, arcuate-ascending, with 4–8 **Br**; racemes cylindrical, 20–25  $\times$  6 cm, lax; **Bra** ovate-acute, 6  $\times$  3 mm; **Ped** 10–14 mm; **Fl** scarlet with a bloom, greenish at the mouth, 26–30 mm, base shortly attenuate, 8 mm  $\varnothing$  across the ovary, slightly narrowed above; **OTep** free for 10 mm; **St** and **Sty** exerted 2–4 mm.

**A. broomii** Schönland (Rec. Albany Mus. 2: 137, 1907). **Type**: RSA, Northern Cape (*Broom* s.n. [not located]). — **Distr**: RSA, Lesotho.

**A. broomii** var. *broomii* — **Distr**: W Lesotho, RSA (Northern Cape, Western Cape, Eastern Cape, S Free State); rocky slopes, amongst grass and bushes, (1000–) 1400–1900 m, flowers in September. **I**: Reynolds (1950: 163–165); Carter & al. (2011: 263); Wyk & Smith (2014: 144–145).

[4] Caulescent, usually simple; stem short or up to 1 m, procumbent, usually simple, sometimes dividing into 2 or 3, covered with dried leaves; **L** densely rosulate, ovate-lanceolate, acuminate with pungent terminal spine, 30  $\times$  10 cm, green, obscurely lineate, with reddish-brown horny margin, **marginal teeth** 1–2 mm, reddish-brown with

paler tips, 10–15 mm apart; **Inf** 1–1.5 m, mostly simple, rarely with 1 **Br**; racemes cylindrical, slightly acuminate, to 100  $\times$  6–8 cm, very dense; **Bra** lanceolate-acute, 30  $\times$  15 mm, rather fleshy, white to pale lemon with brownish tips; **Ped** 1–2 mm; **Fl** pale lemon, 20–25 mm, base rounded, enlarging above the ovary and narrowing to the mouth, completely hidden by the bracts; **OTep** free to the base; **St** and **Sty** exerted 12–15 mm.

Natural hybrids with other species have been reported (Reynolds 1950).

**A. broomii** var. *tarkaensis* Reynolds (J. South Afr. Bot. 2(2): 72–73, ill., 1936). **Type**: RSA, Eastern Cape (Reynolds 1777 [PRE]). — **Distr**: RSA (SE Eastern Cape, adjacent Northern Cape); rocky slopes, 1200–1500 m, flowers February–March. **I**: Reynolds (1950: 166); Carter & al. (2011: 263).

[4] Differs from var. *broomii*: Plants more luxuriant, **L** 2–3 $\times$  broader at the base; **Bra** dry and much shorter; **Ped** 4 mm; **Fl** 30 mm, not hidden by the bracts.

**A. brunneodentata** Lavranos & Collette (Cact. Succ. J. (US) 72(2): 86, ill. (p. 84), 2000). **Type**: Saudi Arabia, Asir Prov. (Collette 5826 [K]). — **Distr**: Saudi Arabia (Asir Prov.); on granite,  $\pm$ 1800 m; known only from the type locality. **I**: Collette (1999: 20); Carter & al. (2011: 258).

[2] Acaulescent, solitary; **L** densely rosulate, 28–35  $\times$  7 cm, pale bluish-green, **marginal teeth** short, brown; **Inf**  $\pm$ 60 cm, simple or with 1 **Br**; racemes cylindrical, lax; **Bra** 12–15  $\times$  4–6 mm; **Fl** reddish, downy, 24–26 (–35) mm, base rounded, not constricted above the ovary; **OTep** free for  $\pm$ 11 mm; **St** and **Sty** not exerted.

**A. brunneostriata** Lavranos & S. Carter (Cact. Succ. J. (US) 64(4): 206–208, ill., 1992). **Type**: Somalia, Bari Region (Migurtein) (Lavranos & Horwood 10187 [K]). — **Distr**: NE Somalia (Puntland: Bari Region); sandy plains on limestone, 640 m. **I**: Carter & al. (2011: 312).

[7] Shortly caulescent, suckering from the base to form small groups; **Br** erect or ascending, 40



cm; **L** up to 10, laxly rosulate, lanceolate, acute, 30 × 7 cm, creamy-yellow with many longitudinal reddish-brown lines, surface smooth, **marginal teeth** absent or <0.5 mm, blunt, yellow; **Inf** 50–60 cm, with 6–7 (–12) **Br**; racemes with subsecund flowers, lax; **Bra** ovate-acute, 5–6 × 5–6 mm; **Ped** 5–6 mm; **Fl** yellow with greenish veins at the lobe tips, 16–20 mm, base shortly attenuate, 5–6 mm  $\emptyset$  across the ovary, slightly narrowed above and enlarging to the mouth; **OTep** free for  $\pm$ 4–6 mm; **St** and **Sty** exerted 5 mm.

**A. bruynsii** P. I. Forster (Bradleya 21: 53–55, ills., 2003). **Type:** Madagascar, Toliara (*Bruyns* 5962A [BRI, BOL, K, MO, P]). — **Distr:** Madagascar (Toliara: Tolanaro); soil pockets on gneiss rock slopes and cliffs, 400–600 m; known only from the type locality. **I:** Castillon & Castillon (2010: 248–249).

[6] Suckering to form dense clumps; stem erect, to 18 cm; **L** 18–28, rosulate, lanceolate-falcate, 16 × 2 cm, lime-green to reddish-green, surface smooth, exudate pale green, drying clear, **marginal teeth** 1 mm, 3–7 mm apart; **Inf** 15–30 cm, erect, simple or with 1 **Br**; racemes semicapitate, to 5 cm, semidense; **Bra** lanceolate, 5 × 1 mm, pale brown; **Ped** 10–12 mm, pale brown; **Fl** lemon-yellow with pale green mid-stripe in the upper  $\frac{1}{3}$ , 19–20 mm, 5–5.5 mm  $\emptyset$ ; **OTep** free for 16 mm; **St** and **Sty** not exerted.

Castillon & Castillon (2010) argue that this species is probably in part based on hybrid material, likely *A. bakeri* × *A. deltoideodonta*.

**A. buchananii** Baker (Bull. Misc. Inform. Kew 1895: 119, 1895). **Type:** Malawi, Southern Prov. (*Buchanan* s.n. [K]). — **Lit:** Lane (2004: 4). **Distr:** S Malawi (Shire Highlands, Kirk Range and Mt. Mulanje), adjacent NW Moçambique; montane woodland, open *Brachystegia* woodland, 1150–1600 (–1940) m. **I:** Reynolds (1966: 29–31); Carter & al. (2011: 146); Klopper & al. (2012: 71, 77, incl. distribution map).

[4] Acaulescent or shortly caulescent, usually simple or 2–3 (rarely up to 9) **Ros** in clumps; **R** fusiform; stem to 20 cm; **L** distichous or becoming rosulate, triangular, 60 × 4–6 cm, green with

few scattered elongated dull white spots towards the base, lower face more copiously spotted, with narrow translucent cartilaginous margin, **marginal teeth** 0.5 mm, 8–15 mm apart, absent towards the leaf tip; **Inf** 60–80 cm, simple; raceme cylindrical-acuminate, 15–20 × 7 cm, dense; **Bra** ovate-acute, apiculate, 25–30 × 10–12 mm, fleshy, pale pink, imbricate in early bud stage; **Ped** 35–40 mm; **Fl** salmon-pink or light coral-red, greenish at the mouth, 30 mm, base shortly attenuate, 10–11 mm  $\emptyset$  across the ovary, narrowing towards the mouth; **OTep** free to or almost to the base; **St** and **Sty** exerted 0–1 mm.

Reported by Lane (2004) to be seriously endangered, now known only as widely separated small populations or isolated individuals.

**A. buchlohii** Rauh (Kakt. and. Sukk. 17(1): 2–4, ills., 1966). **Type:** Madagascar, Toliara (*Rauh* M1381 [HEID]). — **Lit:** Carter & al. (2011: 275). **Distr:** SE Madagascar (Toliara: Tolanaro); bare gneissic or granitic rocks along the coast, 100 m. **I:** Reynolds (1966: 431); Glen & Hardy (1992); Castillon & Castillon (2010: 223).

[4] Acaulescent, simple or in small groups; **L** 10–20, densely rosulate, lanceolate-attenuate with small apical spine, 40–50 × 3 cm, green, sometimes tinged reddish, with a few spots near the base, **marginal teeth** 3 mm, pungent, reddish-brown-tipped, 8 mm apart; **Inf** 60 cm, simple (or with 3 **Br** in cultivation); raceme subcapitate, 10 × 7 cm, subdense; **Bra** ovate-attenuate, 7 × 2.5 mm; **Ped** 15–20 mm; **Fl** pale yellow, or pale rose at the base and yellowish upwards, 25 mm, base shortly attenuate, 7 mm  $\emptyset$  across the ovary, scarcely narrowed above; **OTep** free to the base; **St** and **Sty** exerted 4 mm.

Castillon & Castillon (2016: 115) argue that the species is close to *A. versicolor*.

**A. buettneri** A. Berger (Bot. Jahrb. Syst. 36: 60, 1905). **Type:** Togo (*Büttner* s.n. [B]). — **Lit:** Carter & al. (2011: 151). **Distr:** Benin, Gabon, Ghana, Mali, Nigeria, Togo, Democratic Republic of the Congo [Zaire], Angola, Namibia; grassland and savanna woodland, 250–1800 m. **I:** Reynolds (1966: 45).

**Incl.** *Aloe paedogona* A. Berger (1906); **incl.** *Aloe barteri* var. *dahomensis* A. Chevalier (1952) (*nom. inval.*, ICN Art. 39.1); **incl.** *Aloe barteri* var. *sudanica* A. Chevalier (1952) (*nom. inval.*, ICN Art. 36.1); **incl.** *Aloe paludicola* A. Chevalier (1952) (*nom. inval.*, ICN Art. 39.1).

[5] Acaulescent, simple or rarely suckering at the base forming small groups, the base enlarging to form a bulb towards the end of the growing season; **L** ±16, rosulate, usually dying back in the dry season, triangular, 35–55 cm, green, obscurely lineate, sometimes with few scattered whitish spots, with very narrow white to pale pink cartilaginous margin, surface smooth, **marginal teeth** 3–4 mm, firm, 10–15 mm apart; **Inf** 70–90 cm, with 3–5 **Br**; racemes cylindrical-conical to subcapitate, 15 × 7 cm, subdense; **Bra** deltoid-acute or lanceolate-acuminate, 10–15 × 6–8 mm; **Ped** 20–25 mm; **Fl** greenish-yellow to dull red, 38 mm, base rounded, 9–11 mm Ø across the ovary, narrowed to 6–8 mm above, enlarging to 9–11 mm and narrowing again to the mouth; **OTep** free for 12–13 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Resende 1937).

Reynolds (1966) included *A. bulbicaulis* and *A. paedogona* in this taxon, but Carter (1994) treated them as 3 geographically distinct species. Later *A. paedogona* was included in *A. buettneri*, differing only in the shape of the fruit (Carter & al. 2011).

Until 1963, only 1 species was reported from West Africa, *A. barteri* Baker. Keay (1963) showed that the type of this name was a mixture of 2 taxa, *A. buettneri* (inflorescence) and *A. schweinfurthii* (leaf). The latter is designated as lectotype of *A. buettneri* in this volume, and this removes *A. barteri* as synonym of *A. buettneri* (see comment under *A. schweinfurthii*).

A natural hybrid with *A. schweinfurthii* is known as *A. ×keayi* Reynolds (*pro. sp.*) (Newton 1976).

**A. buhrii** Lavranos (J. South Afr. Bot. 37(1): 37–40, ills., 1971). **Type:** RSA, Northern Cape (*Buhr* s.n. in Lavranos 8163 [PRE]). — **Distr:** RSA (SW Northern Cape: near Calvinia); karroid veld on shale, isolated hilltops, ±650

m. **I:** Carter & al. (2011: 447); Wyk & Smith (2014: 146–147).

[7] Acaulescent, suckering to form dense clumps; **L** ±16, rosulate, lanceolate-deltoid, 40 × 9 cm, glaucous with reddish tinge, distinctly striate and with irregular white elongate or H-shaped spots, with pale red cartilaginous 1.5–2 mm margin, **marginal teeth** < 1 mm, 3.5 mm apart or laterally confluent; **Inf** to 60 cm, with 7–15 **Br**, lower ones rebranched; racemes subcapitate, lax; **Bra** deltoid-acute, yellowish, 5–10 mm; **Ped** 20–25 mm; **Fl** orange-red, 25–27 mm, base truncate, 6 mm Ø across the ovary, abruptly narrowed to 4 mm above, then enlarging towards the mouth; **OTep** free for 6–7 mm; **St** and **Sty** exerted 3–6 mm.

In the protologue the type locality was said to be at ±650 m, and it was stated that the species has a very limited range, restricted to a few isolated hilltops. It is not known if the higher altitudes reported by Wyk & Smith (2014) are based on further discoveries, extending the range.

**A. bukobana** Reynolds (J. South Afr. Bot. 20 (4): 169–171, ills., 1955). **Type:** Tanzania, North-West Prov. (*Reynolds* 7507 [PRE, EA, K]). — **Distr:** NW Tanzania, Ruanda, Burundi, S Uganda; sandstone hills and rock outcrops, 1150–1470 m. **I:** Reynolds (1966: 108–109); Carter & al. (2011: 317); Cole & Forrest (2015: 78); Cole & Forrest (2017: 30–35).

[7] Acaulescent, suckering freely to form small dense groups; **L** ±16, densely rosulate, lanceolate-attenuate with the tip a small spine, 30 × 8 cm, dull green with slight bloom above, grey-green below, exudate drying yellow, **marginal teeth** 4 mm, firm, brownish-tipped, 10 mm apart; **Inf** 70–90 cm, with up to 10 **Br**, lower **Br** sometimes rebranched; racemes narrowly conical-cylindrical, 30–40 cm, very lax; **Bra** ovate-acute, 4 × 3 mm; **Ped** 12 mm; **Fl** dull scarlet, paler at the mouth, 30–35 mm, base rounded or shortly attenuate, 7–8 mm Ø across the ovary, enlarging slightly above; **OTep** free for 7 mm; **St** exerted 1–2 mm; **Sty** exerted 3 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Natural hybrids with *A. macrosiphon* have been reported (Reynolds 1966).

**A. bulbicaulis** Christian (Flow. Pl. South Afr. 16: t. 630 + text, 1936). **Type:** Zambia, Western Prov. (*Porter* s.n. [PRE 20587]). — **Distr:** E Angola (Moxico), N Malawi, NW Moçambique, SW Tanzania, SE Democratic Republic of the Congo [Zaire] (Katanga), N Zambia; seasonally wet grassland in open *Brachystegia* woodland, 1200–1620 m. **I:** Reynolds (1966: 44); Carter & al. (2011: 150); Klopper & al. (2012: 71, 77, incl. distribution map).

**Incl.** *Aloe trothae* A. Berger (1905).

[3] Acaulescent, simple, the base enlarging to form a bulb 8–10 cm  $\varnothing$  towards the end of the growing season; **L**  $\pm 16$ , rosulate, usually dying back in the dry season, ovate-lanceolate, to  $\pm 50 \times 15$  cm, bright green, longitudinally striate, with whitish cartilaginous 1–2 mm margin, surface smooth, **marginal teeth** 1 mm, densely crowded; **Inf** to  $\pm 60$  cm, with 3–4 (–7) **Br**; racemes cylindrical, 10–20  $\times$  7 cm, subdense; **Bra** ovate-acuminate,  $\pm 12 \times 8$  mm; **Ped**  $\pm 20$  mm; **Fl** pale yellow to pinkish- or brownish-yellow, to 40 mm, base rounded, 9–11 mm  $\varnothing$  across the ovary, narrowed to 6–8 mm above, enlarging to 9–11 mm and narrowing again to the mouth; **OTep** free for 12–13 mm; **St** and **Sty** exerted 0–1 mm.

Reynolds (1966) included this in *A. buettneri*, but Carter (1994) treated them as geographically distinct species. Further studies are required to determine their relationships. Carter (1994) suggested that the poorly-known *A. trothae* possibly belongs here, in which case the name would have priority over *A. bulbicaulis*.

The occurrence in Angola was reported by Carter (1994) but was erroneously omitted by Carter & al. (2011). The occurrence in Moçambique was reported by Klopper & al. (2012).

Lebrun & Stork (2012) indicate possible hybrids with *A. christianii* in W Zambia, but fail to cite a reference.

**A. bulbillifera** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 22, 1926). **Type:** Madagascar, Mahajanga (*Perrier* 11017 [P]). — **Distr:** Madagascar.

**A. bulbillifera** var. **bulbillifera** — **Distr:** NW Madagascar (Mahajanga); montane wet forest,

(300–) 400–800 m. **I:** Reynolds (1966: 455–456); Castillon & Castillon (2010: 332–333); Carter & al. (2011: 364).

[5] Acaulescent, simple, or with a short stem and basal branches in shaded situations; **L** 24–30, densely rosulate, acute, 40–60  $\times$  8–10 cm, green, exudate drying deep orange to purple, **marginal teeth** smaller towards the leaf tip, firm, 10–20 mm apart; **Inf** 2–2.5 m, usually curved over sideways and often falling to sprawl on the ground, with up to 30 **Br**, the lowest to 1 m and with up to 12 secondary **Br**, bulbils developing in the axils of sterile bracts on the branches below the racemes; racemes cylindrical-acuminate, 20–25 cm, lax; **Bra** deltoid, 3  $\times$  2 mm; **Ped** 8–10 mm; **Fl** scarlet, 25 mm, base truncate, 5 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 1–3 mm. — **Cytology:** 2n = 14 (Resende 1937).

Bulbil formation is rare in the genus (cf. *A. patersonii*).

**A. bulbillifera** var. **paulianiae** Reynolds (J. South Afr. Bot. 22(1): 26–27, ill., 1956). **Type:** Madagascar, Mahajanga (*Paulian* s.n. in Reynolds 7656 [TAN, K, P, PRE]). — **Distr:** NW Madagascar (Mahajanga); rocky mountain slopes, savanna and basalt hills, 270 m. **I:** Reynolds (1966: 457–458); Carter & al. (2011: 365).

[5] Differs from var. *bulbillifera*: **L**  $\pm 20$ , **marginal teeth** 3 mm, dull white; **Inf** 2 m, with 8–12 compact **Br** in the upper  $\frac{1}{4}$ , the lowest to 30 cm and with 8–12 secondary **Br**, bulbils developing on the main peduncle below the lowest branch; **Bra** ovate-acute, 4  $\times$  3 mm.

**A. bullockii** Reynolds (J. South Afr. Bot. 27 (2): 73–75, ill., 1961). **Type:** Tanzania, Shinyanga Region (*Bullock* 3076 [K]). — **Distr:** NE Tanzania (Shinyanga Region); open woodland amongst grass, seasonal after fires, 1220 m; known only from the region of the type locality. **I:** Reynolds (1966: 39–40); Carter & al. (2011: 118).

[2] Acaulescent, simple, geophytic, base enlarging to form a bulb, 3–4 cm  $\varnothing$ ; **R** thick, fusiform; **L** 8–10, rosulate, linear-lanceolate, 10–20  $\times$  2–3 cm, green, lineate, with narrow cartilaginous margin, **marginal teeth** 0.5–1 mm,

soft, pale pink, 0.5–1 mm apart; **Inf** 35–50 cm, simple or with 1 **Br**; racemes cylindrical, 7–10 × 5 cm, semidense; **Bra** ovate-acute, deflexed, 8–10 × 5–6 mm; **Ped** 4–5 mm; **Fl** pale scarlet to coral-red, 30 mm, base truncate, 6 mm  $\varnothing$  across the ovary, narrowed to 4 mm above, then enlarging and narrowing again towards the mouth; **OTep** free for 8 mm; **St** and **Sty** scarcely exerted.

**A. burgersfortensis** Reynolds (J. South Afr. Bot. 2(1): 31–34, ills., 1936). **Type:** RSA, Mpumalanga (*Reynolds* 1465 [PRE, BOL]). — **Distr:** RSA (N Mpumalanga: Lydenburg Distr.); semi-arid Bushveld vegetation, sandy soil, 760–1400 m. **I:** Reynolds (1950: 274–275); Carter & al. (2011: 184); Wyk & Smith (2014: 220–221).

[7] Acaulescent, simple or suckering to form small to large groups; **L** 10–20, densely rosulate, triangular-acuminate, up to 35–40 cm, upper face brownish-green with oblong scattered white spots  $\pm$  in wavy transverse bands, lower face paler glaucous green, unspotted and somewhat striate, **marginal teeth** 3–5 mm, pungent, brown, 10–14 mm apart; **Inf** 1–1.3 m, with 4–9 arcuate-erect **Br**; racemes cylindrical-acuminate, 20–35 (–40) cm, lax or subdense; **Bra** deltoid-acuminate, slightly longer than the pedicels; **Ped** 10–15 mm; **Fl** dull reddish with a bloom, somewhat white-striped in the upper  $\frac{1}{2}$ , sometimes shading to orange at the mouth, 30 mm, base rounded, 7 mm  $\varnothing$  across the ovary, narrowed above to 5 mm, enlarging

towards the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

Included in *A. parvibracteata* by Glen & Hardy (2000). Natural hybrids with other species have been reported (Reynolds 1950).

**A. bussei** A. Berger (in Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 273, 1908). **Type:** Tanzania, Mpwapwa Distr. (*Busse* 294 [B, BM, KJ]). — **Lit:** Carter (1994). **Distr:** E Tanzania; rock outcrops and cliffs, 580–1500 m. **I:** Reynolds (1966: 72–74, as *A. morogoroensis*); Carter & al. (2011: 419). — Fig. 12.

**Incl.** *Aloe morogoroensis* Christian (1940).

[6,7] Acaulescent, suckering to form dense groups; **L**  $\pm$ 20, rosulate, ovate-lanceolate, attenuate, 20–30 × 5–6 cm, glossy green, usually flushed coppery-red, sometimes with few whitish spots on the lower face, with narrow white cartilaginous margin, **marginal teeth** 2–5 mm, inclining towards the leaf tip, white or pale yellowish, 7–15 mm apart; **Inf** 40–60 (–75) cm, simple or usually with 1–4 **Br**; racemes conical-cylindrical, 15–25 cm,  $\pm$  dense; **Bra** ovate-acute, 4–6 × 3 mm; **Ped** 8–10 mm; **Fl** coral-red, yellowish at the mouth, 28–35 mm, base attenuate, 6 mm  $\varnothing$  across the ovary, slightly narrowed above, enlarging to 8 mm and narrowing again at the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 0–1 mm.

**Fig. 12** *Aloe bussei*.  
(Copyright: L. E. Newton)





**A. butiabana** T. C. Cole & T. G. Forrest (Cact. Succ. J. (US) 83(1): 28–33, ills., 2011). **Type:** Uganda, Masindi Distr. (Cole & Forrest 420 [MHU, EA]). — **Distr:** W Uganda; grassland thickets and on cliffs, 680–920 m. **I:** Cole & Forrest (2017: 36–41).

[7] Acaulescent or with a stem to 50 × 7 cm, suckering to form dense clumps; **L** to 32, rosulate, lanceolate-attenuate, 95 × 9 cm, mid-green, surface smooth, exudate yellow, **marginal teeth** deltoid, 3–4 mm, brick-red, 12–16 mm apart; **Inf** 1.8 m, erect, with (6–) 8–12 (–16) **Br**, lowermost sometimes rebranched; racemes cylindrical, 20–26 cm, subdense; **Bra** triangular-acute, 4 × 3 mm, light brown; **Ped** 9–10 mm, red; **Fl** red, becoming yellow at the mouth, 26–30 mm, 8–9 mm Ø across the ovary, narrowed above to 6 mm; **OTep** free for 15–21 mm; **St** exerted 3–6 mm; **Sty** exerted 2–4 mm.

According to Carter & al. (2011: 705) closest to the Kenyan *A. lolwensis*, and young plants superficially similar.

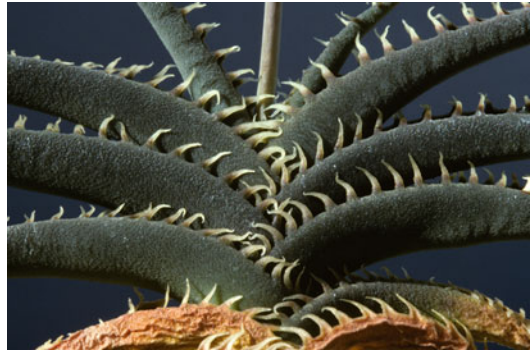
**A. ×buzairiensis** Lodé (Cact.-Avent. Int. 92: 19, ills., 2011). **Type:** Yemen, Socotra (Lodé 1230512 [Herb. Fundación Joel Lodé]). — **Distr:** Yemen (Socotra); in shrubs, 760 m.

[11] Caulescent, branching from the base to form loose clumps, stem to ±1 m; **L** 6–10, rosulate, lanceolate-triangular, dark green with scattered whitish spots; **Inf** erect, simple; raceme cylindrical, lax; **Fl** red.

= *A. perryi* × *A. squarrosa*.

**A. calcairophila** Reynolds (J. South Afr. Bot. 27(1): 5–6, ills., 1961). **Type:** Madagascar, Fianarantsoa (Descoings 2114 [TAN, K]). — **Lit:** Du Puy (2004a: 238–241, t. 507); Du Puy (2004b); Lüthy (2006: 29–30, conservation, with ills.). **Distr:** C Madagascar (Fianarantsoa: E fringe of the Itremo Massif: Amabofinandrahana); rocky marble outcrops, 1300–1400 m. **I:** Reynolds (1966: 408–410); Castillon & Castillon (2010: 120–121); Carter & al. (2011: 209). – Fig. 13.

≡ *Guillauminia calcairophila* (Reynolds) P. V. Heath (1994); **incl.** *Aloe calcairophylla* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1).



**Fig. 13** *Aloe calcairophila*. (Copyright: U. Eggli)

[6] Acaulescent, suckering to form small groups; **L** ±10, distichous, triangular-acuminate, 5–6 × 1.4 cm, dull grey-green, **marginal teeth** 2–3 mm, softly cartilaginous, 2–3 mm apart; **Inf** 20–25 cm, simple; raceme 3–4 cm, lax, with 8–10 flowers; **Bra** ovate-acute, 3 × 2 mm; **Ped** 5–6 mm; **Fl** white, 10 mm, base shortly attenuate, ventricose, enlarging to 4 mm Ø above the ovary, slightly constricted at the mouth; **OTep** free for 5 mm; **St** and **Sty** not exerted.

Vegetatively similar to *A. compressa*.

**A. calidophila** Reynolds (J. South Afr. Bot. 20 (1): 26–28, ills., 1954). **Type:** Ethiopia, Sidamo Prov. (Reynolds 7029 [PRE, K]). — **Distr:** S Ethiopia (Sidamo Region), NE Kenya; open woodland, bushland to open wooded grassland, 360–1620 m. **I:** Reynolds (1966: 217–218); Sebsebe Demissew & Nordal (2010: 93–94); Carter & al. (2011: 626).

[12] Caulescent, branching to form small to large dense groups; stem short or to 2 m, decumbent with ascending tip; **L** ±20, densely aggregated at the stem tip, triangular, deeply canaliculate, strongly recurved, 80 × 16 cm, dull olive-green, exudate drying deep brown, **marginal teeth** 4–5 mm, dull white with reddish-brown tip, 20–25 mm apart; **Inf** 1–1.3 m, with ±12 **Br**; racemes slightly conical-cylindrical, 10–13 × 5 cm, dense; **Bra** ovate-acuminate, 3–4 × 2 mm; **Ped** 10 mm; **Fl** scarlet, becoming orange towards the mouth, 22 mm, clavate, base shortly attenuate, 6 mm Ø across the ovary, enlarging



above; **OTep** free for 11 mm; **St** and **Sty** exerted 3 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

**A. calliantha** T. A. McCoy & Lavranos (Cact. Succ. J. (US) 86(6): 262–263, ills. (pp. 261–263), 2014). **Type**: Saudi Arabia, Medina Prov. (McCoy 523 [FT]). — **Distr**: Saudi Arabia (Medina Prov.); rocky slopes, 1800 m.

[2] Acaulescent, solitary; **L** 20–25, rosulate, lanceolate, 22–25 × 10–11 cm, blue-grey, pruinose, exudate yellowish-orange, drying brownish-yellow, **marginal teeth** 5–7 mm, pinkish-white, 28–35 mm apart; **Inf** 90 cm, erect, usually simple or with 1–2 **Br**; racemes cylindrical, dense; **Bra** ovate-lanceolate, 12–14 × 5–7 mm, with 3–5 brown nerves; **Ped** 2–4 mm, red; **Fl** shiny red, 28–34 mm, cylindrical-ventricose, 10 mm  $\varnothing$  across the middle; **OTep** free for 18 mm; **St** exerted 10–12 mm; **Sty** exerted 11 mm.

**A. cameronii** Hemsley (Curtis's Bot. Mag. 129: t. 7915 + text, 1903). **Type**: Malawi (*Cameron* s.n. [K]). — **Lit**: Campbell-Barker (2003: type locality). **Distr**: Zimbabwe, Malawi, Moçambique, Zambia.

**A. cameronii** var. **bondana** Reynolds (Aloes Trop. Afr. & Madagascar, 353, ills., 1966). **Type**: Zimbabwe, Nyanga Distr. (Reynolds 8585 [SRGH, PRE]). — **Distr**: E Zimbabwe (Nyanga Distr.); exposed on granite outcrops, 1700–2200 m. **I**: Glen & Hardy (1990); Carter & al. (2011: 576).

[8] Differs from var. *cameronii*: Stem mostly simple, 60–180 cm; **Fl** mostly yellowish to orange, 38–40 mm, more fleshy and somewhat clavate.

**A. cameronii** var. **cameronii** — **Distr**: E & S Malawi, W & C Moçambique, E Zambia, E Zimbabwe; shallow soil pockets on granite rocks, 675–2070 m. **I**: Reynolds (1966: 349–351); Lane (2004: 8, 12–13); Carter & al. (2011: 575); Klopper & al. (2012: 73, 79, incl. distribution map).

[16] Caulescent, branching at the base; stem erect, to 150 × 3–4 cm, usually with dried leaf

remains; **L** rosulate and persistent on the apical 30–50 cm of the stem, triangular, tip attenuate-acute, 40–50 × 5–7 cm, green, usually turning copper-red in winter, exudate drying light brown, **marginal teeth** 2–3 mm, pungent, pale brown, 10–15 mm apart; **Inf** 60–90 cm, with 2–3 **Br**; racemes cylindrical, slightly acuminate, 10–15 × 7–8 cm, subdense; **Bra** ovate-acute, 2 × 3 mm; **Ped** 3–5 mm; **Fl** bright scarlet, 45 mm, sometimes slightly clavate, base rounded, 5–7 mm  $\varnothing$  across the ovary, slightly enlarging above, slightly narrowed towards the mouth; **OTep** free for 12–15 mm; **St** and **Sty** exerted 5 mm. — **Cytology**:  $2n = 14$  (Ferguson 1926).

Natural hybrids with other species have been reported (Reynolds 1966).

**A. cameronii** var. **dedzana** Reynolds (J. South Afr. Bot. 31(2): 167–168, ills., 1965). **Type**: Malawi, Central Prov. (Christian 459 [SRGH, PRE]). — **Distr**: Malawi (Central Prov., Southern Prov.), Moçambique?; among rocks in open woodland, 480–1200 m. **I**: Reynolds (1966: 353, flowers only); Lane (2004: 10, 12–13); Carter & al. (2011: 576).

[16] Differs from var. *cameronii*: Dense shrubs; Stems 50–80 cm; **Inf** with racemes 20–25 cm.

Lane (2004) was unable to find this in the wild, and it was last seen in the wild in 1980 according to Hargreaves (2007). Reynolds (1966) cites a specimen from Moçambique as “*Leach* 415 (SRGH) appears to belong here”, but Moçambique is not included in the distribution range by Carter & al. (2011) or Lebrun & Stork (2012). The identity of the Leach specimen is still unresolved.

**A. camperi** Schweinfurth (Bull. Herb. Boissier [sér. 1] 2(app. 2): 67, 1894). **Type**: Eritrea (*Schweinfurth* 514a [B]). — **Distr**: Eritrea, N Ethiopia (Tigray & Welo Regions); rocky slopes and sandy alluvial plains, 550–2700 m; neophyte in RSA (Western Cape). **I**: Reynolds (1966: 212–213); Sebsebe Demissew & Nordal (2010: 90–91); Carter & al. (2011: 621).

**Incl.** *Aloe abyssinica* Salm-Dyck (1817) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe spicata* Baker

(1896) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe albopicta* hort. ex A. Berger (1908); **incl.** *Aloe eru* A. Berger (1908); **incl.** *Aloe eru* fa. *erecta* hort. ex A. Berger (1908); **incl.** *Aloe eru* fa. *glauca* hort. ex A. Berger (1908); **incl.** *Aloe eru* fa. *maculata* hort. ex A. Berger (1908); **incl.** *Aloe eru* fa. *parvipunctata* hort. ex A. Berger (1908); **incl.** *Aloe eru* var. *cornuta* A. Berger (1908).

[12] Caulescent, branching at the base, sometimes forming groups 1–2 m Ø; stem erect, divergent or decumbent, to 100 × 6–10 cm; **L** 12–16, rosulate, persistent for 10–20 cm below, triangular, recurved, 50–60 × 8–12 cm, dark green, sometimes with few dull white lenticular spots, with reddish margin, **marginal teeth** 3–5 mm, pungent, brownish-red, 10–20 mm apart; **Inf** 70–100 cm, with 6–8 **Br**, lower ones sometimes rebranched; racemes cylindrical, 6–9 × 6–7 cm, dense; **Bra** deltoid, 2 × 2 mm; **Ped** 12–18 mm; **Fl** orange to yellow, 20–22 mm, cylindrical-clavate, base shortly attenuate, 5 mm Ø across the ovary, enlarging to 11 mm above; **OTep** free for ±7 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology**: 2n = 14 (Resende 1937: as *A. eru*, Fentaw & al. 2013).

According to Fikre Dessalegn (2006) this species is not clearly distinct from *A. adigratana* and *A. sinana*, and there could be intermediate populations. The taxon is widely cultivated as ornamental in RSA, and Smith & al. (2003) report it as locally naturalized at the foot of the Table Mountain.

**A. canarina** S. Carter (Fl. Trop. East Afr., Aloaceae, 41–42, ills., 1994). **Type**: Uganda, Karamoja Distr. (Reynolds 7951 [K, EA, PRE]). — **Distr**: South Sudan, NE Uganda; open deciduous bushland, 1345–1570 m. **I**: Reynolds (1966: 304–305, as *A. marsabitensis*); Carter & al. (2011: 612); Cole & Forrest (2017: 42–47).

[7] Caulescent, suckering to form small groups; stem decumbent, to 80 cm, with dead leaves persistent; **L** densely rosulate, lanceolate-attenuate, 50–80 × 10–15 cm, dull greyish-green tinged reddish, **marginal teeth** 2–3 mm, pungent, brown-tipped, 10–18 mm apart; **Inf** to ±1 m, with 15–20 **Br**, lower ones rebranched; racemes cylindrical, 10–15 cm, lax; **Bra** ovate-acuminate, 2–3 × 2.5 mm; **Ped** 6–7 mm; **Fl** yellow, 25–30 mm, base truncate, 10–12 mm Ø across the ovary,

narrowed to 8 mm towards the mouth; **OTep** free for ±8–10 mm; **St** and **Sty** exerted 4 mm.

Included by Reynolds (1966) in *A. marsabitensis* (which is now sunk under *A. secundiflora*). The material in South Sudan might represent a distinct species (Carter 1994).

**A. canis** S. Lane (Aloe 40(2): 55, 2003). **Type**: Malawi, Salima Distr. (Lane 1 [MAL, PRE]). — **Distr**: S Malawi (Salima Distr.: Senga Hills); open woodland, 500 m; probably extinct in the wild. **I**: Lane (2004: 29, 38); Carter & al. (2011: 637); Klopper & al. (2012: 73, 79).

**Incl.** *Aloe canii* S. Lane (2002) (*nom. inval.*, ICN Art. 9.1, 40.1).

[8] Caulescent, usually solitary; stem to 2.5 m; **L** densely rosulate, lanceolate, 45 × 5–7 cm, dark green, bronzed, with scattered spots near the base, exudate drying vermilion, **marginal teeth** 2–3 mm, brown-tipped, 15–23 mm apart; **Inf** 1–1.5 m, erect, with 3–4 **Br**; racemes cylindrical-acuminate, 14 × 5 cm; **Bra** 3–4 mm; **Ped** 10–11 mm; **Fl** pinkish-scarlet, 34 mm, 5 mm Ø across the ovary, slightly narrowed above, 5 mm Ø at the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 4 mm.

Described from cultivated material; not relocated at the type locality or elsewhere and possibly extinct in the wild (Lane 2004).

**A. cannellii** L. C. Leach (J. South Afr. Bot. 37 (1): 41–46, ills., 1971). **Type**: Moçambique, Manica e Sofala Distr. (Cannell 33 [SRGH, LISC, PRE]). — **Distr**: Moçambique (Manica e Sofala Distr.); grass tufts on almost vertical cliffs, ±1500 m; known only from the type locality. **I**: Carter & al. (2011: 120).

[6] Acaulescent, suckering to form dense tufts; **R** fleshy, subfusiform, with partially exposed sub-tuberous stock; **L** usually 4–5, rosulate, linear-acute, to 26 × 0.4–0.8 cm, green or with brownish tinge, with narrow hyaline margin, upper face sometimes with a few white spots, lower face more copiously white-spotted, **marginal teeth** ±0.25 mm, whitish, ±1 mm apart; **Inf** 20–30 cm, simple; raceme cylindrical, ±10–12.5 cm, lax, with 10–20 flowers; **Bra** ovate-acute, 4.5–6.5 × 3–3.5 mm; **Ped** 10–15 mm; **Fl**

orange-scarlet becoming greenish towards the mouth, 20–22 (–25) mm, base shortly attenuate, 3.5–4 mm  $\varnothing$  across the ovary, enlarging to  $\pm 5$  mm above, narrowed to 4 mm at the mouth; **OTep** free to the base; **St** and **Sty** not exerted.

**A. capitata** Baker (J. Linn. Soc., Bot. 20: 272, 1883). **Type:** Madagascar, Antananarivo (*Baron* 897 [K]). — **Distr:** Madagascar.

**A. capitata** var. **angavoana** J.-P. Castillon (Cact.-Avent. Int. 81: 12–13, ills., 2009). **Type:** Madagascar, Antananarivo (*Castillon* 34 [TAN, HBG]). — **Distr:** Madagascar (Antananarivo: Imerina); soil pockets on gneiss rock slopes, 1500 m. **I:** Castillon & Castillon (2010: 48–49).

[5] Differs from var. *capitata*: Stem to 15 cm; **L** 35  $\times$  3–4 cm; **Inf** to 70 cm, with 1 **Br**; **Bra** 8–10  $\times$  3–6 mm; **Fl** yellow, 30–35 mm; **Sty** exerted 10–12 mm.

**A. capitata** var. **capitata** — **Distr:** Madagascar (Antananarivo: C Madagascan highlands); rock crevices and soil pockets on granite and gneiss mountains, 1200–1600 m. **I:** Reynolds (1966: 466–467); Glen & Hardy (1988a); Castillon & Castillon (2010: 42–47); Carter & al. (2011: 337). — Fig. 14.

**Incl.** *Aloe cernua* Todaro (1890).

[5] Acaulescent, or caulescent in shady places, usually simple; stem to 60 cm; **L** 20–30, densely rosulate, triangular-attenuate, 50  $\times$  6 cm, green tinged reddish, with brownish-red horny margin, tip slightly twisted, obtuse and shortly dentate, exudate drying yellow, **marginal teeth** 2 mm, pungent, reddish, 8–12 mm apart; **Inf**  $\pm 80$  cm, with 3–4 **Br**; racemes densely capitate, 3–4  $\times$  9–10 cm; **Bra** ovate-acute, 6  $\times$  4 mm; **Ped** 10 mm (lowest) to 25–30 mm (upper); **Fl** orange-yellow, 25 mm, narrowly campanulate, base rounded, 6 mm  $\varnothing$  across the ovary, enlarging to 10 mm at the mouth; **OTep** free to the base but cohering for 24–25 mm; **St** and **Sty** exerted 8–10 mm. — **Cytology:**  $2n = 14$  (Satô 1937: as *A. capitata* var. *typica*).

A natural hybrid with *A. macroclada* has been reported (Bossler 1968: 510).

**A. capitata** var. **quartziticola** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 38, ills., 1926). **Type:** Madagascar, Fianarantsoa



**Fig. 14** *Aloe capitata* var. *capitata*. (Copyright: U. Eggli)

(*Perrier* 11001 [P]). — **Distr:** Madagascar (Fianarantsoa: Ibity and Itremo Mts.); quartzite (mostly) or basalt outcrops, 700–1560 m. **I:** Reynolds (1966: 470–473); Castillon & Castillon (2010: 64–65); Carter & al. (2011: 338).

[5] Differs from var. *capitata*: **L** thick and fleshy, 30–40  $\times$  9–12 cm, glaucous to bluish-grey, **marginal teeth** 3–4 mm, 10–20 mm apart; **Inf** 1 m; racemes 10–12 cm, subdense with more flowers; **Bra** narrowly deltoid, 7–10  $\times$  3–4 mm; lower **Ped** 15–20 mm, uppermost 40–50 mm.

A natural hybrid with *A. macroclada* has been reported (Reynolds 1966).

**A. capitata** var. **silvicola** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 39, 1926). **Type:** Madagascar, Mahajanga (*Perrier* 11012 [P]). — **Distr:** NW Madagascar (Mahajanga); forest, epiphyte on tree trunks, or on very shaded rocks, 1000–1200 m. **I:** Castillon & Castillon (2010: 342–343).

[5] Differs from var. *capitata*: Stem short, lying on tree trunks or rocks; **L** 50–60  $\times$  3–4 cm,

**marginal teeth** very small, sometimes absent; **Bra** 7 × 6 mm, tip rounded; lower **Ped** 8 mm, uppermost to 40 mm; **Fl** 20 mm.

**A. capmanambatoensis** Rauh & Gerold (Kakt. and. Sukk. 51(11): 293–294, ill., 2000). **Type:** Madagascar, Antsiranana (*Rauh & Gerold* 73669a [HEID]). — **Distr:** NE Madagascar (Antsiranana: N of Iharana); on granite near the coast, 50 m; known only from the type locality. **I:** Carter & al. (2011: 411).

[6] Acaulescent or shortly caulescent; **Ros** to 40 cm Ø, 10 cm tall, suckering to form groups; **L** ±10, densely rosulate, long-attenuate, 20–25 × 4 cm, upper face dark reddish-green with longitudinal whitish flecks, lower face grey-green with less distinct flecks, **marginal teeth** small, broadly triangular, continuous; **Inf** to 1.2 m, simple or with short **Br**; racemes cylindrical, to 40 cm, lax, with ±20 flowers; **Bra** narrowly lanceolate-attenuate, shorter than the pedicels; **Ped** to 45 mm; **Fl** cinnabar-red, lobes white with wide green veins, 25–40 mm, 7 mm Ø, not narrowed above the ovary; **OTep** free for 15–30 mm; **St** and **Sty** not exerted.

Included in *A. fragilis* by Castillon & Castillon (2010), but much larger and with spotted leaves (Carter & al. 2011: 411).

**A. carnea** S. Carter (Kew Bull. 51(4): 784–785, 1996). **Type:** Zimbabwe, Eastern Prov. (*Leach & Wild* 11135 [K, LISC, PRE, SRGH]). — **Distr:** Zimbabwe (E highlands to border with Moçambique); usually rocky ground, in grass and light *Brachystegia* woodland, 900–1375 m. **I:** Carter & al. (2011: 174).

[5] Acaulescent or caulescent, simple or in small groups; stem to ±20 cm, with dead leaf remains; **L** densely rosulate, ovate-lanceolate, to ±30 × 6–10 cm, apical 10 cm soon drying, upper face glossy dark greyish-green with conspicuous elongated whitish spots, often in transverse bands towards the base, lower face pale milky green without spots, ± lineate esp. near the margin, with horny, often reddish-brown margin, surface smooth, exudate drying yellow, **marginal teeth** ±6 mm, pungent, dark red-brown, 8–12 mm apart; **Inf** 75–200 cm, with 6–12 (–15) **Br**, the lowest sometimes rebranched; racemes capitate,

3–5 × ±7 cm, dense, more lax at the base; **Bra** linear-lanceolate, 8–12 × 2.5 mm; **Ped** 18–28 mm; **Fl** dull pale coral-pink (flesh-coloured) with whitish segment margins to the base, 25–30 mm, 6–7 mm Ø across the ovary, abruptly narrowed above the ovary, then enlarging to the mouth; **OTep** free for up to 10 mm; **St** and **Sty** exerted ±2 mm.

**A. carolineae** L. E. Newton (Brit. Cact. Succ. J. 20(4): 205, ill., 2002). **Type:** Kenya, North-Eastern Prov. (*Newton & al.* 5764 [EA]). — **Distr:** Kenya (North-Eastern Prov.: Manderu Distr.: Lugh Burborgebiss gorge); rocky ledges, 460 m. **I:** Carter & al. (2011: 487).

[13] Caulescent, branching to form dense clumps; stem to 100 cm, sprawling or pendulous; **L** laxly rosulate, persistent to 15 cm below the shoot apex, lanceolate, 22 × 3.5 cm, light green with numerous elongated whitish spots in irregular transverse bands, surface smooth, exudate yellow, drying brownish, **marginal teeth** 1 mm, white, 3–6 mm apart; **Inf** 55 cm, spreading almost horizontally, with 4–7 **Br**; racemes cylindrical with secund flowers, 19 cm, lax; **Bra** triangular, 3 mm; **Ped** 5 mm; **Fl** scarlet with yellow margins on the lobes, 27 mm, 7 mm Ø across the ovary, 5 mm Ø above, widening to 6 mm at the mouth; **OTep** free for 10.5–12 mm; **St** and **Sty** exerted 3–5 mm.

**A. castanea** Schönland (Rec. Albany Mus. 2: 138, 1907). **Type:** RSA, Mpumalanga (*Burtt-Davy* 2856 [GRA]). — **Distr:** RSA (E Gauteng, NW Mpumalanga, S Limpopo), Swaziland; woodland and bushland slopes, often in open flat country, 1000–2000 m. **I:** Reynolds (1950: 439, t. 44); Carter & al. (2011: 674); Wyk & Smith (2014: 88–89). – Fig. 15.

[16] Caulescent, branching near the base, sometimes rebranched with 10–20 crowns; stem 3–4 m; **L** densely rosulate, attenuate, 100 × 10 cm, glaucous, with thin pale brownish-red margin, **marginal teeth** 1.5 mm, uncinat, 8–10 mm apart; **Inf** 1.5–2 m, usually oblique, simple; raceme narrowly cylindrical, slightly acuminate, 70–100 cm, dense; **Bra** ovate-acute, 12 × 8 mm; **Ped** 3 mm; **Fl** reddish-brown, campanulate, 18 mm, base rounded, 6 mm Ø across the ovary, enlarging to





**Fig. 15** *Aloe castanea*. (Copyright: G. F. Smith)

15 mm at the tip; **OTep** free to the base or almost so, nectar dark brown; **St** and **Sty** exerted 12–15 mm. — **Cytology**:  $2n = 14$  (Müller 1945).

Natural hybrids with other species have been reported (Reynolds 1950).

**A. castellorum** J. R. I. Wood (Kew Bull. 38 (1): 25–26, t. 2, 1983). **Type**: Yemen (Wood 2504 [K]). — **Lit**: McCoy & Lavranos (2010). **Distr**: SE Saudi Arabia, NW Yemen; exposed W-facing slopes with high incidence of mist, 1400–2400 m. **I**: Collenette (1999: 20, 22 (as *A. hijazensis*); Carter & al. (2011: 250).

**Incl.** *Aloe hijazensis* Lavranos & Collenette (2000).

[2] Acaulescent, simple; **L** rosulate, ensiform, acuminate,  $30 \times 3.5$  cm, yellow-green, **marginal teeth** small, pale brown,  $\pm 6$  mm apart; **Inf** 1–1.5 m, with up to 3 **Br**; racemes cylindrical, subdense; **Bra** ovate-cuspidate,  $\pm 10 \times 6$  mm; **Ped**  $\pm 5$  mm; **Fl** yellow with green veins,  $\pm 25$  mm, not narrowed above the ovary; **St** and **Sty** scarcely exerted. — **Cytology**:  $2n = 14$  (protologue).

In the protologue of *A. castellorum*, the inflorescence is described as ‘branched’, but the photograph shows a simple inflorescence. For the synonymous *A. hijazensis*, inflorescences with up to 3 branches are described.

**A. castilloniae** J.-B. Castillon (Succulentas 2006(3): 21–24, ills., 2006). **Type**: Madagascar, Toliara (Castillon 24 [HBG, P]). — **Distr**: SW Madagascar (Toliara: Mahafaly Plateau); limestone cliffs, 100–250 m; known only from the type locality. **I**: Castillon & Castillon (2010: 276–277); Castillon (2011); Carter & al. (2011: 470).

[13] Caulescent, branching from the base, forming groups to 1 m  $\varnothing$ ; stem prostrate or pendulous, to 40 cm, usually with persistent dried leaves; **L** 30–40, triangular, strongly recurved in the dry season,  $6 \times 1.5$  cm, apex acute, with 1–3 small spines, blue-green, surface with scattered red prickles 1–2 mm, **marginal teeth** deltoid, 2 mm, red, 3–6 mm apart; **Inf** 6.5 cm, erect, simple; racemes cylindrical, with 2–9 flowers, lax; **Bra** 2 mm; **Ped** 8 mm; **Fl** orange-red, 23 mm, 6 mm  $\varnothing$  across the ovary, constricted to 4 mm above, widening to 8 mm at the mouth; **OTep** free to shortly united above the base; **St** and **Sty** exerted 1–3 mm.

**A. cataractarum** T. A. McCoy & Lavranos (Aloe 44(1): 53, ills., 2007). **Type**: Tanzania, Mbeya Prov. (McCoy 1923 [FT]). — **Distr**: SW Tanzania (Mbeya Prov.); steep rock faces, 1200 m; known only from the type locality. **I**: Carter & al. (2011: 497).

[13] Caulescent, branching freely from the base; stem pendulous, to 50 cm; **L** 12–15, in loose apical rosettes, ensiform-falcate,  $35 \times 2.5$  cm, dark green to reddish, with a few white spots, exudate bright yellow, drying dark yellow, **marginal teeth** deltoid, 2 mm, white, 4–5 mm apart; **Inf** 40 cm, oblique, with up to 10 **Br**, lower ones often rebranched; racemes cylindrical, with secund flowers, 5 cm, dense; **Bra** lanceolate, acute, 5 mm; **Ped** 8–10 mm, red; **Fl** bright red, 20–25 mm, 7 mm  $\varnothing$  across the ovary, slightly constricted at the mouth; **OTep** free for 8 mm; **St** and **Sty** exerted 2.5–3 mm.

**A. catengiana** Reynolds (Kirkia 1: 160, 1961). **Type**: Angola, Benguela Distr. (Reynolds 9307)



[PRE, K]). — **Distr:** SW Angola (Benguela, Namibe), N Namibia (Kaokoveld); hot arid bush country, 520 m (Angola), or sandstone rock crevices among savanna vegetation, 1760–1900 m (Namibia). **I:** Reynolds (1966: 373–374); Carter & al. (2011: 634).

[16] Caulescent, branching to form thickets 1–2 m Ø or more; stem ascending, divergent or sprawling, 1.5–2 m, to 3 m when supported by bushes; **L** 16–20, scattered along the stem for 30 cm, lanceolate-attenuate, 30 × 3–5 cm, pale yellowish grey-green, with very pale green lenticular spots, more numerous in the lower ½, **marginal teeth** 3 mm, firm, reddish-brown-tipped, 8–10 mm apart, sheathing leaf base 15–20 mm, lineate; **Inf** 40 cm, with ±6 **Br**; racemes cylindrical-acuminate, laterals with subsecund flowers, to 16 × 4 cm, lax; **Bra** ovate-acute, 5 × 3 mm; **Ped** 10 mm; **Fl** dull scarlet, 28 mm, base rounded, 7 mm Ø across the ovary, very slightly narrowed above, then enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. cephalophora** Lavranos & Collette (Cact. Succ. J. (US) 72(1): 20–21, ill., 2000). **Type:** Saudi Arabia, Hijaz Prov. (Collette 4981 [K, ZSS]). — **Distr:** Saudi Arabia (Hijaz Prov.: Jabal Auf); steep rocky granite slopes, ±1400 m. **I:** Collette (1999: 21); Carter & al. (2011: 420).

[6,7] Acaulescent, suckering at the base; **L** 8–10, densely rosulate, arcuate-ascending, triangular-attenuate, 34–36 × 4–4.5 cm, olive-green, surface rough, **marginal teeth** small, white; **Inf** ±25 cm, erect, simple or with up to 2 **Br**; racemes capitate or subcapitate, dense; **Bra** ovate, 10 × 8 mm, whitish with 3–5 brown nerves; **Ped** 12–14 mm; **Fl** coral-red at the base, becoming cream-yellow with green nerves towards the apex, ±35 mm, base shortly attenuate, funnel-shaped, 5 mm Ø across the ovary, widening to 10 mm at the mouth; **OTep** free for ±20 mm; **St** and **Sty** exerted 4 mm.

**A. chabaudii** Schönland (Gard. Chron., ser. 3, 38: 102, 1905). **Type:** Zimbabwe (Brown s.n. [GRA]). — **Distr:** Botswana, Tanzania, Democratic Republic of the Congo [Zaire], Zambia,



**Fig. 16** *Aloe chabaudii* var. *chabaudii*. (Copyright: G. F. Smith)

Zimbabwe, Malawi, Moçambique, Swaziland, RSA.

**A. chabaudii** var. *chabaudii* — **Distr:** Botswana, SW Tanzania, Democratic Republic of the Congo [Zaire], Zambia, Zimbabwe, Malawi, Moçambique, E Botswana, Swaziland, RSA (Limpopo, E Mpumalanga, NE KwaZulu-Natal); on or at the base of granite outcrops, and shady wooded slopes, 0–2130 m. **I:** Reynolds (1950: 340–341, t. 27); Reynolds (1966: 103–104); Lane (2004: 15, 18, 20); Carter & al. (2011: 457–458); Klopper & al. (2012: 74); Wyk & Smith (2014: 148–149). – Fig. 16.

[7] Acaulescent or very shortly caulescent, suckering to form small to large dense groups; **L** ±20, densely rosulate, ovate-lanceolate, acuminate, to 50 × 10 cm, dull grey-green to glaucous-green, obscurely lineate, sometimes with few scattered H-shaped spots, with narrow greyish cartilaginous margin, **marginal teeth** 1–2 mm, near the base pale brownish, 5–10 mm apart,

more brownish, more uncinat, and further apart towards the leaf tip; **Inf** 60–80 (–100) cm, with 6–12 **Br**, the lowest 1–3 rebranched; racemes broadly cylindrical, slightly acuminate, 8–15 × 10 cm, sublux with 30–40 flowers; **Bra** ovate-acute or deltoid-acuminate, 3–5 mm; **Ped** lowest 20–25 mm, shorter upwards, oblique to almost horizontal; **Fl** pale brick-red, paler at the mouth, 35–40 mm, base shortly attenuate, 7 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, enlarging towards the mouth; **OTep** free for 8 mm; **St** and **Sty** exerted 2–3 mm. — **Cytology**:  $2n = 14$  (Müller 1945).

A very variable species. Natural hybrids with other species have been reported (Reynolds 1950, Reynolds 1966).

Hargreaves (2010) reports the taxon for 2 sites in Botswana, first reported in a paper by Hargreaves (1990). The same author also reports that a hybrid with *A. buchananii* was seen once in the wild.

The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984), and local use in herbal medicine has caused deaths (Drummond & al. 1975).

**A. chabaudii** var. **mlanjeana** Christian (Flow. Pl. South Afr. 18: t. 698 + text, 1938). **Type**: Malawi, Southern Prov. (Everett s.n. in Christian 274 [PRE 23025]). — **Distr**: Malawi (Mulanje Mts. and surrounding hills); steep granite slopes, in grass patches, 900–1525 m. **I**: Reynolds (1966: 106); Lane (2004: 17–18, 20); Carter & al. (2011: 458); Klopper & al. (2012: 74, 79–80, 82, incl. distribution map).

[7] Differs from var. *chabaudii*: **L** 30–40 × 9 cm, green turning brick-red in the upper part, with white horny margin, **marginal teeth** 3 mm, 10–15 mm apart; **Inf** 40–50 cm, oblique; **Ped** 18–20 mm; **Fl** coral-red, 30–32 mm, 9 mm  $\varnothing$  across the ovary; **OTep** free for 12 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

**A. chabaudii** var. **verekeri** Christian (Flow. Pl. South Afr. 18: t. 699 + text, 1938). **Type**: Zimbabwe, Manicaland (Vereker s.n. [PRE 23027]). — **Distr**: Moçambique (Manica), E Zimbabwe (Manicaland): Sabi gorge; fire-

protected habitats on rocky ground. **I**: Reynolds (1966: 107).

[7] Differs from var. *chabaudii*: **L** olive-green turning reddish in the upper ½ in the dry season, with white margin, **marginal teeth** 4 mm, uncinat; **Inf** subcapitate racemes, ±8 cm; **Ped** 15–17 mm; **Fl** various shades of red and yellow, 32 mm.

Carter & al. (2011) note that this variety is known only from the type locality, while Court (2000) reports the taxon also from Vila de Manica in Moçambique.

**A. challisii** Van Jaarsveld (Aloe 43(2–3): 36–37, ills., 2006). **Type**: RSA, Mpumalanga (Van Jaarsveld & Challis 19801 [PRE]). — **Distr**: RSA (N Mpumalanga); SE-facing quartzite sandstone cliffs, 1700–1800 m; known from the region of the type locality only. **I**: Carter & al. (2011: 112); Wyk & Smith (2014: 300–301).

[10] Caulescent, suckering below the ground, forming dense groups to 20 cm  $\varnothing$ ; stem short, tufted, pendulous; **L** rosulate, linear, 10–20 (–25) × 0.8–1 (–2) cm, bluish-/purplish-green, with white spots at the base, striate, apex with 5–6 teeth, **marginal teeth** 0.4–1 mm, white, 1–3 mm apart; **Inf** 14–16 cm, curving upwards, simple; racemes subcapitate, 4–4.5 cm, dense; **Bra** deltoid-acuminate, 8–9 × 4 mm; **Ped** 10–15 mm; **Fl** orange-red, yellow at the apex, 25 mm, 7 mm  $\varnothing$  across the ovary; **OTep** free to the base; **St** and **Sty** not exerted.

Craib (2007) considers *A. challisii* to be synonymous with *A. woolliana* (here treated as *A. chortolirioides* var. *woolliana*), and argues that *A. woolliana* should be accepted at species rank, though he suggests that further work is required before implementing these changes.

**A. charlotteae** J.-B. Castillon (Bradleya 24: 67–69, ills., 2006). **Type**: Madagascar, Fianarantsoa (Castillon 22 [HBG, P]). — **Distr**: Madagascar (Fianarantsoa: Andringitra Mts.); on granite rocks in forest, ±2000 m. **I**: Castillon & Castillon (2010: 154–155); Carter & al. (2011: 611).

[3] Solitary, shortly caulescent; stem 30–70 × 3–8 cm, erect or decumbent; **L** 15–40, rosulate, triangular, acuminate, 30–50 × 5–10 cm,

glaucous-green, red-tinged, **marginal teeth** 2 mm, 7–10 mm apart; **Inf** 70–110 cm, erect, with 2–5 **Br**; racemes cylindrical, 10–17 cm, dense; **Bra** triangular, 3–6 mm; **Ped** 45 mm; **Fl** yellow, 40 mm, slightly campanulate; **OTep** free almost to the base; **St** and **Sty** exerted 2 mm.

**A. cheranganiensis** S. Carter & Brandham (Cact. Succ. J. Gr. Brit. 41(1): 4–6, ill., 1979). **Type:** Kenya, Rift Valley Prov. (Brandham 1727 [K, EA]). — **Distr:** N Kenya, E Uganda; open deciduous woodland on rocky sandy plains and rocky slopes, 1220–1980 m. **I:** Carter & al. (2011: 572); Cole & Forrest (2017: 48–55).

[16] Caulescent, branching from the base; stem to 2 m × 4 cm; **L** laxly crowded at the stem tip, ovate-attenuate, to 40 × 5 cm, glaucous-green, with scattered whitish spots on young shoots, exudate yellow, **marginal teeth** 3 mm, green with brown tips, 8–13 mm apart; **Inf** 60 cm, usually with 2 **Br**; racemes cylindrical-acuminate, ±20 × 7 cm, dense; **Bra** ovate-acuminate, 5–8 × 3–4 mm; **Ped** to 10–20 mm; **Fl** bright orange, yellow at the mouth, 27–30 mm, base shortly attenuate, 7 mm Ø across the ovary, not narrowed above; **OTep** reflexed, free for 22–25 mm; **St** and **Sty** exerted 6–7 mm. — **Cytology:** 2n = 28 (Cutler & al. 1980).

**A. chlorantha** Lavranos (J. South Afr. Bot. 39 (1): 85–90, ill., 1973). **Type:** RSA, Northern Cape (Lavranos 10024 [PRE]). — **Distr:** RSA (S Northern Cape: around Fraserburg); dolerite outcrops, 1200–1500 m. **I:** Carter & al. (2011: 262); Wyk & Smith (2014: 150–151).

[4] Acaulescent or caulescent, simple or up to 10 **Ros** in groups; stem to 1.5 m, procumbent; **L** rosulate, deltoid, acute, slightly falcate, to 40 × 8 cm, bright green shading into purplish, ± striate, lower face often with white spots, with dark brown-red cartilaginous margin, **marginal teeth** 2 mm, dark brown-red, 10–30 mm apart; **Inf** to 1.6 m, simple or rarely with 1 **Br**; racemes cylindrical, to 35 cm, subdense; **Bra** ovate-deltoid, acute, fleshy, yellow-green, 12–20 × 5–8 mm; **Ped** 15–22 mm; **Fl** yellow-green, 10 mm, base attenuate, enlarged to 4 mm Ø above the ovary, narrowing to the mouth; **OTep** free to the base; **St** and **Sty** slightly exerted.

**A. chortolirioides** A. Berger (in Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 171, 1908). **Type:** RSA, Mpumalanga (Galpin 490 [K]). — **Distr:** RSA (Mpumalanga), Swaziland.

Reynolds (1950) cites *Thorncroft* s.n. (BOL) as type, and this was followed by Glen & Hardy (1987), but only *Galpin* 490 is cited in the protologue and so this is automatically the type (ICN Art. 9.1). — **Cytology:** 2n = 14 (Müller 1945).

**A. chortolirioides** var. **chortolirioides** — **Distr:** RSA (Mpumalanga, Limpopo), Swaziland; rocky ridges and slopes in grassland, 1300–2000 m. **I:** Reynolds (1950: 124–125); Craib (2006: 36–39); Carter & al. (2011: 128); Wyk & Smith (2014: 302–303); Smith & al. (2016: 56–57).

**Incl.** *Aloe boastii* Letty (1934) ≡ *Aloe chortolirioides* var. *boastii* (Letty) Reynolds (1950).

[10] Caulescent, branching to form dense tufts of up to 50 stems; **R** fusiform; stem 10–20 × 2–3 cm, usually branching about the middle; **L** 15–20, multifarious, linear, 10–25 cm × 3–5 mm, dull green, lower face sometimes with few small white spots near the base, **marginal teeth** 0.5 mm, white, cartilaginous, 2–3 mm apart; **Inf** 25 cm, simple; raceme capitate, ±5 × 5–7 cm, with 18–20 flowers; **Bra** ovate-acuminate, 10–13 mm; **Ped** 20–25 mm; **Fl** scarlet to yellow, 30–35 mm, base shortly attenuate, enlarging above the ovary; **OTep** free almost to the base; **St** and **Sty** slightly exerted.

Flowering is induced by burning of surrounding grass (Reynolds 1950). A natural hybrid with *A. arborescens* has been reported (Reynolds 1950) and was recently formally described as *A. ×inopinata* (Smith & al. 2016).

**A. chortolirioides** var. **woolliana** (Pole-Evans) Glen & D. S. Hardy (South Afr. J. Bot. 53(6): 489–490, 1987). **Type:** RSA, Mpumalanga (Pole-Evans s.n. [PRE 8320]). — **Distr:** RSA (Mpumalanga, Limpopo), Swaziland; grassy cliff-faces, 1100–2000 m. **I:** Reynolds (1950: 128, as *A. woolliana*); Craib (2006: 123–126); Carter & al. (2011: 128).

≡ *Aloe woolliana* Pole-Evans (1934).

[10] Differs from var. *chortolirioides*: Stem 15–25 cm; **L** 37 cm × 5–8 mm; **Inf** to 45 cm; **Fl** Jasper-red or rose-pink, sometimes yellowish at the mouth, 30–40 mm.

Craib (2006) suggests that this variety is (in contrast to the typical variety) not dependent on fire for flowering and establishment, but fires do enhance flower production. Craib (2007) argues that *A. woolliana* should be accepted at species rank, though he suggests that further work is required before implementing the change.

**A. christianii** Reynolds (J. South Afr. Bot. 2 (4): 171–173, ills., 1936). **Type:** Zimbabwe (Reynolds 1885 [PRE, K, SAM, SRGH]). — **Distr:** E Angola (Moxico), Botswana, Malawi, NW Moçambique, E Tanzania, S & E Democratic Republic of the Congo [Zaire], Zambia, N Zimbabwe; in partial shade in woodland or tall grass subject to annual burning, 300–2000 m. **I:** Reynolds (1950: 309–311); Reynolds (1966: 187–188); Lane (2004: 29, 32, 39); Carter & al. (2011: 624); Klopper & al. (2012: 75, 82, incl. distribution map).

[8] Caulescent, simple or in small groups; stem erect or procumbent, to 150 × 10–15 cm, with dead leaf remains; **L** 30–40, densely rosulate, lanceolate-attenuate, 30–75 × 10–15 cm, upper face dull green, obscurely lineate, lower face dull bluish-green, very obscurely lineate, **marginal teeth** 3–5 mm, pungent, sometimes slightly uncinatate, pinkish to pale brown, 10–20 mm apart; **Inf** 2–3 m, with 5–10 **Br**, lower ones sometimes rebranched; racemes cylindrical-acuminate, 25–30 cm, subdense with 40–50 flowers; **Bra** ovate-acute, 5–6 × 3 mm; **Ped** 8–12 mm; **Fl** coral-red with a bloom, 40–45 mm, base shortly attenuate, 9–10 mm Ø across the ovary, not narrowed above; **OTep** free for 15 mm; **St** and **Sty** exerted 4 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Confused with *A. pretoriensis* by Reynolds (1966) (Carter & al. 2011). Hybrids with *A. bulbicaulis* (in Zambia) and *A. cameranii* (in Zimbabwe) are reported by Lebrun & Stork (2012). Hargreaves (2007) records the species from Botswana, close to the border with Zimbabwe.

**A. chrysostachys** Lavranos & L. E. Newton (Cact. Succ. J. (US) 48 (6): 278–279, ills., 1976). **Type:** Kenya, Eastern Prov. (*Classen* 14 [EA, ZSS [clono]]). — **Lit:** Newton (1996). **Distr:** E Kenya; soil pockets on isolated gneissic outcrops, 900–1200 m. **I:** Carter & al. (2011: 314).

**Incl.** *Aloe meruana* Lavranos (1980).

[7] Acaulescent or with very short stem, suckering sparsely from the base forming small groups; **L** 14–18, densely rosulate, lanceolate-attenuate, ±30 × 8–10 cm, bluish-green, usually purplish in exposed situations, with reddish cartilaginous margin, surface smooth, exudate drying yellow, **marginal teeth** 4 mm, firm, uncinatate, 8–12 mm apart; **Inf** 30–40 cm, with 5–10 **Br**; racemes 6–10 cm, lax, with secund flowers; **Bra** deltoid-acute, 5–7 × 1.5 mm; **Ped** 10–12 mm; **Fl** dull red or yellow, 35 mm, base attenuate, 8 mm Ø across the ovary, narrowed to 7 mm above, enlarging to 8 mm at the mouth; **OTep** free for 11–13 mm; **St** and **Sty** exerted 5 mm. — **Cytology:** 2n = 14 (protologue).

Plants with red and yellow flowers occur in the same population, with yellow predominating. In Kenya, planted in rows on slopes to control soil erosion (Newton 2004).

**A. ciliaris** Haworth (Philos. Mag. J. 66: 281, 1825). **Type:** RSA, Eastern Cape (*Bowie* s.n. [K [Duncanson drawing]]). — **Distr:** RSA.

≡ *Aloiampelos ciliaris* (Haworth) Klopper & Gideon F. Smith (2013).

The species includes plants representing 3 levels of ploidy, recognised as varieties, the origin of which was discussed by Brandham & Carter (1990). Silva & al. (2015) report its appearance as a neophyte in Portugal and Aymerich (2016) reports it from Spain.

**A. ciliaris** var. *ciliaris* — **Distr:** RSA (Western Cape, S Eastern Cape); amongst and supported by bushes and trees, 0–600 m. **I:** Reynolds (1950: 353–354, t. 29); Carter & al. (2011: 540); Wyk & Smith (2014: 108–109).

**Incl.** *Aloe ciliaris* var. *flanaganii* Schönland (1903) ≡ *Aloe ciliaris* fa. *flanaganii* (Schönland) Resende (1943); **incl.** *Aloe ciliaris* fa. *gigas* Resende (1938).



[14] Caulescent, branching, scrambling; stem to 5 m or more, 1–1.5 cm Ø; **L** scattered along the stem for 30–60 cm, linear-lanceolate, long-acuminate, 10–15 × 1.5–2.5 cm, green, **marginal teeth** 1 mm, shorter towards the leaf tip, firm, white, 3 mm apart, leaf sheath 5–15 mm, obscurely green-lineate, upper margin opposite the lamina with a fringe of 2–4 mm long cilia; **Inf** 20–30 cm, usually simple, sometimes with 1 **Br**; racemes cylindrical, 8–15 × 4–5 cm, subdense with 24–30 flowers; **Bra** ovate-acuminate; **Ped** ±5 mm; **Fl** scarlet, yellowish-green at the mouth, 28–35 mm, slightly clavate, base very shortly attenuate, gradually enlarging above the ovary; **OTep** free for 6 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology**: 2n = 42 (hexaploid) (Müller 1945).

There is no evidence supporting reports such as Reynolds (1950) that *A. ciliaris* occurs wild in Kenya.

**A. ciliaris** var. **redacta** S. Carter (Kew Bull. 45 (4): 643, 1990). **Type**: RSA, Eastern Cape (*Wisura* 2640 [K]). — **Distr**: RSA (S Eastern Cape: Kei River region); sand dunes, 0–100 m. **I**: Carter & al. (2011: 541).

≡ *Aloiampelos ciliaris* var. *redacta* (S. Carter) Klopper & Gideon F. Smith (2013).

[14] Differs from var. *ciliaris*: **L** sheath cilia 1–2 mm; **Bra** 4–5 mm; **Ped** 12–14 mm; **Fl** 21–25 mm. — **Cytology**: 2n = 28 (tetraploid) (protologue).

Morphologically and cytologically intermediate between the other 2 varieties, but apparently not of hybrid origin.

**A. ciliaris** var. **tidmarshii** Schönland (Rec. Albany Mus. 1: 41, 1903). **Type**: RSA, Eastern Cape (*Schönland* 1587 [GRA, BOL]). — **Distr**: RSA (S Eastern Cape: Uitenhage & Grahamstown); temperate mountain slopes, 0–600 m. **I**: Reynolds (1950: 355–356, as *A. tidmarshii*); Carter & al. (2011: 541).

≡ *Aloe ciliaris* fa. *tidmarshii* (Schönland) Resende (1943) ≡ *Aloe tidmarshii* (Schönland) F. S. Müller ex R. A. Dyer (1943) ≡ *Aloiampelos ciliaris* var. *tidmarshii* (Schönland) Klopper & Gideon F. Smith (2013).

[14] Differs from var. *ciliaris*: **L** 7–10 × 1.5–2 cm, sheath cilia <1 mm; **Inf** racemes subclax; **Fl** 16–25 mm. — **Cytology**: 2n = 14 (Müller 1945).

**A. cipolinicola** (H. Perrier) J.-B. Castillon & J.-P. Castillon (Aloe Madagascar, 28, 2010). **Type**: Madagascar, Antananarivo (*Perrier* 13225 [P]). — **Distr**: Madagascar (Antananarivo); “cipolin” marble outcrops, 1250–1400 m. **I**: Reynolds (1966: 474–475, as *A. capitata* var.); Castillon & Castillon (2010: 104–105); Carter & al. (2011: 338–339, as *A. capitata* var.).

≡ *Aloe capitata* var. *cipolinicola* H. Perrier (1926).

[9] Caulescent, stem 2–4 m, simple; **L** 60–100, densely rosulate, linear-lanceolate, tip acute with 2–3 teeth, 60 × 5–6.5 cm, glossy green, sometimes tinged reddish, with red horny edge, **marginal teeth** deltoid, 3–4 mm, pink to red, 10 mm apart; **Inf** to 1 m, with 6–10 **Br**; racemes capitate, 8–12 cm Ø, very dense; **Ped** lowest 2–3 mm, uppermost to 20 mm; **Fl** golden-yellow, campanulate, to 30 mm, 4 mm Ø across the ovary; **OTep** free for 18 mm; **St** and **Sty** exerted ±10 mm. — **Cytology**: 2n = 14 (Brandham 1971).

**A. citrea** (Guillaumin) L. E. Newton & G. D. Rowley (Excelsa 17: 61, 1997). **Type**: Madagascar, Toliara (*Boiteau* 227 [P ?]). — **Distr**: S Madagascar (Toliara: Tolanaro?); not presently known from the wild. **I**: Rauh (1995: 329); Castillon & Castillon (2010: 233); Carter & al. (2011: 242).

≡ *Lomatophyllum citreum* Guillaumin (1944).

[2] Acaulescent; **L** ±16, densely rosulate, lanceolate-attenuate, often contorted towards the tips, to 28 × 2.5 cm, dark green, **marginal teeth** 3 mm, green, 1–2 mm apart; **Inf** 15 cm, simple; racemes cylindrical, 6 cm, dense, with ±20 flowers; **Bra** triangular, <5 mm; **Ped** 6–8 mm; **Fl** lemon-yellow with green midrib, 25 mm, narrowed slightly above the ovary, then enlarging slightly to the mouth; **OTep** free for ±5 mm; **St** and **Sty** slightly exerted; **Fr** yellow berries.

In cultivation, but type locality not recorded, and not found again in the wild.

**A. citrina** S. Carter & Brandham (Bradleya 1: 21–23, ill., 1983). **Type**: Somalia, Hiraan (*Bally*



& *Melville* 15287 [K]). — **Distr:** S Ethiopia (Sidamo), NE Kenya, S Somalia; sandy plains with open deciduous thorn bush, 90–200 (–990) m. **I:** Sebsebe Demissew & Nordal (2010: 56–57); Carter & al. (2011: 372).

[5] Acaulescent, simple or with a few suckers; **L** rosulate, lanceolate-attenuate, to 60 × 15 cm, glaucous with many elongated white spots, exudate drying purple, **marginal teeth** 1.5 mm, green, brown-tipped, 15–35 mm apart; **Inf** to 2 m, with 2–6 **Br**; racemes cylindrical-acuminate, 25–50 × 5 cm, ± dense; **Bra** ovate-acute, to 12 × 4 mm, pubescent; **Ped** to 10 mm, pubescent; **Fl** pale lemon-yellow, shortly tomentose, 28–35 mm, base rounded, 6 mm Ø across the ovary, slightly narrowed above, enlarging to 8 mm at the mouth; **OTep** free for 18 mm; **St** and **Sty** exerted 1 mm. — **Cytology:** 2n = 14 (protologue).

**A. clarkei** L. E. Newton (Haseltonia 9: 15–16, ill., 2003). **Type:** Ethiopia, Kefa Region (*Clarke* s.n. in *Newton* 5676 [EA]). — **Distr:** SW Ethiopia (Kefa Region: Naita Mt.); light shade in openings in montane forest, 1980 m; known from the type collection only. **I:** Carter & al. (2011: 480).

[12] Caulescent, freely branching at the base to form a dense clump; stem to 30 cm, erect at first, later leaning over; **L** laxly rosulate, persistent below the shoot apex, 1–1.5 cm apart, lanceolate, 18 × 3 cm, green with scattered elongated whitish spots, surface smooth, exudate yellow, **marginal teeth** 3 mm, green, white-tipped, 6–9 mm apart; **Inf** 52 cm, erect, with 2–5 **Br** arching upwards; racemes cylindrical, terminal 10 cm, laterals 4–7 cm, lax; **Bra** ovate-attenuate, 6 × 3 mm; **Ped** 15 mm; **Fl** red or yellow, 25–26 mm, base shortly attenuate, 6 mm Ø across the ovary; **OTep** free for 10–12 mm; **St** and **Sty** exerted 2–5 mm.

Found on top of Naita, a mountain that straddles the Ethiopia/South Sudan border. Red- and yellow-flowered plants occur in the same population.

**A. classenii** Reynolds (J. South Afr. Bot. 31 (4): 271–273, ill., 1965). **Type:** Kenya, Coast Prov. (*Classen* 128 in *Reynolds* 10117 [PRE, EA, K]). — **Distr:** SE Kenya (Coast Prov.: Taita

Distr.); soil pockets on gneissic outcrops in deciduous bushland, ±600 m; known from the area of the type locality only. **I:** Reynolds (1966: 255–256); Carter & al. (2011: 446).

[7] Acaulescent or with short stem to 50 cm, suckering from the base forming dense groups; **L** ±24, densely rosulate, lanceolate, tip with a spine, 35–40 × 7–8 cm, dark olive-green, becoming reddish in exposed situations, lower face sometimes with few elongated pale spots near the base, surface smooth, exudate drying yellow, **marginal teeth** 5 mm, pungent, pale brownish, 10–15 mm apart; **Inf** ±60 cm, with ±10 **Br**, lower ones rebranched; racemes cylindrical-acuminate, ±7 × 4 cm, lax; **Bra** ovate-acute, 3 mm; **Ped** 8–10 mm; **Fl** dark wine-red with powdery bloom, 20–25 mm, base rounded, 7 mm Ø across the ovary, not narrowed above; **OTep** free for 10 mm; **St** and **Sty** exerted 3–4 mm.

**A. claviflora** Burchell (Trav. South. Afr. 1: 272, 1822). **Type:** RSA, Northern Cape (*Burchell* s.n. [not located]). — **Lit:** Arena (2018: ecology). **Distr:** S Namibia, RSA (Northern Cape, NE Western Cape, NW Eastern Cape, W Free State, North-West Prov.); well-drained flat stony ground or rocky slopes, 300–1300 m. **I:** Reynolds (1950: 320–321); Carter & al. (2011: 408); Wyk & Smith (2014: 90–91). — Fig. 17.

**Incl.** *Aloe schlechteri* Schönland (1903); **incl.** *Aloe decora* Schönland (1905).

[6,7] Acaulescent or with decumbent stems, usually forming hollow circular groups 1–2 m Ø; stem 10–20 cm; **Ros** decumbent; **L** 30–40, densely rosulate, ovate-lanceolate, ±20 × 6–8 cm, glaucous, lower face 1- to 2-carinate in the upper 1/3, the keel with 4–6 brownish prickles, 2–4 mm, **marginal teeth** 2–4 mm, pungent, brownish, ±10 mm apart; **Inf** to 50 cm, oblique, almost horizontal, simple or with 1–4 **Br**; racemes cylindrical-acuminate, 20–30 cm, dense; **Bra** ovate-acute, reflexed, ±15 × 6–8 mm; **Ped** 7–10 mm; **Fl** red with a bloom, green-tipped, paler and turning lemon-yellow to ivory after pollination, 30–40 mm, base long-attenuate, enlarging above the ovary to 10 mm Ø; **OTep** free for 1/4–1/2 of their length; **St** and **Sty** exerted 10–15 mm. — **Cytology:** 2n = 14 (Riley 1959: 241).



**Fig. 17** *Aloe claviflora*. (Copyright: D. J. Supthut)

Natural hybrids with other species have been reported (Reynolds 1950). Arena (2018) reports the Round-eared Elephant Shrew (*Macroscelides proboscideus*) as nocturnal flower visitor.

**A. collenetteae** Lavranos (Cact. Succ. J. (US) 67(1): 32–33, ills., 1995). **Type:** Oman, Dhofar (*Collenette* 8945 [E]). — **Distr:** Oman (Dhofar); limestone cliffs and rocky grassy hillsides,  $\pm 800$  m; known only from the region of the type locality. **I:** Carter & al. (2011: 496).

[11] Caulescent, suckering from the base; stem to 20 cm; **L** 5–8, rosulate, triangular-acute,  $30\text{--}32 \times 3$  cm, bright green, sometimes with a few pale spots, **marginal teeth** 0.5 mm, cartilaginous, white, 10 mm apart, obsolete in the upper  $\frac{1}{3}$ ; **Inf**  $\pm 20$  cm, usually with 2 **Br**; racemes to 7 cm, lax, with up to 22 flowers; **Bra** deltoid-acute, 2–4 mm; **Ped** 5–6 mm; **Fl** bright orange-red with green veins,  $\pm 20$  mm, base rounded, 4 mm  $\varnothing$  across the ovary, not narrowed above, narrowing slightly

at the mouth; **OTep** free for  $\pm 7$  mm; **St** and **Sty** exerted 1–3 mm.

**A. collina** S. Carter (Kew Bull. 51(4): 781–782, 1996). **Type:** Zimbabwe, Eastern Prov. (*Leach* 269 [K, B, LISC, SRGH]). — **Distr:** E Zimbabwe (Nyanga Distr.: Nyanga Downs); rocky hillsides, often in the shelter of bushes, 1980–2200 m; known only from the type locality. **I:** Reynolds (1966: 88–89, as *A. saponaria*); Carter & al. (2011: 168).

[3] Acaulescent, simple; **L** densely rosulate, ovate-lanceolate, to  $\pm 25 \times 7\text{--}11$  cm plus apical portion soon drying, upper face dark green with conspicuous elongated whitish spots in transverse bands, lower face pale green usually without spots, exudate drying purplish-brown, **marginal teeth**  $\pm 6$  mm, pungent, reddish-brown, 1–1.5 mm apart; **Inf** to 75 cm, with 3–7 **Br**, lowest ones sometimes rebranched; racemes capitate-corymbose,  $3\text{--}4 \times \pm 10\text{--}12$  cm, very dense; **Bra** lanceolate-acuminate,  $15\text{--}20 \times 4\text{--}6$  mm; **Ped** 30–40 mm; **Fl** bright orange-red, 35–40 mm,  $\pm 9$  mm  $\varnothing$  across the ovary, abruptly narrowed above the ovary, then enlarging slightly to the mouth; **OTep** free for 27–30 mm; **St** and **Sty** exerted  $\pm 2$  mm.

This is included in *A. saponaria* in the sense of Reynolds (1966).

**A. commixta** A. Berger (in Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 260–261, ills., 1908). **Type:** RSA, Western Cape (*Wright* s.n. [K]). — **Distr:** RSA (SW Western Cape: Cape Peninsula); between rocks and low shrubs, 0–200 m. **I:** Reynolds (1950: 360–361); Carter & al. (2011: 548); Wyk & Smith (2014: 110–111).

$\equiv$  *Aloiampelos commixta* (A. Berger) Klopper & Gideon F. Smith (2013)  $\equiv$  *Aloe gracilis* Baker (1880) (*nom. illeg.*, ICN Art. 53.1). **incl.** *Aloe perfoliata* var.  $\alpha$  Linné (1753).

[15] Caulescent, branching to form dense shrubs; stem suberect to erect,  $\pm 100 \times 2\text{--}2.5$  cm; **L** scattered along the stem for  $\pm 30$  cm, lanceolate-acuminate, to  $20 \times 3$  cm, dull green, **marginal teeth** 1–2 mm, firm, white, 2–4 mm apart, leaf sheath green-striatulate; **Inf** 30–35 cm, simple; raceme subcapitate, 5–7 cm, dense;

**Bra** ovate-deltoid, acuminate; **Ped**  $\pm 6$  mm; **Fl** yellowish to orange, to 40 mm, base shortly attenuate, not narrowed above the ovary; **OTep** free for 20 mm almost to the base. — **Cytology**:  $2n = 14$  (Snoad 1951).

**A.**  $\times$  **commutata** Todaro *pro sp.* (Hort. Bot. Panorm. 1: 75, t. 18, 1878). **Type**: [icono] l.c. t. 18. — **Lit**: Figueiredo & Smith (2012: with ills.). **Distr**: RSA.

**Incl.** *Aloe tricolor* Baker (1877) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe commutata* var. *tricolor* A. Berger (1908).

Probably *A. maculata*  $\times$  *A. grandidentata* (Reynolds 1950, Figueiredo & Smith 2012). A plant seen in cultivation in California seems to match the description (which is very incomplete and lacks measurements almost completely) according to Figueiredo & Smith (2012).

**A. comosa** Marloth & A. Berger (Bot. Jahrb. Syst. 38: 86, 1905). **Type**: RSA, Western Cape (Marloth 3787 [BOL, GRA, PRE]). — **Distr**: RSA (SW Northern Cape, Western Cape); slopes of hills and valleys, 300–600 m. **I**: Reynolds (1950: 387–388); Carter & al. (2011: 656); Wyk & Smith (2014: 58–59).

[8] Caulescent, simple; stem to 2 m, with dead leaf remains persistent; **L** densely rosulate, lanceolate-ensiform, to  $65 \times 12$  cm, upper face glaucous to somewhat brownish-pinkish, obscurely lineate, lower face bluish-green, with pinkish margin, **marginal teeth** 1–2 mm, brownish-red, 5–10 mm apart; **Inf** to 2.5 m or more, usually simple, sometimes with 1 **Br**; raceme narrowly cylindrical,  $100 \times 8$  cm, dense; **Bra** lanceolate, long-acuminate, 40 mm, imbricate in bud stage and tufted at the tip of the raceme; **Ped** 20 mm, almost erect, at anthesis with the base remaining appressed to the axis and the upper  $\frac{1}{3}$  markedly decurved; **Fl** usually rosy-cream to pinkish-ivory, sometimes deep pink with a bloom, 35 mm, ventricose, base very shortly attenuate, enlarging above the ovary to 12 mm  $\varnothing$  in the middle, narrowing to the mouth; **OTep** free for  $\pm 23$  mm; **St** and **Sty** exerted 10–12 mm. — **Cytology**:  $2n = 14$  (Riley 1959).

**A. compressa** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 33, 1926). **Type**: Madagascar, Antananarivo (Perrier 12556 [P]). — **Lit**: Du Puy (2004b: t. 506, 233–237, with ills.) Lüthy (2006: 31–32, conservation, with ills.). **Distr**: C Madagascar.

**A. compressa** var. **compressa** — **Distr**: C Madagascar (Antananarivo: Mt. Ibity, Itremo Massif, Mania River); quartzite rock crevices, gullies, or gravel, 1000–1500 m. **I**: Reynolds (1966: 425–425); Castillon & Castillon (2010: 72–73); Carter & al. (2011: 226).

[2] Acaulescent or shortly caulescent, simple; **L** 15–20, distichous, triangular, tip rounded,  $12\text{--}15 \times 5$  cm, glaucous, surface smooth, **marginal teeth** 2 mm, flattened, green- or red-tipped, 4–5 mm apart; **Inf** 60–70 cm, simple, rarely with 1 **Br**; raceme almost ovate,  $7\text{--}8 \times 6$  cm, dense, with 40–60 flowers; lower **Bra** long-acute, upper obtuse and emarginate,  $20\text{--}24 \times 10\text{--}17$  mm, white with 3 brown veins; **Ped** 1–2 mm; **Fl** white, with red midstripe in the upper  $\frac{1}{2}$ , 25–33 mm; **OTep** free to the base, connivent in the lower  $\frac{1}{2}$ , recurved in the upper  $\frac{1}{2}$ ; **St** and **Sty** not exerted.

**A. compressa** var. **paucituberculata** Lavranos (Kakt. and. Sukk. 49(7): 158–159, ills., 1998). **Type**: Madagascar, Antananarivo (Rössli & Hoffmann 7/95 [P, MO, TAN]). — **Distr**: C Madagascar (Antananarivo: Ibity Massif: Antsirabe Region); quartzite mountain, 1725–1950 m; known only from the type locality. **I**: Castillon & Castillon (2010: 75); Carter & al. (2011: 227).

[2] Differs from var. *compressa*: **L**  $9 \times 4$  cm, sparsely tuberculate.

**A. compressa** var. **schistophila** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 34, 1926). **Type**: Madagascar, Fianarantsoa (Perrier 11005 [P]). — **Distr**: Madagascar (Fianarantsoa: Itremo Range); quartzite schistose rocks,  $\pm 1400$  m. **I**: Reynolds (1966: 427–428); Castillon & Castillon (2010: 122); Carter & al. (2011: 227).

[2] Differs from var. *compressa*: **L** more numerous, more compressed,  $12 \times 2\text{--}2.5$  cm,

**marginal teeth** almost confluent; **Inf** with racemes 4 cm; **Fl** reddish, 22 mm.

**A. condyae** Van Jaarsveld & P. Nel (Bradleya 30: 169, ill. (pp. 168, 170), 2012). **Type:** RSA, Mpumalanga (*Van Jaarsveld & Nel* 24252 [PRE]). — **Distr:** RSA (E Mpumalanga: S of Barberton); rock crevices on quartzitic sandstone cliffs, 1700–1800 m. **I:** Wyk & Smith (2014: 304–305).

[1] Caulescent, solitary or with subterranean suckers, forming small groups; stem ascending or spreading; **L** 8–14, rosulate, linear-lanceolate, apex acuminate, 20–30 × 1–1.5 (–2) cm, green, densely white-spotted, **marginal teeth** triangular, 0.7 mm, 1–3 mm apart; **Inf** 22–29 cm, decumbent, simple; racemes capitate, 4–6 cm, dense; **Bra** deltoid, acuminate, 15 × 5 mm; **Ped** 20–25 mm; **Fl** orange-red, 30 mm, tubular; **OTep** free to the base; **St** and **Sty** not exerted.

**A. confusa** Engler (Pfl.-welt Ost-Afr., Teil C, 141, 1895). **Type:** Tanzania, Moshi Distr. (*Volkens* 410 [B?, BM]). — **Distr:** S Kenya, N Tanzania: around the base of Mt. Kilimanjaro; rocky slopes and cliff faces in riverine forest and dense bushland, 885–1000 m. **I:** Reynolds (1966: 166–167); Carter & al. (2011: 494).

[13] Caulescent, branching mostly at the base to form dense tangled masses to 4 m Ø; stem decumbent or pendulous, to 1 m, 1.8 cm Ø; **L** scattered along the stem for 20–30 cm, lanceolate-attenuate, mostly falcate, to 30 × 3–4 cm, grey-green, lower face usually with a few small white spots near the base, surface smooth, with narrow white cartilaginous margin, exudate yellow, rapidly turning deep purple in air, **marginal teeth** 1–2 mm, firm, whitish, ±10–15 mm apart, leaf sheath ±15 mm, usually green-striate, sometimes spotted; **Inf** ±45 cm, oblique with racemes erect, simple or with 2–3 **Br**; racemes cylindrical-acuminate, 10–20 × 7 cm, subdense, with ±25 flowers; **Bra** deltoid-acuminate, 4–7 × 2–3 mm; **Ped** 12–15 mm; **Fl** yellow, sometimes red, ±25–30 mm, base shortly attenuate, ±6 mm Ø across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 11 mm; **St**

and **Sty** exerted 3–4 mm. — **Cytology:** 2n = 14 (Müller 1945).

**A. congdonii** S. Carter (Fl. Trop. East Afr., Aloaceae, 18, 20, ill. (p. 10), 1994). **Type:** Tanzania, Iringa Distr. (*Congdon* 281 [K, EA, NHT, SRGH]). — **Distr:** S Tanzania; rock outcrops, 1500–2375 m. **I:** Carter & al. (2011: 412).

[6] Acaulescent, suckering to form large groups; **L** ±8–10, densely rosulate, ovate-lanceolate, 15–25 × 3–5 cm, greyish-green tinged red, with many elongated whitish spots, **marginal teeth** 1–2 mm, pale, minutely brown-tipped, 5–8 mm apart; **Inf** 20–30 (–50) cm, simple or occasionally with 1–2 **Br**; racemes subcapitate to cylindrical, 5–10 cm, ± dense; **Bra** ovate-acuminate, 6–8 × 3–3.5 mm; **Ped** 18–22 mm; **Fl** orange-pink, 32–38 mm, base rounded, 8 mm Ø across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for ±10–13 mm; **St** and **Sty** slightly exerted.

**A. conifera** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 47, 1926). **Type:** Madagascar, Fianarantsoa (*Perrier* 13123 [P]). — **Distr:** Madagascar (Fianarantsoa).

**A. conifera** ssp. **conifera** — **Distr:** Madagascar (Fianarantsoa); soil pockets on eroded granite; 1300–1500 (–2000) m. **I:** Reynolds (1966: 478–479); Castillon & Castillon (2010: 132–137); Carter & al. (2011: 230).

[2] Acaulescent or with short stem to 10 cm, simple; **L** 20–24, densely rosulate, lanceolate-attenuate, upper surface often with teeth, tip rounded with few short teeth, 16 × 4–4.5 cm, bluish-grey tinged reddish, **marginal teeth** 2–3 mm, pungent, reddish, 5–10 mm apart; **Inf** 50 cm, usually simple, rarely with 1–2 **Br**; racemes cylindrical, 10–15 (–20) × 3.5 cm, very dense, young raceme at first conical with densely imbricate bracts, resembling a narrow pine-cone; **Bra** obovate-cuspidate, 12 mm; **Ped** none; **Fl** lower ½ lemon, yellow near the mouth, 14 mm, slightly campanulate-clavate, base rounded, 4 mm Ø across the ovary, enlarging above; **OTep** free to the base; **St** and **Sty** exerted 3 mm.



**A. conifera** ssp. **pervagata** J.-B. Castillon (CactusWorld 31(1): 45–46, ills., 2013). **Type:** Madagascar, Fianarantsoa (*Reynolds* 7692 [P]). — **Distr:** Madagascar (Fianarantsoa); granite hill.

[2] Differs from ssp. *conifera*: **L** distichous on young plants, 18–20 × 3–6 cm, green-red, upper surface without teeth.

**A. cooperi** Baker (Gard. Chron., ser. nov. 1: 628, 1874). **Type:** RSA, KwaZulu-Natal (*Cooper* 1193/3263 [K]). — **Lit:** Craib (2006: 39–43). **Distr:** RSA (KwaZulu-Natal, Free State, Mpumalanga, SW Limpopo), Lesotho, Swaziland, S Moçambique; grassland, sometimes marshy, and rocky slopes, 0–1980 m. **I:** Carter & al. (2011: 148).

**Incl.** *Aloe schmidtiana* Regel (1879).

[4] Acaulescent or shortly caulescent, usually simple, sometimes suckering to form small groups; stem to 15 cm; **L** 16–20, distichous, sometimes spirally twisted to rosulate with age, triangular, plicate-carinate and V-shaped in cross section, 60–80 × 5–6 cm, upper face green, sometimes with few scattered spots near the base, obscurely lineate, lower face with many white spots near the base, with narrow white cartilaginous margin, **marginal teeth** 1–2 mm, firm, white, 1–2 mm apart; **Inf** to 1 m or more, simple; raceme broadly conical, to 20 × 10–14 cm, subdense, with ±40 flowers; **Bra** ovate-acuminate, 20–32 mm; **Ped** 40–45 mm; **Fl** salmon-pink with green tips, 38–40 mm, base attenuate, 12 mm Ø across the ovary, narrowing to ±9 mm near the mouth; **Tep** free almost to the base; **St** exerted 0–1 mm. — **Cytology:** 2n = 14 (Kondo & Megata 1943).

**A. corallina** I. Verdoorn (Flow. Pl. Afr. 45: t. 1788 + text, 1979). **Type:** Namibia, Kaokoland (*Leistner & al.* 179 [PRE]). — **Distr:** N Namibia (Kaokoland), adjacent S Angola: banks of the Kunene River; vertical dolomite cliff faces, 600–1200 m. **I:** Carter & al. (2011: 513).

[5] Caulescent, usually simple; stem 0.5 cm Ø; **L** densely rosulate, lanceolate-acuminate, ±50 × 11 cm, grey-green with light bloom, upper face obscurely lineate, **marginal teeth** on

young leaves minute, red-brown, on mature leaves absent; **Inf** with 2–3 **Br**; racemes cylindrical, 17–28 cm, subdense; **Bra** oblong-acute, 10–15 mm; **Ped** 10–17 mm; **Fl** coral-red, ±30 mm, base shortly attenuate, enlarged above the ovary to the middle, then narrowing to the mouth; **OTep** free for 20 mm; **St** and **Sty** exerted 5 mm.

In the protologue the length of the stem is not given, but the habit drawing suggests that it is quite short.

**A. × corderoyi** A. Berger (Monatsschr. Kakt.-kunde 14: 61, 1904). **Type** [neo]: Ex cult. (*Anonymous* s.n. [HMGBH]). — **Lit:** Smith & al. (2018). **Distr:** Cultivated only.

≡ ×*Kumalista corderoyi* (A. Berger) G. D. Rowley (2014) ≡ ×*Gonimara corderoyi* (A. Berger) Gideon F. Smith & Moltano (2018).

[15] Stem ±10 cm, dichotomously branched; **L** spirally arranged, narrow, ensiform, bow-like curved to patent, 3 × 0.7 cm, bluish-green, margin cartilaginous, untoothed; **Inf** ±30 cm; racemes cylindrical, lax; **Ped** 10–15 mm; **Fl** pinkish-red, ±40 mm; **St** hardly exerted.

= *A. variegata* × *A. plicatilis* (Smith & al. 2018).

**A. craibii** Gideon F. Smith (Bradleya 21: 26–28, ills., 2003). **Type:** RSA, Mpumalanga (*Condy & Craib* 148 [PRE]). — **Lit:** Smith & Craib (2005); Craib (2006: 44–46, with ills.). **Distr:** RSA (Mpumalanga: SE of Barberton); short grassland on rocky slopes in the mist-belt, 1500–1800 m; known only from the type locality. **I:** Carter & al. (2011: 127); Wyk & Smith (2014: 308–309).

[10] Caulescent, forming clumps; stem erect to decumbent, to 16 cm; **L** 6–20, distichous, rarely rosulate, linear, 21–30 × 1–2.5 cm, light yellowish-green, rarely with few scattered white spots near the base, exudate colourless, **marginal teeth** 1.5 mm, whitish, 1–2 mm apart; **Inf** 23–30 cm, erect, simple; racemes capitate, 4–10 × 5–6 cm, dense; **Bra** 12–35 mm; **Ped** 12–20 mm; **Fl** yellow, 15–18 mm, base slightly stipitate, 5 mm Ø across the ovary, widening slightly to the



mouth; **OTep** free almost to the base; **St** and **Sty** not exerted.

Regular fires are needed in order that seeds can germinate and thus for the establishment of new plants. Populations at places with dense grass cover and few fires consist mostly of well-established, old, large plants and few or no juveniles (Smith & Craib 2005).

**A. crassipes** Baker (J. Linn. Soc., Bot. 18 (108): 162, 1880). **Type:** South Sudan, Equatoria Prov. (*Schweinfurth* 3765 [K]). — **Distr:** South Sudan; thick grass in woodland, ±1280 m. **I:** Reynolds (1966: 185); Carter & al. (2011: 319).

[3] Acaulescent or very shortly caulescent; **L** ±20–24, densely rosulate, triangular, 40 × 7 cm, dull glaucous-green, **marginal teeth** 5 mm, firm, brown-tipped, 15 mm apart; **Inf** 50–60 cm, with ±5 **Br**; racemes cylindrical-conical, 17–25 × 8 cm, dense; **Bra** deltoid-acute, 10 × 4 mm; **Ped** 14 mm; **Fl** dull yellowish-green, 38 mm, base truncate, 10 mm Ø across the ovary, very slightly narrowed above, very slightly enlarging to the mouth; **OTep** free for 13 mm; **St** and **Sty** exerted 0–1 mm.

Reported occurrence of this species in Zaïre and Zambia (Reynolds 1966, Williamson 2003a) would be an unlikely disjunction. Carter (2001) suggested that the plant in Zambia could be a hybrid, *A. christianii* × *A. bulbicaulis*.

**A. cremnophila** Reynolds & P. R. O. Bally (J. South Afr. Bot. 27(2): 77–79, tt. 13–14, 1961). **Type:** Somalia, Erigavo Distr. (Reynolds 8450B [PRE]). — **Lit:** Brandham & al. (1994). **Distr:** N Somalia (Erigavo Distr.); limestone cliff faces in *Juniperus-Pistacia* forest, 1980–2130 m; known from the type locality only. **I:** Carter & al. (2011: 473).

[13] Caulescent, branching at the base; stem pendulous, 10–20 × 0.8–1 cm; **L** 6–8, rosulate, lanceolate-attenuate, 10 × 2 cm, grey-green, **marginal teeth** 2 mm, pungent, pale brown, 3–5 mm apart; **Inf** 25–30 cm, base pointing downwards, then arcuate-ascending, simple; raceme cylindrical-conical, 10–12 × 5.5 cm, lax; **Bra** ovate-acute, 10 × 5 mm; **Ped** 10–12 mm; **Fl**

scarlet, yellowish-green at the mouth, 25 mm, very slightly clavate, base rounded, 5 mm Ø across the ovary, very slightly narrowed and then enlarging above; **OTep** free for 5 mm; **St** and **Sty** exerted 0–2 mm. — **Cytology:** 2n = 28 (Brandham & al. 1994).

**A. cryptoflora** Reynolds (J. South Afr. Bot. 31 (4): 281–284, ill., 1965). **Type:** Madagascar, Fianarantsoa (*Fievet* s.n. in Reynolds 11619 [PRE, K]). — **Distr:** Madagascar (Fianarantsoa); granite plateau, 1300 m; known only from the area of the type locality. **I:** Reynolds (1966: 480–481); Castillon & Castillon (2010: 138–139); Carter & al. (2011: 241).

[3] Acaulescent or shortly caulescent, simple; **L** 15–20, densely rosulate with slight spiral twist, lanceolate-attenuate, 20–25 × 6.5 cm, deep green slightly tinged reddish, with brownish-red margin, **marginal teeth** 2–3 mm, brownish-red, 5–10 mm apart; **Inf** 40–60 cm, usually with 1 **Br**; racemes cylindrical, very slightly conical, 14 × 3 cm, very dense; **Bra** ovate-orbicular-cuspidate, rounded and somewhat cupped, fleshy, pale green, 11 × 12 mm, closely imbricate in bud stage; **Ped** none; **Fl** greenish-yellow, becoming orange-yellow at the mouth, 10 mm, cylindrical-campanulate, base rounded, 3.5 mm Ø across the ovary; **OTep** free to the base; **St** and **Sty** exerted 3 mm.

**A. cryptopoda** Baker (J. Bot. 22: 52, 1884). **Type:** Moçambique (*Kirk* 96 [K]). — **Distr:** Botswana, Malawi, W & C Moçambique, S & E Zambia, Zimbabwe; rocky slopes and inselbergs with little or no grass, 60–1525 m. **I:** Reynolds (1950: 331–333); Lane (2004: 19, 21); Carter & al. (2011: 383); Klopper & al. (2012: 75, 82–83, incl. distribution map). — Fig. 18.

[5] Caulescent or very shortly caulescent, usually simple, sometimes suckering to form small groups; **L** ±40–50, densely rosulate, lanceolate-ensiform, or gradually attenuate from the base, to 120 × 7–12 cm, deep green to dull dark greyish-green, **marginal teeth** 1–3 mm, pungent, reddish-brown, 2–10 mm apart; **Inf** 1.25–1.75 m, with 1–4 **Br**; racemes cylindrical-conical to cylindrical-

**Fig. 18** *Aloe cryptopoda*.  
(Copyright: L. E. Newton)



acuminate, 25–45 cm, dense; **Bra** ovate-acuminate, 10–15 mm; **Ped** 15–20 mm; **Fl** scarlet or orange-scarlet, greenish-tipped, upper ½ becoming yellowish at anthesis, 28–35 mm, base truncate, 8–9 mm Ø across the ovary, not narrowed above; **OTep** free to the base; **St** exerted 2–10 mm; **Sty** exerted to 5 mm. — **Cytology**: 2n = 14 (Müller 1945).

Natural hybrids with other species have been reported (Reynolds 1950). The plants in RSA featured by Wyk & Smith (2014) as this species are *A. wickensii*.

**A. cyrtophylla** Lavranos (Kakt. and. Sukk. 49 (7): 159–161, ills., 1998). **Type**: Madagascar, Fianarantsoa (Röösli & Hoffmann 36/95 [P, MO, TAN]). — **Distr**: SW Madagascar (Fianarantsoa: Ambatofinandrahana); “cipolin” marble limestone, ±1400 m; known only from the type locality. **I**: Castillon & Castillon (2010: 110–111); Carter & al. (2011: 545).

[11] Caulescent, much branched from the base; stems erect, up to 30 cm; **L** in lax rosettes, lanceolate, tip acute, the distal ½ strongly rolled back, 12–18 × 2 cm, dark green, **marginal teeth** 1.5 mm, whitish, 5–6 mm apart; **Inf** 30–50 cm, simple; raceme 22 cm, lax; **Bra** acute, 10 × 7 mm, whitish with 5 brown veins; **Ped** 7 mm; **Fl** coral-red, becoming yellowish and then green above, ±28 mm, 4 mm Ø across the ovary, slightly constricted above the ovary, then enlarging to 7

mm Ø, base shortly attenuate; **OTep** free for 9 mm; **St** and **Sty** exerted 1 mm.

**A. dabenorisana** Van Jaarsveld (J. South Afr. Bot. 48(3): 419–424, ills., 1982). **Type**: RSA, Northern Cape (Van Jaarsveld & Kritzinger 6426 [NBG]). — **Distr**: RSA (Northern Cape: N Bushmanland: Dabenoris Mts.); vertical S- and SW-facing quartz cliffs, 900–1000 m. **I**: Carter & al. (2011: 240); Wyk & Smith (2014: 128–129).

[5] Acaulescent or shortly caulescent, simple or in dense groups; stem to 30 × 2.7 cm; **Ros** hanging down or ascending; **L** in 4–5 vertical ranks when young, later spirally arranged, lanceolate-acuminate, to 24 × 5 cm, green, tinged red, obscurely striate, exudate drying orange-yellow, **marginal teeth** 2 mm, white, ±10 mm apart; **Inf** 25–30 cm, arcuate and ascending, rarely simple, usually with 2–4 **Br**; racemes conical, 12 × 7–9 cm, lax; **Bra** lanceolate-acuminate, 7 × 2 mm; **Ped** 20–28 mm; **Fl** yellowish with red keel, 25 mm, 5 mm Ø across the ovary, enlarging to 8 mm near the mouth; **OTep** free to the base; **St** and **Sty** slightly exerted.

**A. darainensis** J.-P. Castillon (CactusWorld 27(3): 177–178, ills., 2009). **Type**: Madagascar, Antsiranana (Castillon 44 [TAN]). — **Distr**: Madagascar (Antsiranana: Daraina near Iharana); dry woodland. **I**: Castillon & Castillon (2010: 345); Carter & al. (2011: 705).

[11] Caulescent, suckering freely at the base; stem to 2–12 cm; **L**  $\pm 15$ , scattered along the stem, narrowly triangular, 6–10  $\times$  0.5 cm, dark green, **marginal teeth** 1 mm, white, 5–8 mm apart, leaf sheath 5 mm; **Inf** 10 cm, erect, simple; racemes cylindrical, 3.5 cm, lax; **Bra** 5  $\times$  1.5 mm; **Ped** 6–8 mm; **Fl** red, 26 mm, base obtuse, 5 mm  $\varnothing$  across the ovary, slightly narrowed above; **OTep** free for 5 mm; **St** exerted 1–2 mm; **Sty** not exerted; **Fr** unknown.

Possibly a member of Sect. *Lomatophyllum* according to Castillon & Castillon (2010: 345), but fruit not described.

**A. dawei** A. Berger (Notizbl. Königl. Bot. Gart. Berlin 4: 246, 1906). **Type** [neo]: Uganda, Mengo Distr. (*Reynolds* 7511 [PRE, EA, K]). — **Distr**: Kenya, Rwanda, Uganda, Democratic Republic of the Congo [Zaire]; grassland and thickets, 800–1525 m. **I**: Reynolds (1966: 369–370); Carter & al. (2011: 635); Cole & Forster (2017: 56–61).

**Incl.** *Aloe beniensis* De Wildeman (1921); **incl.** *Aloe pole-evansii* Christian (1940).

[16] Caulescent, branching; stem erect or decumbent, to 2 m  $\times$  6–8 cm, with dead leaf remains; **L** 16–20, laxly rosulate and persisting 30 cm below, lanceolate-attenuate, 40–60  $\times$  6–9 cm, olive-green to dark green, sometimes tinged reddish, with dull white spots on young shoots, exudate drying yellow, **marginal teeth** 2–4 mm, pungent, reddish-brown, 10–15 mm apart; **Inf** 60–90 cm, with 3–8 **Br**; racemes broadly cylindrical-conical, 8–20  $\times$  8 cm, subdense; **Bra** ovate-acute, 3–4  $\times$  3–5 mm; **Ped** 10–15 mm; **Fl** scarlet, paler at the mouth, 33–35 mm, base shortly attenuate, 8 mm  $\varnothing$  across the ovary, very slightly narrowed above; **OTep** free for 11–12 mm; **St** and **Sty** exerted 4 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

**A. debrana** Christian (Flow. Pl. Afr. 26: t. 1016 + text, 1947). **Type**: Ethiopia, Shewa Region (*McLoughlin* 812A [PRE 27173]). — **Lit**: Gilbert & Sebsebe Demissew (1997). **Distr**: C Ethiopia; grassland and low scrub on volcanic (basaltic) rocks, usually gentle slopes, 2000–2700 m. **I**: Reynolds (1966: 279–280, as



**Fig. 19** *Aloe debrana*. (Copyright: M. G. Gilbert)

*A. berhana*); Carter & al. (2011: 358); Starha (2014b). — Fig. 19.

**Incl.** *Aloe berhana* Reynolds (1957).

[5] Acaulescent or with very short stem, simple or suckering to form small groups; **L** 24 or more, densely rosulate, lanceolate-attenuate, 25–60  $\times$  7.5–15 cm, dull green, with reddish-brown horny margin, exudate drying brownish, **marginal teeth** 2–4 mm, reddish-brown, pungent, 0.8–15 mm apart; **Inf** 1 m, with 8–12 **Br**, lower ones sometimes rebranched; racemes subcapitate, 5–10  $\times$  6–7 cm, dense; **Bra** ovate-triangular, 3–5  $\times$  1.5–2 mm; **Ped** 10–15 mm; **Fl** scarlet, paler at the mouth, 17–20 (–35) mm, base very shortly attenuate, 8 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 5–9 mm; **St** and **Sty** scarcely exerted. — **Cytology**:  $2n = 14$  (Fentaw & al. 2013).

**A. decaryi** Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 12: 318, 1941). **Type**:



Madagascar, Toliara (*Decary* f.346). — **Distr:** S Madagascar (Toliara: Androy); coastal scrub, in sand. **I:** Castillon & Castillon (2010: 262–263); Carter & al. (2011: 381).

[10] Caulescent, branching at the base to form small groups; stem 1–1.5 m, erect; **L** 10–14 at the stem apices, narrowly triangular, 15–19 × 0.8–1.2 cm, dull green, **marginal teeth** white, 5–10 mm apart, leaf sheath prominently striate; **Inf** 20–30 cm, erect, simple; racemes cylindrical, lax; **Bra** 8 × 3 mm; **Ped** 10 mm; **Fl** rose-red to scarlet, 20 mm, 6 mm Ø across the ovary; **OTep** free to the base; **St** and **Sty** exerted 2 mm.

Regarded as conspecific with *A. antandroi* by Reynolds (1966).

**A. decorsei** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 43, 1926). **Type:** Madagascar, Fianarantsoa (*Perrier* 11002 [P]). — **Lit:** Castillon & Castillon (2010: 155). **Distr:** Madagascar (Fianarantsoa: Andringitra Massif); gneiss slopes, 1600–2200 m; not presently known from the wild nor from cultivation. **I:** Reynolds (1966: 451).

[2] Acaulescent, simple; **L** 12–15, rosulate, slightly falcate, 60–70 × 5–6 cm, green, **marginal teeth** 1–1.5 mm; **Inf** 80–120 cm, simple; raceme 18–30 cm, lax; **Bra** oblanceolate, shortly acute, 15 × 6 mm; **Ped** 3–4 mm; **Fl** yellow becoming green with white margins at the tips, 20–22 mm, campanulate, base shortly attenuate; **OTep** free for 18–20 mm; **St** and **Sty** not exerted.

Little known, and type locality not recorded precisely, but close to or identical with *A. andringitrensis* (Carter & al. 2011: 289).

**A. decumbens** (Reynolds) Van Jaarsveld (Aloe 45(1): 7, ills., 2008). **Type:** RSA, Western Cape (*Muir* 5383 [PRE]). — **Distr:** RSA (Western Cape: S Langeberg); Fynbos vegetation on sandstone rocks and cliffs, 500–1000 m. **I:** McDonald (1994: as *A. gracilis* var.); Carter & al. (2011: 539); Wyk & Smith (2014: 112–113).

≡ *Aloe gracilis* var. *decumbens* Reynolds (1950) ≡ *Aloiampelos decumbens* (Reynolds) Klopper & Gideon F. Smith (2013).

[13] Caulescent, branching from the base and above; stem to 75 cm, decumbent with ascending

leafy tips; **L** scattered along the stems, lanceolate-deltoid, 15 × 1.5 cm, green, **marginal teeth** 0.5 mm, white, leaf sheath 1 cm, obscurely green-striate; **Inf** 30 cm, erect, simple; racemes cylindrical, 10–12 cm, sublux; **Bra** 4–5 mm, pale brownish; **Ped** 4–5 mm; **Fl** scarlet, 28–33 mm, 5–6 mm Ø across the ovary; **OTep** free for 6 mm; **St** and **Sty** exerted 2–3 mm.

**A. decurva** Reynolds (J. South Afr. Bot. 23(1): 15–17, ills., 1957). **Type:** Moçambique, Manica e Sofala (*Reynolds* 8200 [PRE, K, SRGH]). — **Distr:** Moçambique (Manica e Sofala: Mt. Zembe); soil pockets on steep granite slopes, 915–1060 m. **I:** Reynolds (1966: 247–248); Carter & al. (2011: 281).

[4] Acaulescent or very shortly caulescent, simple, sometimes dividing into 2 rosettes; **L** 20–24, densely rosulate, ensiform-attenuate, to 55 × 9 cm, dull green tinged reddish, exudate drying yellow, **marginal teeth** 3 mm, pungent, 8–15 mm apart; **Inf** to 90 cm, simple, rarely with 1 **Br**; raceme broadly cylindrical to slightly acuminate, 15–20 × 10–12 cm, very dense, pointing downwards on the decurved peduncle; **Bra** ovate-obtuse, 2 × 3 mm; **Ped** 1 mm; **Fl** bright red or orange, 38 mm, ventricose, base narrowly rounded, 5 mm Ø across the ovary, enlarging above to 11 mm in the middle, narrowing to the mouth; **OTep** free for 33 mm; **St** and **Sty** exerted 15 mm.

**A. deinacantha** T. A. McCoy & al. (Kakt. and Sukk. 59(2): 45–46, ills., 2008). **Type:** Madagascar, Mahajanga (*Razafindratsira* s.n. in *Lavranos* 32230 [Herb. Univ. Antananarivo, FT]). — **Distr:** Madagascar (Mahajanga); habitat not stated but apparently in forested area (Castillon & Castillon 2010: 303). **I:** Castillon & Castillon (2010: 303); Carter & al. (2011: 649).

≡ *Aloe divaricata* ssp. *deinacantha* (T. A. McCoy & al.) J.-B. Castillon & J.-P. Castillon (2010) (*nom. inval.*, ICN Art. 36.1b, 41.5) ≡ *Aloe divaricata* var. *deinacantha* (T. McCoy & al.) J.-B. Castillon & J.-P. Castillon (2010) (*nom. inval.*, ICN Art. 36.1b, 41.5).

[12] Caulescent, branching from the base; stem to 1.75 m, with persistent dry leaves; **L** 12–16, in

lax rosettes, ensiform, 50 × 6 cm, dull pale green, exudate bright yellow, **marginal teeth** 4 mm, pinkish, white-tipped, 10–15 mm apart; **Inf** 70 cm, ascending, with 3–8 **Br**; racemes cylindrical, 30 cm, lax; **Bra** obovate, 1–2 mm; **Ped** 5 mm, reddish-green; **Fl** coral-red, yellow-tipped, 25 mm, 4–5 mm Ø across the ovary; **OTep** free to the base; **St** and **Sty** exerted 5 mm.

Considered as synonym of *A. divaricata* ssp. *divaricata* by Castillon (2012: 19).

**A. delicatifolia** J.-B. Castillon (CactusWorld 31(4): 260, ill. (pp. 259–261), 2013). **Type:** Madagascar, Fianarantsoa (Castillon 58 [TAN, TAN]). — **Distr:** Madagascar (Fianarantsoa); amongst rocks; known only from the type locality.

[10] Caulescent, suckering to form groups of up to 20 **Ros**; stem 5 cm; **L** 8–15, rosulate, linear-attenuate, 10–18 × 0.3–0.5 cm, green, reddish in the sun, surface densely muricate, **marginal teeth** 0.5–1 mm, white, 1–1.5 mm apart; **Inf** 25–40 cm, erect, simple; racemes subcapitate, 3 cm, lax; **Bra** triangular, 4–6 mm; **Ped** 2 mm; **Fl** red, lobes with white margin at the mouth, 24 mm, base obconical, 5 mm Ø across the ovary, widening above to 7 mm, to 12 mm at the mouth; **OTep** free almost to the base; degree of exertion of **St** and **Sty** not described.

**A. delphinensis** Rauh (Cact. Succ. J. (US) 62 (5): 230–232, ill., 1990). **Type:** Madagascar, Toliara (Rauh 68629a [HEID]). — **Lit:** Forster (2000); Lüthy (2006: 33–34, conservation, with ill.). **Distr:** S Madagascar (Toliara: Tolanaro: Pic St. Louis); granite rocks, 100–500 m; known only from the type locality. **I:** Castillon & Castillon (2010: 236); Carter & al. (2011: 488).

[11] Caulescent, branching at the base forming lax groups; stem erect or ascending, to 30 × 1 cm; **L** scattered along the stem, linear-acute, 15–25 × 1.5 cm, green to red-green, **marginal teeth** small, reddish, crowded, leaf sheath ±1 cm, red-brown with darker veins; **Inf** 18–28 cm, simple; racemes cylindrical, ±8 × 6 cm, lax, with ±15 flowers; **Bra** triangular, 2 mm, red-brown; **Ped** 15–18 mm, almost horizontal in bud stage; **Fl** red becoming whitish with green midrib towards the tip, 25 mm, narrowed very slightly above the ovary; **St**

slightly exerted; **Sty** not exerted; **Fr** berries, elongate-trigonous; **Se** wingless as in the *Lomatophyllum* group, black and polished.

**A. deltoideodonta** Baker (J. Linn. Soc., Bot. 20: 271–272, 1883). **Type** [lecto]: Madagascar, Antananarivo? (*Baron* 946 [K]). — **Lit:** Rebmann (2009). **Distr:** Madagascar.

Rebmann (2009) changed all varieties to subspecies status, but one new combination was invalid, and so the changes are not adopted here.

The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984).

**A. deltoideodonta** ssp. **amboahangyensis** Rebmann (Cact.-Avent. Int. 84: 28–29, ill., 2009). **Type:** Madagascar (Rebmann 17 [BR]). — **Lit:** Carter & al. (2011: 706, with ill.). **Distr:** Madagascar; on granite, 320 m.

≡ *Aloe horombensis* ssp. *amboahangyensis* (Rebmann) J.-P. Castillon (2014) (*incorrect name*, ICN Art. 11.4).

[18] Differs from var. *deltoideodonta*: **L** patent to recurved; **Br** shorter; **Ped** longer; **Fl** shorter.

**A. deltoideodonta** var. **brevifolia** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 24, 1926). **Type:** Madagascar, Toliara (Perrier 12740 [P, P]). — **Lit:** Carter & al. (2011: 217). **Distr:** SW Madagascar (Toliara); denuded sandstone rocks, ±100 m. **I:** Reynolds (1966: 437); Castillon & Castillon (2010: 179).

≡ *Aloe deltoideodonta* ssp. *brevifolia* (H. Perrier) Rebmann (2009); ≡ *Aloe horombensis* J.-P. Castillon (2014) (*nom. illeg.*, ICN Art. 52.1).

[18] Differs from var. *deltoideodonta*: **L** 10 × 5 cm; **Inf** 30 cm; racemes 6–10 cm, denser.

Little-known. The type specimen has narrower leaves (2.5 cm) than given in the protologue. Probably not distinct from var. *intermedia* (Castillon & Castillon 2010: 179).

**A. deltoideodonta** var. **candicans** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 25, 1926). **Type** [lecto]: Madagascar, Fianarantsoa (Perrier 11026 [P, P]). — **Distr:** SW Madagascar (Fianarantsoa: Ankaramena–Zazafotsy); semi-denuded rocky slopes and pavements, 800–1100 m.



**I:** Reynolds (1966: 435–436); Castillon & Castillon (2010: 174–175); Carter & al. (2011: 218).

≡ *Aloe deltoideodonta* ssp. *candicans* (H. Perrier) Rebmann (2009) ≡ *Aloe candicans* (H. Perrier) J.-B. Castillon & J.-P. Castillon (2010) (*nom. inval.*, ICN Art. 36.1b, 41.5) ≡ *Aloe horombensis* ssp. *candicans* (H. Perrier) J.-P. Castillon (2014) (*incorrect name*, ICN Art. 11.4).

[18] Differs from var. *deltoideodonta*: **L** 15–20 × 5–6 cm; **Inf** racemes cylindrical-conical, 10–20 cm; **Bra** ovate-acute, ±15 × 7–8 mm, very white, usually deflexed near the base. — **Cytology**: 2n = 14 (Brandham 1971).

**A. deltoideodonta** var. **deltoideodonta** —

**Lit:** Carter & al. (2011: 217–219). **Distr:** C Madagascar (Antananarivo?). **I:** Reynolds (1966: 434); Castillon & Castillon (2010: 172–173); Carter & al. (2011: 217).

**Incl.** *Aloe madecassa* H. Perrier (1926); **incl.** *Aloe deltoideodonta* var. *typica* H. Perrier (1926) (*nom. inval.*, ICN Art. 24.3); **incl.** *Aloe madecassa* var. *lutea* Guillaumin (1955).

[18] Acaulescent or shortly caulescent, probably suckering; **L** 12–16, densely rosulate, lanceolate-deltoid, 10–13 × 2.5–3 cm, green, probably without spots, with narrow straw-coloured cartilaginous margin, **marginal teeth** 2 mm, straw-coloured, 3–5 mm apart; **Inf** 40–60 cm, simple or with 1–2 **Br**; racemes narrowly cylindrical-acuminate and narrowing almost to a point, 15–20 cm, subdense; **Bra** lanceolate-deltoid, ±10 mm, white; **Ped** 10–12 mm; **Fl** probably scarlet, ±25 mm, base attenuate; **OTep** free for 10 mm; **St** and **Sty** exerted 0–1 mm.

Little-known; type locality unknown, given as “Central Madagascar” in the protologue, and as Imerina by Perrier (1938: 86). The white frothy leaf exudate appears to be unique in the genus. Castillon & Castillon (2010: 53, as *A. madecassa*) report natural hybrids with *A. capitata*

**A. deltoideodonta** var. **fallax** J.-B. Castillon (Succulent 2006(1): 20–21, *ills.*, 2006). **Type:** Madagascar, Fianarantsoa (Castillon 19 [HBG]). — **Distr:** SW Madagascar (Fianarantsoa: Ambalavao); among grass on granitic rocks, 800 m.

**I:** Castillon & Castillon (2010: 176–177); Carter & al. (2011: 219).

≡ *Aloe deltoideodonta* ssp. *fallax* (J.-B. Castillon) Rebmann (2009) (*nom. inval.*, ICN Art. 41.5, Note 1) ≡ *Aloe candicans* var. *fallax* (J.-B. Castillon) J.-B. Castillon & J.-P. Castillon (2010) (*nom. inval.*, ICN Art. 36.1b, 41.5) ≡ *Aloe horombensis* ssp. *fallax* (J.-P. Castillon) J.-P. Castillon (2014) (*incorrect name*, ICN Art. 11.4).

[18] Differs from var. *deltoideodonta*: **L** distinctly lineate, reddish when dry.

**A. deltoideodonta** var. **intermedia** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 24–25, 1926). **Type:** Madagascar, Toliara (Perrier 12690 [P, P]). — **Lit:** Castillon (2009b); Castillon & Castillon (2010: 178, with *ills.*). **Distr:** Madagascar; on rocks, 600 m.

≡ *Aloe intermedia* (H. Perrier) Reynolds (1957) (*nom. illeg.*, ICN Art. 53.1); ≡ *Aloe subacutissima* G. D. Rowley (1973).

[18] Differs from var. *deltoideodonta*: **L** 15–35 × 3–5 cm, dull green, bluish- or red-tinged, **marginal teeth** 3–4 mm, reddish-brown, 5–10 mm apart; **Inf** 50–70 cm, with 2–4 **Br**; racemes cylindrical-acuminate, 10–15 cm; **Bra** 15–20 mm; **Ped** 15–20 mm; **Fl** 30 mm.

Reynolds (1957) raised this to species rank as *A. intermedia*, but this name was illegitimate as it was a later homonym to *A. intermedia* Haworth, and so Jacobsen & Rowley (1973) published a new name as *A. subacutissima*. Reynolds did not reach the type locality, and Castillon (2009b) claimed that the plants collected by Reynolds were not identical to Perrier’s taxon. He therefore described the Reynolds gathering as *A. newtonii*, but see the note after this name. Castillon & Castillon (2010: 178) argue that this variety is not distinct from var. *deltoideodonta*.

**A. deltoideodonta** var. **ruffingiana** (Rauh & Petignat) J.-B. Castillon & J.-P. Castillon (Aloe Madagascar, 28, 2010). **Type:** Madagascar, Toliara (Petignat 671 [HEID]). — **Distr:** Madagascar (Toliara); on granite in open bush, 450 m. **I:** Castillon & Castillon (2010: 211); Carter & al. (2011: 706, as ssp. *esomonyensis*).

≡ *Aloe ruffingiana* Rauh & Petignat (1999) ≡ *Aloe horombensis* ssp. *ruffingiana* (Rauh & Petignat) J.-P. Castillon (2014) (*incorrect name*, ICN Art. 11.4); **incl.** *Aloe deltoideodonta* ssp. *esomonyensis* Rebmann (2009).

[18] Differs from var. *deltoideodonta*: **L** 10–25 × 4 cm, obscurely striate, densely spotted, **marginal teeth** < 1 mm, reddish, closer together; **Inf** 25 cm; racemes 6 cm, lax; **Fl** 25–28 mm; **St** and **Sty** exerted 2–4 mm.

Possibly just a shade forest variant of the species (Castillon & Castillon 2010: 211).

**A. descoingsii** Reynolds (J. South Afr. Bot. 24(2): 103–105, ill., 1958). **Type:** Madagascar, Toliara (*Descoings* 2440 [TAN, PRE]). — **Lit:** Lüthy (2006: 35–36, conservation, with ill.). **Distr:** Madagascar. **I:** Carter & al. (2011: 392–293).

≡ *Guillauminia descoingsii* (Reynolds) P. V. Heath (1994).

**A. descoingsii** ssp. *augustina* Lavranos (Cact. Succ. J. (US) 67(3): 158–161, ill., 1995). **Type:** Madagascar, Toliara (*Lavranos & al.* 29194 [P]). — **Distr:** S Madagascar (Toliara: near St. Augustin); limestone, in the shade of bushes, ±100 m; known only from the region of the type locality. **I:** Castillon & Castillon (2010: 286–287); Carter & al. (2011: 393).

[11] Differs from ssp. *descoingsii*: **L** narrower, greyish-green, with many white tubercles each bearing a bristle-like prickle, especially on a lower surface keel towards the tip; **Fl** almost cylindrical, with wide mouth.

**A. descoingsii** ssp. *descoingsii* — **Lit:** Du Puy (2004b). **Distr:** SW Madagascar (Toliara: Mahafaly Plateau escarpment); shallow soil at top of limestone cliffs, ±350 m; known only from the region of the type locality. **I:** Reynolds (1966: 411–412); Castillon & Castillon (2010: 285); Carter & al. (2011: 392).

[11] Acaulescent or very shortly caulescent, suckering freely forming dense groups; **L** ±8–10, densely rosulate, ovate-attenuate, to 3 × 1.5 cm, dull green with many dull white tubercles, surface rough, **marginal teeth** 1 mm,

cartilaginous, white, 1–1.5 mm apart, smaller and becoming obsolete towards the tip; **Inf** 12–15 cm, simple; raceme capitate, 1.2 × 2.5 cm, with ±10 flowers; **Bra** ovate-acute, 2 × 1 mm; **Ped** 5 mm; **Fl** scarlet, paler to slightly orange at the mouth, 7–8 mm, urceolate, base flat and shortly attenuate, 4 mm Ø across the ovary, narrowed to 3 mm at the mouth; **OTep** free for 2 mm; **St** and **Sty** not exerted. — **Cytology:** 2n = 14 (Brandham 1971).

Highly endangered and known only from 3 populations (Du Puy 2004b).

**A. deserti** A. Berger (Bot. Jahrb. Syst. 36: 61, 1905). **Type:** Tanzania, Pare Distr. (*Volkens* 2378 [B]). — **Distr:** S Kenya, NE Tanzania; sandy stony soil in grass or at the edge of thickets, 550–1825 m. **I:** Reynolds (1966: 338–340); Carter & al. (2011: 613).

[15] Caulescent, branching sparsely; stem erect to 75 × 4–5 cm or decumbent to 1 m; **L** ±16–20, laxly rosulate and persistent for 20–30 cm, lanceolate-attenuate, 40–45 × 7–8 cm, dull green tinged brownish, with or without elliptic whitish spots, surface slightly rough, **marginal teeth** 2–3 mm, pungent, pale brown, 10–15 mm apart; **Inf** 1.2–1.5 m, with 3–8 **Br**; racemes cylindrical to slightly acuminate, to 25 × 7 cm, somewhat lax, limp and drooping in bud stage, becoming stiff and erect as the flowers open; **Bra** ovate-acute, 12–15 × 6–8 mm, conspicuously white, closely imbricate in bud stage, becoming deflexed later; **Ped** 7–10 mm; **Fl** dull rose-pink with a bloom, paler at the mouth, 28–35 mm, base shortly attenuate, 8 mm Ø across the ovary, narrowed slightly above and enlarging to the mouth; **OTep** free for 14–18 mm; **St** and **Sty** exerted 3–4 mm.

**A. dewetii** Reynolds (J. South Afr. Bot. 3(3): 139–141, ill., 1937). **Type:** RSA, KwaZulu-Natal (*Reynolds* 2319 [PRE, BOL]). — **Distr:** RSA (N KwaZulu-Natal, SE Mpumalanga), S Swaziland; open gently sloping grassland, 200–1000 m. **I:** Reynolds (1950: 267–268); Carter & al. (2011: 189); Wyk & Smith (2014: 224–225).

[3] Acaulescent, simple; **L**  $\pm 20$ , densely rosulate, lanceolate-attenuate, to  $48 \times 13$  cm, dull green, upper face with many dull white elongated spots in irregular transverse bands or scattered irregularly, lower face without spots and obscurely lineate, with prominent horny brown margin, whole surface with dull glossy appearance, **marginal teeth** to 10 mm, pungent, brown, 10–15 mm apart; **Inf** to 2 m or more, with 10 **Br**, lower ones rebranched; racemes cylindrical-acuminate, to  $40 \times 7$  cm; **Bra** deltoid,  $20 \times 3$  mm; **Ped** to 15 mm; **Fl** dull scarlet with a bloom, 35–42 mm, base truncate, 14 mm  $\varnothing$  across the ovary, abruptly narrowed above to 6–7 mm, enlarging towards the mouth; **OTep** free for 6 mm; **St** and **Sty** exerted to 1 mm. — **Cytology**:  $2n = 14$  (Müller 1945).

**A. dewinteri** Giess (Bothalia 11: 120–122, ill., 1973). **Type**: Namibia, Kaokoland (*Buhr* s.n. in *Giess* 10990 [WIND, M, PRE]). — **Distr**: NW Namibia (Kaokoland); vertical limestone cliff faces, 600–1200 m. **I**: Carter & al. (2011: 280).

[2,3] Acaulescent or shortly caulescent, simple; stem to 10 cm; **L** 14–22, rosulate, lanceolate-attenuate, to  $50 \times 15$  cm, grey-green with light powdery bloom, with yellowish-brown horny margin, surface smooth, **marginal teeth** 1–2 mm, brown, 10–20 mm apart; **Inf** to 85 cm, simple or with 2–3 **Br**; racemes cylindrical-acuminate,  $25\text{--}40 \times 5$  cm, dense; **Bra** oblong-obovate, obtuse to apiculate; **Ped** to 4 mm; **Fl** coral-pink, becoming yellowish to white when open, 30–33 mm, base attenuate, enlarging above the ovary to 8 mm  $\varnothing$  in the middle, narrowing to the mouth; **OTep** free for 20–25 mm; **St** and **Sty** exerted 4–6 mm.

**A. dhufarensis** Lavranos (Cact. Succ. J. (US) 39(5): 167–171, ill., 1967). **Type**: Oman, Dhofar (*Lavranos* 4337 [PRE]). — **Distr**: Oman (Dhofar), Yemen (Al-Mahrah); dry water courses and gravel banks on a limestone plateau,  $\pm 250$  m. **I**: Carter & al. (2011: 271).

[3] Acaulescent, simple; **L** 14–20, rosulate, deltoid-acuminate,  $45 \times 14$  cm, bluish-grey, **marginal teeth** absent except for a few white teeth in

very young plants; **Inf** to 90 cm, with 1–2 **Br**; racemes cylindrical-acuminate,  $\pm 20$  cm, lax; **Bra** deltoid-acute, to 12 mm; **Ped** 12–15 mm; **Fl** coral-red with a bloom, 28–30 mm, base attenuate, 9 mm  $\varnothing$  across the ovary, not narrowed above; **OTep** free for 22 mm; **St** and **Sty** exerted 8 mm.

**A. dichotoma** Masson (Philos. Trans. 66: 310, 1776). **Type**: RSA, Northern Cape (*Thunberg* 8587 [UPS, PRE [photo]]). — **Lit**: Zonneveld (2002). **Distr**: Namibia, RSA (Northern Cape).

$\equiv$  *Rhipidodendrum dichotomum* (Masson) Willdenow (1811)  $\equiv$  *Aloidendron dichotomum* (Masson) Klopper & Gideon F. Smith (2013).

**A. dichotoma** ssp. **dichotoma** — **Lit**: Jaarsveld & Judd (2015: 48–51, ill., as *Aloidendron*). **Distr**: Namibia, NW RSA (Northern Cape); rocky slopes. **I**: Reynolds (1950: 489–494); Carter & al. (2011: 690);

**Incl.** *Aloe ramosa* Haworth (1804); **incl.** *Aloe montana* Schinz (1896)  $\equiv$  *Aloe dichotoma* var. *montana* (Schinz) A. Berger (1908).

[17] Caulescent, copiously branching dichotomously and forming dense rounded crowns; stem erect, to 9 m, to 1 m  $\varnothing$  at the base; **L**  $\pm 20$ , densely rosulate, lanceolate-linear,  $25\text{--}35 \times 5$  cm, glaucous green, with very narrow brownish-yellow margin, **marginal teeth** 1 mm, smaller and becoming obsolete towards the apex, brownish-yellow; **Inf** 30 cm, with 3–5 **Br**; racemes broadly cylindrical, slightly acuminate, to  $15 \times 9$  cm; **Bra** acuminate,  $5\text{--}7 \times 3$  mm; **Ped** 5–10 mm; **Fl** bright canary-yellow, 33 mm, ventricose, base shortly attenuate, enlarging to 14 mm  $\varnothing$  in the middle; **OTep** free for 25 mm; **St** and **Sty** exerted 12–15 mm. — **Cytology**:  $2n = 14$  (Riley 1959: 241).

The N limit of *A. dichotoma* is in the Brandberg region of Namibia, but the species is absent from C Namibia (Smith & Steyn 2005). *A. dichotoma* is, together with *A. pillansii* and *Pachypodium namaquanum*, an important keystone species and provides perching sites to raptors and nesting sites for birds, etc. (Midgley & al. 1997). Foden & al. (2007) found high degrees of population-level mortality, with increasing mortality rates from S to N populations. Mortality is most pronounced in low-altitude populations.

From repeat photographs, population decrease has been found to be as much as 4.73% per year in N populations, while S populations are stable or show a small (0.91% per year) increase.

Jack & al. (2014) show that mortality is attributable to a large extent to windthrow caused by high summer rainfall associated with high wind speeds. Windthrow mortality is much smaller in the more S populations. Jack & al. (2016) argue that the population decline observed is not the result of climate change.

**A. dichotoma** ssp. **ramosissima** (Pillans) Zonneveld (Bradleya 20: 10, 2002). **Type:** RSA, Northern Cape (*Reynolds* 2547 [BOL, BOL, K, PRE]). — **Lit:** Rebelo & al. (1989); Zonneveld (2002); Carter & al. (2011: 659); Jaarsveld & Judd (2015: 56–59, *ills.*, as *Aloidendron*). **Distr:** Namibia, RSA (Northern Cape); hot arid mountain slopes. **I:** Reynolds (1950: 487, as *A. ramosissima*).

≡ *Aloe ramosissima* Pillans (1937) ≡ *Aloe dichotoma* var. *ramosissima* (Pillans) Glen & D. S. Hardy (2000) ≡ *Aloidendron ramosissimum* (Pillans) Klopper & Gideon F. Smith (2013).

[16] Differs from ssp. *dichotoma*: Much branched at the base and above; stem erect or ascending, to 3 m × 8 cm; **L** 15–20 × 2.2 cm; **Inf** 15–20 cm, with 1–2 **Br**. — **Cytology:** 2n = 14 (Riley 1959).

**A. dinteri** A. Berger (in Dinter, *Neue Pfl. Deutsch-SWA*, 14, 1914). **Type:** Namibia, Outjo (*Dinter* 2791a [SAM]). — **Distr:** NW Namibia, SW Angola (Namibe, Cunene); limestone rocks in low bush, 600–1500 m. **I:** Reynolds (1950: 211–212); Carter & al. (2011: 310).

≡ *Gonialoe dinteri* (A. Berger) Boatwright & J. C. Manning (2014) ≡ *Tulista dinteri* (A. Berger) G. D. Rowley (2014).

[3] Acaulescent, simple, 26 × 26 cm; **L** ±12, trifarious, lanceolate-acuminate, plicate-carinate, towards the tip V-shaped in cross section, 20–30 × 5–8 cm, chocolate-brown or deep brownish-green, with many elongated white spots in ± broken transverse bands, with narrow white cartilaginous margin, keel on the lower face with 1 mm white cartilaginous margin, **marginal teeth**

0.5 mm, firm, white, 1–2 mm apart, becoming smaller and more crowded upwards, with similar teeth on the keel; **Inf** 50–85 cm, with 3–8 **Br**; racemes cylindrical-acuminate, 15–20 × 7 cm, lax, with 30–40 flowers; **Bra** lanceolate-deltoid, very acuminate, a little shorter than the pedicels; **Fl** pale rose-pink with bluish bloom, paler to almost white at the mouth, 28–30 mm, base rounded, 6.5 mm Ø across the ovary, narrowed to 3.5 mm above, enlarging towards the mouth; **OTep** free for 5–10 mm; **St** and **Sty** exerted 0–1 mm.

Klopper & al. (2009a) report the taxon for SW Angola (Namibe, Cunene).

**A. diolii** L. E. Newton (*Cact. Succ. J. (US)* 67 (5): 277–279, *ills.*, SEM-*ills.*, 1995). **Type:** South Sudan, Equatoria Prov. (*Powys & Dioli* 824 [K, EA]). — **Distr:** South Sudan (Equatoria region); montane forest, deep shade; 1760 m; known only from the type locality. – Fig. 20.



**Fig. 20** *Aloe diolii*. (Copyright: L. E. Newton)



[11] Caulescent, branching at the base to form loose clumps; stem sprawling, rooting on contact with the soil, to 35 cm; **L** 8–10, laxly rosulate, triangular to slightly falcate, 25 × 2.5 cm, dull green with few scattered elongated white spots in young growth, few spots near the base or none on older shoots, surface slightly rough, exudate yellow, drying brown, **marginal teeth** 1 mm, firm, uncinete, red-tipped, 2–8 mm apart, to 13 mm apart towards the leaf tip; **Inf** 36 cm, simple or usually with 2–6 **Br**; racemes cylindrical, 9 cm, lax; **Bra** triangular, attenuate, 4–5 × 2 mm; **Ped** 10 mm; **Fl** light scarlet with light bloom at the base, becoming pale yellow with red mid-stripe above, 20–25 mm, base truncate, 8 mm  $\varnothing$  across the ovary, narrowed gradually to 6 mm above, lobes spreading to 8 mm; **OTep** free for 5–8 mm; **St** and **Sty** exerted 3 mm. — **Cytology**:  $2n = 14$  (protologue).

**A. divaricata** A. Berger (Bot. Jahrb. Syst. 36: 65, 1905). **Type**: Madagascar, Mahajanga (Hildebrandt 3047 [P, BM, K]). — **Lit**: Castillon (2012). **Distr**: Madagascar.

**A. divaricata** ssp. **divaricata** — **Lit**: Ratsirarson (1995: pollination ecology). **Distr**: SW & W Madagascar; widespread in arid bush and coastal thickets, to 800 m. **I**: Reynolds (1966: 504–506); Castillon & Castillon (2010: 200–202); Carter & al. (2011: 667). — Fig. 21.

**Incl.** *Aloe saundra* Bojer (1837) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Aloe vahontsohy* Decorse ex Poisson (1912); **incl.** *Aloe vahontsohy* H. Perrier (1938) (*nom. illeg.*, ICN Art. 53.1).

[16] Caulescent, simple or sparsely branching at the base or low down; stem to 3 m or more, with dead leaf remains; **L** 30 or more, rosulate and persistent for 50–100 cm below, ensiform, obtuse-attenuate, 60–65 × 7 cm, dull grey-green tinged reddish, exudate drying yellow, **marginal teeth** 5–6 mm, pungent, reddish-brown, 15–20 mm apart; **Inf** ±1 m, with many spreading **Br**, the lowest with 8–10 secondary branches, producing a total of 60–80 racemes; racemes cylindrical-acuminate, 15–20 cm, lax, with ±20 flowers; **Bra** deltoid, 4 × 2 mm; **Ped** 6 mm; **Fl** scarlet, 28 mm, base slightly rounded, 7 mm  $\varnothing$  across the ovary,



**Fig. 21** *Aloe divaricata* ssp. *divaricata*. (Copyright: B. Descouings)

narrowed to 6 mm above, enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 3–4 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

Flowers are visited by nectar birds and a species of bee (Ratsirarson 1995), the latter is considered a nectar thief.

**A. divaricata** ssp. **tulearensis** (T. A. McCoy & Lavranos) J.-P. Castillon (Adansonia, sér. 3, 34 (1): 18–19, fig. 4, 2012). **Type**: Madagascar, Toliara (McCoy 2523 [TAN, FT]). — **Lit**: Carter & al. (2011: 606). **Distr**: Madagascar (Toliara); on limestone, 90 m. **I**: Castillon & Castillon (2010: 272, as *A. tulearensis*).

≡ *Aloe tulearensis* T. A. McCoy & Lavranos (2007).

[13] Differs from ssp. *divaricata*: Branching to form large groups; stem to 150 cm; **L** 15–20, 30–40 × 3 cm; **Inf** 40–50 cm; racemes cylindrical, 8–15 cm; **Fl** 18–20 mm.



**A. divaricata** ssp. **vaotsohy** (Decorse & Poisson) J.-P. Castillon (*Adansonia*, sér. 3, 34(1): 18, fig. 1 (p. 15), 2012). **Type:** Madagascar, Toliara (*Decorse* s.n. [[lecto — icono]: Decorse, Notes Reconnaiss. & Explor., 620, 1900]). — **Distr:** S Madagascar (Toliara).

≡ *Aloe vaotsohy* Decorse & Poisson (1912).

[13] Differs from ssp. *divaricata*: Stems longer and thicker; **L** longer, larger at the base, darker in colour, **marginal teeth** more reddish; racemes more numerous and shorter, denser; **Fr** smaller.

A hybrid with *A. helenae* has recently been described as *A. ×anosyana* (Castillon 2012).

**A. divaricata** var. **rosea** (Decary) Reynolds (*Aloes Madagascar Revis.*, 133, 1958). **Type:** not typified. — **Distr:** S Madagascar (Toliara: Ambovombe); known only from the type. **I:** Carter & al. (2011: 667).

≡ *Aloe vaotsohy* var. *rosea* Decary (1921).

[16] Differs from var. *divaricata*: **Fl** light pink.

**A. djiboutiensis** T. A. McCoy (Cact. Succ. J. (US) 79(6): 270, ills. (p. 269), 2007). **Type:** Djibouti (*McCoy* 3019 [FT]). — **Distr:** Djibouti, SE Eritrea; among basalt rocks, 780 m. **I:** Carter & al. (2011: 304).

[5] Acaulescent, solitary or forming small groups; **L** to 30, rosulate, spreading-recurved, attenuate, 15 × 4 cm, dark jade-green with elliptical white spots, exudate orange-yellow, drying brown, **marginal teeth** 3 mm, reddish-tipped, 8 mm apart; **Inf** 30 cm, with up to 12 horizontal or oblique **Br**; racemes with subsecund flowers, 5–25 cm, subdense; **Bra** acute, 3 mm, brownish-white; **Ped** 6 mm, red; **Fl** reddish-pink with small white spots, 18–22 mm, 7–8 mm Ø across the ovary; **OTep** free for 8 mm; **St** and **Sty** exerted 2 mm.

**A. doddsiorum** T. A. McCoy & Lavranos (*CactusWorld* 25(4): 209–211, ills., 2007). **Type:** Kenya, Samburu Distr. (*Dodds* 1 [EA, FT]). — **Distr:** N Kenya (E escarpment of the Rift Valley); near-vertical W-facing rock faces, 2675 m; known only from the type collection. **I:** Carter & al. (2011: 503).

[13] Caulescent, sparsely branching from the base; stem to 2 m and 6 cm Ø, procumbent and pendulous; **L** 16–20, dense at and just below the stem apices, broadly deltoid, 30 × 11 cm, bluish-grey, occasionally with few pale spots near the base, surface smooth, exudate clear, drying colourless, **marginal teeth** deltoid, 5–6 mm, red, 5–15 mm apart; **Inf** 90–100 cm, erect or ascending, with up to 4 **Br**; racemes conical, to 25 cm, dense; **Bra** ovate-lanceolate, 18–22 × 5–6 mm, pale pink with brownish nerves; **Ped** 12–15 mm, reddish; **Fl** bright orange-pink, cream at the mouth, 30–35 mm, 4.5 mm Ø across the ovary; **OTep** free for 12 mm; **St** and **Sty** exerted 3–5 mm.

**A. dominella** Reynolds (*J. South Afr. Bot.* 4(4): 101–103, ills., 1938). **Type:** RSA, KwaZulu-Natal (*Reynolds* 2094 [PRE]). — **Distr:** RSA (C & NW KwaZulu-Natal); short grassland on rocky slopes, 1000–2000 m. **I:** Reynolds (1950: 129–130); Craib (2006: 47–49); Carter & al. (2011: 129); Wyk & Smith (2014: 310–311).

[10] Caulescent, suckering freely forming tufts of up to 50 stems; stem to 15 cm, covered with dead leaf remains; **L** ±20, multifarious, linear-lanceolate, ±35 × 1 cm, dull green, lower face with many small white spots near the base, with very narrow white cartilaginous margin, **marginal teeth** 0.5–1 mm, firm, white, 2–5 mm apart; **Inf** ±35 cm, simple; raceme capitate, ±4 × 8 cm, with ±20 flowers; **Bra** ovate-acuminate, to 15 × 3 mm; **Ped** to 20 mm; **Fl** yellow, 18 mm, slightly clavate, base shortly attenuate; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

According to Hargreaves & al. (2012) this is one of the few species with scented flowers, and is likely pollinated by bees. Flowering is enhanced by the occurrence of fires (Craib 2006: 47–49).

**A. dorotheae** A. Berger (in Engler, A. (ed.), *Pflanzenr.* IV.38 (Heft 33): 263–264, 1908). **Type:** Tanzania, Tanga (*Strauss* 435 [B]). — **Distr:** NE Tanzania (Tanga Region: Kideliko Rock area); soil pockets on rock slabs, 600–685 m. **I:** Reynolds (1966: 69–70); Carter & al. (2011: 418).

**Incl.** *Aloe harmsii* A. Berger (1908).

[6,7] Shortly caulescent, suckering to form dense groups; stem to 25 cm; **L**  $\pm 20$ , rosulate, lanceolate-attenuate, to  $30 \times 5\text{--}6$  cm, bright glossy green becoming reddish in drought, with scattered white spots, with narrow white cartilaginous margin, surface smooth, exudate drying yellow, **marginal teeth** 3–5 mm, uncinatate, white-tipped, 10–15 mm apart; **Inf** to 40–60 cm, simple or rarely with 1–3 **Br**; racemes conical-cylindrical, 10–25 cm, subdense; **Bra** ovate-acute,  $3\text{--}6 \times 2\text{--}3$  mm; **Ped** 4–10 mm; **Fl** coral-red becoming greenish-yellow at the tip, or entirely yellow, to 27–35 mm, base shortly attenuate, 6 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to 8 mm and narrowed slightly to the mouth; **OTep** free for 13–17 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

Probably only cultivated at the reported type locality, but matching plants are known in the wild elsewhere in Tanzania. *A. harmsii* is placed here with a question mark according to Carter (1994).

**A. downsiana** T. A. McCoy & Lavranos (CactusWorld 25(3): 139, ill. (pp. 137–139), 2007). **Type**: Ethiopia, Oromia (McCoy 1146 [FT]). — **Distr**: C Ethiopia (Oromia: Harer–Asbe Teferi); vertical rock faces, 2175 m; known only from the type collection.

[13] Caulescent, solitary or 1- to 2-branched from the base; stem decumbent or pendulous, to 1.5 m and 5–7 cm  $\varnothing$ ; **L** 12–15, crowded at the stem apices, lanceolate,  $50 \times 15$  cm, dull dark green, exudate yellow, drying almost clear, **marginal teeth** 5 mm, reddish-brown-tipped, 20 mm apart; **Inf** 1.2 m, erect, with up to 5 **Br**; racemes cylindrical-acuminate, to 35 cm, subdense; **Bra** narrowly lanceolate,  $10\text{--}12 \times 4$  mm, white with brown nerves; **Ped** 10 mm, pink; **Fl** pink, yellow at the mouth, minutely puberulent, 30–35 mm, 7 mm  $\varnothing$  across the ovary; **OTep** free for 12 mm; **St** and **Sty** exerted 2–3 mm.

**A. droseroides** Lavranos & T. A. McCoy (Cact. Succ. J. (US) 75(6): 256–258, ill., 2003). **Type**: Madagascar, Fianarantsoa (Lavranos & McCoy 31680 [MO, P, TAN]). — **Distr**: C

Madagascar (Fianarantsoa: Ambatofinandrahana); rock ledges on SW-facing “cipolin” marble cliffs in seasonally wet conditions, 1400 m; known only from the type locality. **I**: Castillon & Castillon (2010: 118–119); Carter & al. (2011: 207).

[6] Acaulescent or with short mostly subterranean stems, suckering to form small clumps; **L** 8–15, rosulate, narrowly deltoid to linear,  $2.5\text{--}4.5 \times 0.2\text{--}0.4$  cm, purplish- or grey-green to dark green, covered with erect bristle-like hairs 0.5 mm long, **marginal teeth** 1–1.5 mm, pellucid, cilia-like, closely set; **Inf** 30 cm, erect, simple; racemes cylindrical, 4–6 cm, lax; **Bra** deltoid-acute,  $3 \times 1$  mm; **Ped** 5–6 mm, reddish; **Fl** white, 10 mm, 9 mm  $\varnothing$  at the mouth; **OTep** free to near the base; **St** and **Sty** exerted 0–1 mm.

**A. duckeri** Christian (J. South Afr. Bot. 6(4): 179–180, ill., 1940). **Type**: Malawi, Northern Prov. (Ducker s.n. in Burt 5862 [SRGH, BM, K]). — **Distr**: N Malawi, SW Tanzania, NE Zambia; grassland and open *Brachystegia* woodland, (1000–) 1370–2440 m. **I**: Reynolds (1966: 87); Lane (2004: 33, 41); Carter & al. (2011: 198); Klopper & al. (2012: 76, 83–85, incl. distribution map).

[5] Acaulescent or shortly caulescent, simple, rarely suckering sparsely; stem to 30 cm; **L**  $\pm 20$ , rosulate, lanceolate-attenuate, to  $50 \times 10\text{--}12$  cm, dull green, obscurely lineate, usually with scattered white spots, with cartilaginous margin, **marginal teeth** 4–5 mm, pungent, red-brown, 10–20 mm apart; **Inf** 1–2 m, with 3–10 **Br**; racemes capitate,  $5\text{--}6 \times 8\text{--}10$  cm, dense; **Bra** deltoid-attenuate,  $10\text{--}12 \times 3$  mm; **Ped** 30 mm; **Fl** scarlet, orange or pink, 35–40 mm, base truncate, 10 mm  $\varnothing$  across the ovary, abruptly narrowed to 5–6 mm above, then enlarging to the mouth; **OTep** free for 12–13 mm; **St** and **Sty** exerted 0–1 mm.

**A. dyeri** Schönland (Rec. Albany Mus. 1: 289, 1905). **Type**: RSA, Mpumalanga (Burt Davy s.n. [GRA]). — **Distr**: RSA (E Mpumalanga, Limpopo), Swaziland; in long grass or amongst trees

and bushes on shady rocky slopes, 500–1500 m. **I:** Reynolds (1950: 249–250); Carter & al. (2011: 199); Wyk & Smith (2014: 226–227).

[5] Acaulescent or shortly caulescent, usually simple; **L** ±20, densely rosulate, lanceolate-attenuate, ±60–70 × 10–15 cm, upper face green to yellowish-green, usually with small elongated whitish spots scattered or in irregular transverse bands, lower face paler and usually more copiously spotted, **marginal teeth** 5–6 mm, pungent, light brown, 10–15 mm apart; **Inf** 1.5–2 m, with up to 15 **Br**, lower ones rebranched; racemes cylindrical-acuminate, 12–25 × 9 cm, subdense near the tip, lax below; **Bra** deltoid-acuminate, 10–13 mm; **Ped** 10–13 mm; **Fl** dull brick-red, 35 mm, base truncate, 9 mm Ø across the ovary, abruptly narrowed to 4.5 mm above, enlarging to 8 mm at the mouth; **OTep** free for 8 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Müller 1945).

**A. ecklonis** Salm-Dyck (Monogr. Gen. Aloes & Mesembr. 5: t. 5 + text, 1849). **Type:** RSA, Eastern Cape? (*Ecklon* s.n. [[icono:]] l.c. t. 5]). — **Lit:** Fritz (2009: with ill.). **Distr:** Lesotho, Swaziland, RSA (Eastern Cape, KwaZulu-Natal, E Free State, Limpopo, Mpumalanga, Gauteng); summer rainfall grassland, rarely on rocky slopes, 0–2500 m. **I:** Reynolds (1950: 145–147); Craib (2006: 50–53); Carter & al. (2011: 141); Wyk & Smith (2014: 312–313).

[4] Acaulescent or very shortly caulescent, simple or suckering to form groups of 12 or more shoots; **L** 14–20, multifarious, lanceolate, to 40 × 9 cm, dull green, somewhat veined, lower face sometimes with a few small white spots near the base, with white cartilaginous margin, **marginal teeth** 1–3 mm, firm, white; **Inf** to 50 cm, usually simple or with up to 3 **Br**; racemes densely capitate, ±5 × 10–12 cm, with ±40 flowers; **Bra** ovate-acuminate, ±10–13 mm; **Ped** 30–40 mm; **Fl** yellow to red, 20–24 mm, ventricose, base attenuate, 7 mm Ø in the middle; **OTep** free almost to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Vosa 1982: 413).

Craib (2006) states that this is the most common and widely distributed grass aloe in RSA.

According to Wyk & Smith (2014), it is cold-hardy down to –8 °C.

**A. edouardii** Rebmann (Cact.-Avent. Int. 79: 4–5, ill., 2008). **Type:** Madagascar, Fianarantsoa (*Rebmann* 15 [BR]). — **Distr:** Madagascar (Fianarantsoa); granite domes, 1100–1200 m; known only from the type locality. **I:** Castillon & Castillon (2010: 146–147); Carter & al. (2011: 375).

**Incl.** *Aloe fianarantsoae* J.-B. Castillon (2007) (*nom. inval.*, ICN Art. 40.2).

[3] Acaulescent or with a short stem to 20 cm; **L** 30–35, densely rosulate, ovate-lanceolate, 60–65 × 7–10 cm, dark green to bluish, upper surface reddish, surface with prominent waxy bloom, **marginal teeth** deltoid, 2 mm, red, 7–10 mm apart; **Inf** 70–100 cm, with 4–6 **Br**; racemes conical to cylindrical, 10–25 cm, dense; **Bra** 6 × 2 mm; **Ped** 10–25 mm; **Fl** yellow (orange in bud), 18–33 mm; **OTep** free for 5 mm; **St** and **Sty** not described.

Castillon & Castillon (2010: 146) state that this species is apparently extinct in the wild, and suggest that it was a hybrid, *A. capitata* × *A. acutissima* or *A. arborescens* (though *A. arborescens* is not native to Madagascar).

**A. elata** S. Carter & L. E. Newton (in S. Carter, Fl. Trop. East Afr., Aloaceae, 56–57, t. 4: lower right, 1994). **Type:** Tanzania, Mbulu Distr. (*Greenway & Kanuri* 11776 [K, EA]). — **Lit:** Newton & Kamiti (2003). **Distr:** SW Kenya, N Tanzania: Along the W wall of the Rift Valley Escarpment; dense bush and dry forest on rocky slopes, 1050–1500 m. **I:** Reynolds (1966: 325, Fig. 321, as *A. ballyi*); Carter & al. (2011: 686). — Fig. 22.

[9] Caulescent, usually simple, sometimes suckering at the base; stem unbranched, to 6 (–10) m, to 12 cm Ø, without persistent dead leaves; **L** densely rosulate, becoming strongly recurved, lanceolate, to 100 × 10 cm, dark greyish-green, surface smooth, exudate colourless, **marginal teeth** 4–5 mm, uncinat, white-tipped, 10–26 mm apart; **Inf** to 65 cm, with up to 9 **Br**, lower ones rebranched; racemes



**Fig. 22** *Aloe elata*. (Copyright: L. E. Newton)

cylindrical, 6–14 cm, lax; **Bra** ovate, 4–7 × 3–5 mm; **Ped** 8–10 mm; **Fl** scarlet in bud, becoming yellow at anthesis, 30–32 mm, base rounded, 10 mm  $\varnothing$  across the ovary; **OTep** free for 24–26 mm; **St** and **Sty** exerted 3–7 mm.

Broken leaves give off a slight odour reminiscent of rats or mice, and the sap is poisonous. Material of this species was included in *A. ballyi* by Reynolds (1966).

**A. elegans** Todaro (Hort. Bot. Panorm. 2: 25, t. 29 (1886), 1882). **Type:** Ethiopia, Tigray Prov. (*Schimper* 927 [[lecto — icono]: l.c. t. 29]). — **Lit:** Gilbert & Sebsebe Demissew (1997). **Distr:** Eritrea, N & C Ethiopia; evergreen open bush or wooded grassland, on stony slopes, mostly sandstone or limestone, 1615–2500 m. **I:** Reynolds (1966: 204–206); Sebsebe Demissew & Nordal (2010: 88–89); Carter & al. (2011: 373).

**Incl.** *Aloe abyssinica* var. *peacockii* Baker (1880); **incl.** *Aloe vera* var. *aethiopica*

Schweinfurth (1894)  $\equiv$  *Aloe aethiopica* (Schweinfurth) A. Berger (1905); **incl.** *Aloe schweinfurthii* Hooker fil. (1899) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe peacockii* A. Berger (1905); **incl.** *Aloe percrassa* var. *saganeitiana* A. Berger (1908); **incl.** *Aloe abyssinica* A. Berger (1908) (*nom. illeg.*, ICN Art. 53.1).

[5] Acaulescent or shortly caulescent with age, usually simple, rarely dividing into 2 or 3 **Ros**; stem (when present) to 30 cm, decumbent; **L** 16–20, densely rosulate, lanceolate-attenuate, tip with short teeth,  $\pm 60 \times 15$ –18 cm, grey-green, with reddish margin, exudate drying reddish-brown, **marginal teeth** 3–4 mm, pungent, brownish-red, 15–25 mm apart; **Inf** 1 m, with 8 **Br**, lower ones sometimes rebranched; racemes broadly cylindrical, subcapitate, to 8 × 7 cm, dense, buds spreading horizontally to slightly nutant; **Bra** ovate-acuminate,  $\pm 8 \times 2$ –3 mm; **Ped** 15 mm; **Fl** yellow, orange or scarlet, 25–30 mm, slightly clavate, base shortly attenuate, 6 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 13–15 mm; **St** and **Sty** exerted 3–4 mm. — **Cytology:** 2n = 14 (Fentaw & al. 2013).

Gilbert & Sebsebe Demissew (1997) consider the closely similar *A. sinkatana* from the Sudan as possibly conspecific.

**A. elegantissima** T. A. McCoy & Lavranos (Cact. Succ. J. (US) 80(3): 118, ill. (pp. 116–117), 2008). **Type:** Somalia, Sanaag (*McCoy* 3169 [FT]). — **Distr:** N Somalia (Sanaag: Mait Escarpment); on heavily forested hillside, 2050 m; known from the type collection only. **I:** Carter & al. (2011: 316).

[7] Acaulescent, forming small groups; **L** 12–15, lanceolate-attenuate, 30 × 8 cm, bright green with numerous whitish spots, surface somewhat glossy, exudate orange-yellow, drying brown, **marginal teeth** deltoid, 3 mm, red, 5–8 mm apart; **Inf** 70 cm, erect, with 12–15 **Br**; racemes capitate, 6 cm, dense; **Bra** deltoid-acute, 6 × 1.5 mm; **Ped** 10 mm; **Fl** lemon-yellow with prominent green nerves, 25 mm, 7 mm  $\varnothing$  across the ovary; **OTep** free for 10 mm; **St** exerted 1–2 mm; **Sty** exerted 3.5 mm.

**A. elgonica** Bullock (Bull. Misc. Inform. Kew 1932: 503, 1932). **Type:** Kenya, Trans-Nzoia Distr. (*Lugard* 299 [K]). — **Distr:** W Kenya (Mt. Elgon); rocky slopes, often in grass, 1980–2380 m. **I:** Reynolds (1966: 360–361); Carter & al. (2011: 628).

[12] Caulescent, branching to form dense clumps sometimes to 2 m Ø; stem erect or decumbent, to 1 m or more; **L** 20–24, densely rosulate, triangular-attenuate, to 40 × 9 cm, dark green, often reddish tinged, surface smooth, exudate drying yellow, **marginal teeth** 8–9 mm, pungent, 10–15 mm apart; **Inf** 50–70 cm, simple or with 3–4 **Br**; racemes cylindrical-conical, 18 × 8–9 cm, dense; **Bra** ovate-acute, 5 × 4 mm; **Ped** 20–25 mm; **Fl** orange-scarlet, yellowish at the mouth, 40 mm, base shortly attenuate, 7–8 mm Ø across the ovary, narrowed slightly above, then enlarging to the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 3–5 mm. — **Cytology:** 2n = 28 (Brandham 1971).

Mount Elgon straddles the Kenya-Uganda border, but *A. elgonica* is known only from the Kenyan side of the mountain. Newton (1998a) reports a hybrid with *A. wollastonii*.

**A. elkerriana** Dioli & T. A. McCoy (Haseltonia 13: 35–37, ills., 2008). **Type:** Ethiopia, Bale Region (*Dioli* 28 [O † ?]). — **Distr:** E Ethiopia (Bale Region); on cliff face, 1000 m; known only from the type collection. **I:** Sebsebe Demissew & Nordal (2010: 107–108); Carter & al. (2011: 628).

[13] Caulescent, branching at the base; stem 3–5 m, procumbent or pendulous; **L** 9–23, in open rosettes, lanceolate, 20–30 × 4.5 cm, greyish-green, surface smooth, exudate yellow-orange, drying almost black, **marginal teeth** 1–2 mm, whitish-pink, 4 mm apart; **Inf** 50–60 cm, oblique, with 4–5 **Br**; racemes cylindrical, 10–15 cm, lax, with subsecund flowers; **Bra** 5 mm; **Ped** 10–17 mm; **Fl** dark coral-red, yellow at the mouth, 25 mm, 5 mm Ø across the ovary; **OTep** free for 12 mm; **St** and **Sty** exerted 4 mm.

**A. ellenbeckii** A. Berger (Bot. Jahrb. Syst. 36: 59, 1905). **Type:** Somalia (*Ellenbeck* 2340 [B]). — **Distr:** S Ethiopia, N Kenya, S Somalia

(Jubbada Dhexe); sandy soils in deciduous bushland, 700–1600 m. **I:** Glen & Hardy (1990: t. 2012, as *A. dumetorum*); Carter & al. (2011: 156).

**Incl.** *Aloe dumetorum* B. Mathew & Brandham (1977).

[6] Acaulescent, suckering to form clumps; **L** 6–12, rosulate, linear-lanceolate, 15–27 × 1–2.5 (–3) cm, yellowish-green with many white spots sometimes in irregular transverse bands, with cartilaginous margin, surface smooth, exudate pale yellow, **marginal teeth** 0.5–1 mm, 2–6 mm apart; **Inf** 50–75 cm, simple; racemes conical-cylindrical, 5–8 × 6 cm, lax; **Bra** linear-lanceolate, 5–10 × 2 mm; **Ped** 7–10 mm; **Fl** orange-red, becoming yellow at the mouth, 24–30 mm, base truncate, 7–10 mm Ø across the ovary, abruptly narrowed to ±5 mm above, then enlarging to the mouth; **OTep** free for 8–10 mm; **St** and **Sty** exerted 2–4 mm.

Lavranos (1995) treats this as a “species of uncertain position”, preferring to reserve judgement on its relationship with *A. dumetorum* until more material is found at or near the type locality. It should also be noted that Kenyan material currently in cultivation as *A. dumetorum* does not agree closely with the protologue of that name and could prove to be an as yet undescribed taxon. Grace & al. (2008) report that a particular form of the compound nataloin is present in this and some related E African species, and that this compound has potential value as marker for the “maculate Aloes”, as previously suggested by Wabuye (2006a).

**A. eminens** Reynolds & P. R. O. Bally (J. South Afr. Bot. 24: 187–189, tt. 30–32, 1958). **Type:** Somalia, Sanaag (*Reynolds* 8435 [PRE, EA, K]). — **Lit:** Jaarsveld & Judd (2015: 44–47, ills., as *Aloidendron*). **Distr:** N Somalia (Sanaag: near Erigavo); forested slopes, 1300–1830 m. **I:** Reynolds (1966: 386–388); Carter & al. (2011: 694).

≡ *Aloidendron eminens* (Reynolds & P. R. O. Bally) Klopper & Gideon F. Smith (2013).

[17] Caulescent, irregularly branched; stem erect, to 1.5 m, to 15 cm Ø at the base, more slender above; **L** 16–20, rosulate, triangular-obtuse, deeply canaliculate and recurved, 40–45



× 5 cm, dull green, with narrow white cartilaginous margin, surface smooth, exudate yellow, **marginal teeth** 2–3 mm, blunt, white, 3–5 mm apart, becoming smaller to obsolescent above except for a few short crowded teeth in the apical 4–5 cm; **Inf** 50–60 cm, with 3–5 **Br**; racemes cylindrical-acuminate, 16 × 8–9 cm, subdense; **Bra** deltoid, 6 × 3 mm; **Ped** 10 mm; **Fl** red, 40 mm, base rounded, 12 mm Ø across the ovary, slightly narrowing towards the mouth; **OTep** free for 32 mm; **St** and **Sty** exerted 3–5 mm.

**A. eremophila** Lavranos (J. South Afr. Bot. 31(1): 71–74, ills., 1965). **Type:** Yemen, Hadhramaut (*Rauh & Lavranos* 13348 [HEID, K, PRE]). — **Distr:** Yemen (Hadhramaut); high limestone plateau, 1375–1950 m. **I:** Reynolds (1966: 137–138); Carter & al. (2011: 320).

[5] Acaulescent or with a short procumbent stem, usually simple, sometimes forming groups of up to 6 **Ros**; **L** 10–22, rosulate, deltoid-acute, 35 × 10 cm, grey-green tinged brownish, **marginal teeth** 4 mm, pungent, dark brown, 10–15 mm apart, smaller and more crowded near the base; **Inf** 40–75 cm, with 3–5 **Br**; racemes conical-cylindrical, to 22 × 5 cm, dense; **Bra** deltoid, 12 × 5 mm; **Ped** 7–8 mm; **Fl** scarlet, 30 mm, base shortly attenuate, 8 mm Ø across the ovary, slightly narrowed above, not enlarging to the mouth; **OTep** free for 14 mm; **St** exerted 4 mm; **Sty** exerted 5 mm.

**A. erensii** Christian (Flow. Pl. South Afr. 20: t. 797 + text, 1940). **Type:** Kenya, Rift Valley Prov. (*Pole-Evans & Erens* 1587 [PRE]). — **Distr:** NW Kenya (Rift Valley Prov.: Turkana Distr.), South Sudan; rocky slopes and cliffs, open succulent shrubland and deciduous bushland, 670–800 m. **I:** Reynolds (1966: 59–60).

[5] Acaulescent, simple or with a few suckers; **L** ±16–19, densely rosulate, ovate-acute, 21 × 8–9 cm, grey-green with many elongated white spots in transverse bands, with narrow whitish translucent margin, **marginal teeth** 1–1.5 mm, whitish, 4–6 mm apart; **Inf** to 50 cm, with 2–7 **Br**; racemes cylindrical, laterals with subsecund flowers, to 21 cm, lax; **Bra** ovate-acuminate, 5–6 × 3 mm; **Ped** 8–9 mm; **Fl** pink with a bloom,

29 mm, base rounded, 10 mm Ø across the ovary, narrowed to 8 mm above, then enlarging to 9 mm at the mouth; **OTep** free for 13 mm; **St** and **Sty** exerted 2 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. ericahenriettae** T. A. McCoy (Cact. Succ. J. (US) 79(6): 271, ills. (p. 270–271), 2007). **Type:** Djibouti (*McCoy* 3130 [FT]). — **Distr:** Djibouti; lava plateau in sandy lava soil, 200 m; known only from the type locality. **I:** Carter & al. (2011: 297).

[5] Acaulescent, solitary or with 2–3 **Ros**; **L** 15–25, deltoid-acute, 100 × 25 cm, grey-green, exudate yellow, drying greenish-yellow, **marginal teeth** 4 mm, white, brown-tipped, 20–30 mm apart, pointing backwards; **Inf** 2.4 m, erect, with 3 **Br**; racemes cylindrical, to 1 m, subdense; **Bra** lanceolate-acute, 5–10 × 4 mm, white with brown nerves; **Ped** 7 mm, pink, minutely puberulent; **Fl** red, yellow-green at the mouth, puberulent at the base, 30 mm, 6–7 mm Ø across the ovary; **OTep** free for 15 mm; **St** and **Sty** exerted 5–6 mm.

**A. ericetorum** Bosser (*Adansonia*, n.s. [sér. 2], 8(4): 508–509, ills., 1968). **Type:** Madagascar, Toamasina (*Bosser* 17143 [P]). — **Distr:** C Madagascar (Toamasina); sandy heath and moorland. **I:** Castillon & Castillon (2010: 50–51); Carter & al. (2011: 235).

[3] Acaulescent, simple; **L** 15–20, rosulate, lanceolate, 18–19 × 3.5–4.5 cm, glaucous, with narrow cartilaginous margin, **marginal teeth** 1.5–2.5 mm, pale yellow, 0.7–1 mm apart; **Inf** 50–70 cm, with 1–2 **Br**; racemes cylindrical and lax to densely capitate, to 15 cm; **Bra** ovate-acute, 8–10 mm; **Ped** 15–30 mm; **Fl** yellow, 35–37 mm, base rounded, very slightly narrowed above the ovary and slightly enlarging to the mouth; **OTep** free for ±18–24 mm; **St** and **Sty** exerted 0–1 mm.

**A. erinacea** D. S. Hardy (*Bothalia* 10: 366, 1971). **Type:** Namibia, Lüderitz Distr. (*Hardy* 2619 [PRE]). — **Distr:** S Namibia; rocky hills in very arid country, 900–1350 m. **I:** Hardy (1984: t. 1885); Carter & al. (2011: 224).

≡ *Aloe melanacantha* var. *erinacea* (D. S. Hardy) G. D. Rowley (1980).

[13] Caulescent, solitary or forming small groups; stem to 60 cm, prostrate; **L** densely rosulate, narrowly triangular, 8–16 × 2–4 cm, pale greyish-green, surface slightly rough, lower surface with a few blackish-brown spines along the keel, exudate lemon-yellow, **marginal teeth** 5–9 mm, blackish-brown; **Inf** 1 m, erect, simple; racemes conical-cylindrical, 26 cm, dense; **Bra** ovate, 27 × 4.5 mm, scarious; **Ped** 19 mm; **Fl** yellow (red in bud), 28 mm, base rounded; **OTep** free almost to the base; **St** exerted 4 mm; **Sty** exerted 7 mm.

**A. erythrophylla** Bosser (*Adansonia*, n.s. [sér. 2], 8(4): 508–511, ill., 1968). **Type:** Madagascar, Antananarivo/Fianarantsoa? (*Bosser* 19583 [P]). — **Distr:** C Madagascar.

**A. erythrophylla** ssp. *erythrophylla* — **Distr:** C Madagascar (Antananarivo/Fianarantsoa: W Itremo Mts.); montane gneiss and quartzite, 1500–1600 m. **I:** Castillon & Castillon (2010: 108–109); Carter & al. (2011: 225).

[2] Acaulescent or shortly caulescent, simple; **L** 6–8, rosulate, lanceolate-linear, acuminate, 10–17 × 2–4 cm, dark brownish-red or in the centre green tinged red, **marginal teeth** 1–1.5 mm, red, 4–6 mm apart; **Inf** 15–40 cm, simple or with 1 **Br**; raceme pyramidal, 6–20 cm, lax, with 20 flowers; **Bra** ovate-subacute, 6–9 mm; **Ped** 7–12 mm; **Fl** red, 20–25 mm, base rounded, slightly narrowed above the ovary; **OTep** free for 7–8 mm; **St** and **Sty** not exerted.

**A. erythrophylla** ssp. *major* J.-B. Castillon (*CactusWorld* 29(1): 54–55, ill. (pp. 53–54), 2011). **Type:** Madagascar, Fianarantsoa (*Castillon* 50 [TAN]). — **Distr:** C Madagascar (Fianarantsoa: Saronara); on quartzitic mountain. **I:** Carter & al. (2011: 706).

[2] Differs from ssp. *erythrophylla*: More compact; **Ros** more open; **L** to 30, 28 × 6 cm; **Inf** with 5–6 **Br**; raceme 15–20 cm with 25–40 flowers.

**A. esculenta** L. C. Leach (*J. South Afr. Bot.* 37 (4): 249–259, ill., 1971). **Type:** Angola, Huila

(*Leach & Cannell* 13818 [PRE, BM, K, LISC, SRGH]). — **Distr:** S Angola (Cunene, Huila), NW Botswana, N Namibia, SW Zambia; sandy flats, ±1000 m. **I:** Rothmann (2004: 62–63).

[7] Acaulescent or shortly caulescent, dividing and sometimes suckering at the base, forming dense clumps; stem often decumbent, to 40 cm; **L** ±20, rosulate, triangular-lanceolate, acute, 40–60 × 7–10.5 cm, grey or grey-green to pinkish-brown, with many white spots in irregular ± transverse bands, lower face usually with a row of sharp blackish-brown prickles with white bases on a median line for ½ to ⅓ of the leaf length, often sharply keeled, **marginal teeth** 3–5 mm, shiny brown, 10–20 mm apart; **Inf** 1.5 (–2.2) m, with 3–5 **Br**, lower ones sometimes rebranched; racemes cylindrical-acuminate, 30–40 × ±6 cm, subdense; **Bra** ovate-acute, 20–27 × 10–11 mm; **Ped** 5–6 mm; **Fl** deep pink with pale yellow border on the lobes, 28–30 mm, subclavate, base rounded, ±6 mm Ø across the ovary, enlarging to ±8 mm above the middle; **OTep** free for 15–18 mm; **St** and **Sty** exerted 6–8 mm.

According to Leach (1971) there is a strong possibility that this could be *A. baumii* Engler & Gilg, at present treated as a taxon of uncertain status, though some authors regard *A. baumii* as a synonym of *A. zebrina*. Leach (1971) reported that the leaves of some plants were less bitter and could be eaten. Lebrun & Stork (2012: 226) report that the flowers are eaten as spinach-like vegetable.

**A. estevei** Rebmann (*Cact.-Avent. Int.* 79: 6–8, ill., 2008). **Type:** Madagascar, Fianarantsoa (*Rebmann* 14 [BR]). — **Distr:** Madagascar (Fianarantsoa); steep S-facing slopes of granite domes, 1200 m; known only from the type locality. **I:** Carter & al. (2011: 554).

[13] Caulescent, suckering from the base; stem erect to 50 cm, decumbent to 150 cm, with persistent dried leaves; **L** 15–30, laxly rosulate, lanceolate-attenuate, 22–28 × 1.2 cm, bright green, **marginal teeth** deltoid, small, yellowish, 6–10 mm apart, leaf sheath 2–2.5 cm; **Inf** 35–45 cm, ascending, with 0–3 **Br**; racemes subcapitate, sublax with 25–35 flowers; **Bra** 3–5 mm; **Ped** 15–20 mm; **Fl** yellow (orange in bud),

30 mm, 5 mm  $\varnothing$  across the ovary; **St** and **Sty** exerted 0–1 mm.

In Castillon (2009b: 29) and Castillon & Castillon (2010: 294) treated as a synonym of *A. fievetii* var. *altimatsiatrae*, from which it differs only in having shorter leaves with yellowish marginal teeth, a shorter inflorescence with more lax racemes, and shorter pedicels. Further study could confirm this synonymization.

**A. eumassawana** S. Carter & al. (Kew Bull. 51(4): 776, 1996). **Type:** Eritrea (*Ash* 1816 [K]). — **Lit:** Medhanie & Dioli (2006); McCoy (2007); both with ills. **Distr:** S Eritrea (incl. Dahlak Islands), N Djibouti; coastal bushland with *Acacia* and *Euphorbia cactus* on sandy soil, near sea level. **I:** Reynolds (1966: 154, as *A. massawana*); Sebsebe Demissew & Nordal (2010: 58–59); Carter & al. (2011: 428).

[7] Acaulescent, or nearly so, suckering to form large groups; **L**  $\pm$ 16, rosulate, lanceolate, 45–50  $\times$  7–18 cm, dull grey-green, sometimes with few pale spots, surface smooth, **marginal teeth** 3 mm, tip reddish-brown, 1.5–2 mm apart; **Inf** 1.2–1.5 m, with 1–2 **Br**, all parts minutely papillose-puberulent when young, later glabrescent; racemes cylindrical-conical, (15–) 20–25 cm, lax; **Bra** ovate-triangular, tip acute to acuminate, 6.5–7  $\times$  2.5–4 mm; **Ped** 3–4.5 (–7) mm; **Fl** pale scarlet or orange, lobes with paler yellowish margins, very minutely papillose, (18–) 20–21 mm, base rounded, uniformly  $\pm$ 7 mm  $\varnothing$  (when pressed); **OTep** free for  $\pm$ 12 mm; **St** and **Sty** exerted 0–1 mm.

Reynolds included this taxon in his *A. massawana*, forming the epithet from the old locality name Massawa (now Mits'iwa) in Eritrea, but selecting a specimen from Tanzania as type. The Eritrean and Tanzanian plants are not conspecific, however. As the name *A. massawana* must be used for the Tanzanian material, the name of the newly described Eritrean species indicates that it is the true Massawa plant. Medhanie & Dioli (2006) report that around Massawa the species is only found in graveyards, according to McCoy (2007) a single clone (hence non-fruiting) originally introduced

from Djibouti, where an apparently natural and fruiting population was seen.

**A. excelsa** A. Berger (Notizbl. Königl. Bot. Gart. Berlin 4: 247, 1906). **Type** [lecto]: Zimbabwe, Bulawayo Distr. (*Eyles* 1240 [PRE]). — **Lit:** Leach (1977: 386–389). **Distr:** Moçambique, Malawi, Zambia, Zimbabwe, RSA.

**A. excelsa** var. **breviflora** L. C. Leach (Kirkia 10(2): 387–389, ill., 1977). **Type:** Moçambique, Zambesia (*Royle* s.n. in *Leach* 14111 [SRGH, PRE]). — **Distr:** S Malawi, Moçambique (Zambesia: Morrumbala Distr.): lower reaches of Ruo River; fire-protected granite rocky outcrops, 230–615 m. **I:** Klopper & al. (2012: 76, 85, incl. distribution map).

[9] Differs from var. *excelsa*: **L** narrower, both faces without prickles; **Inf** with racemes narrower, usually less dense; **Fl**  $\pm$ 20 mm.

**A. excelsa** var. **excelsa** — **Distr:** Moçambique, C Zambia, Zimbabwe, NE RSA (NE Limpopo); rocky granite hills and plains in open bush, 300–1525 m. **I:** Reynolds (1966: 315–316); Carter & al. (2011: 687); Wyk & Smith (2014: 60–61).

[9] Caulescent, simple; stem erect, to 4 m, with dried leaf remains; **L**  $\pm$ 30, densely rosulate, oldest becoming recurved, triangular-attenuate, to 80  $\times$  15 cm, dull green, lower face usually tuberculate-aculeate, **marginal teeth** 5–6 mm, pungent, reddish-brown, 15–20 mm apart; **Inf** 80–100 cm, with up to 14 **Br**; racemes cylindrical, 15–25 cm, very dense; **Bra** reflexed, 4–6  $\times$  4–6 mm; **Ped**  $\pm$ 1 mm; **Fl** red or orange, 30 mm, slightly ventricose, base rounded, 5 mm  $\varnothing$  across the ovary, enlarging to 7 mm in the middle, then narrowing to the mouth; **OTep** free for 22–23 mm; **St** and **Sty** exerted 8–10 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

**A. eximia** Lavranos & T. A. McCoy (CactusWorld 24(4): 199–200, ills., 2006). **Type:** Madagascar, Antananarivo (*Pronk* s.n. in *Lavranos* 32025 [TAN]). — **Distr:** Madagascar (Antananarivo: Ibity region); montane, >1200 m;

known from the area of the type locality only. **I**: Castillon & Castillon (2010: 78–79); Carter & al. (2011: 680).

[9] Caulescent; stem to 5 (–7) m, 8–14 cm Ø, unbranched; **L** 20–25, rosulate, narrowly lanceolate, acuminate, 45 × 5–6 cm, bright green with reddish tinge, surface smooth, exudate brownish-yellow, drying darker, **marginal teeth** deltoid, 2 mm, yellowish-white, 5–12 mm apart; **Inf** 18–20 cm, erect, simple; racemes cylindrical to subcapitate, 7–10 × 8–9 cm, dense; **Bra** narrow, 8–10 × 6–7 mm; **Ped** 20–25 mm; **Fl** yellow (orange or brick-red in bud), 20–22 mm, 5 mm Ø across the ovary; **OTep** free for 10–12 mm; **St** and **Sty** exerted 5–6 mm.

Reminiscent of *A. helenae* in overall architecture, but with shorter almost globose racemes.

**A. falcata** Baker (J. Linn. Soc., Bot. 18(108): 181–182, 1880). **Type**: RSA, Northern Cape (Zeyher 1678 [K]). — **Dist**: RSA (Northern Cape, NW Western Cape); arid plains, 0–1000 m. **I**: Reynolds (1950: 316–317); Carter & al. (2011: 438); Wyk & Smith (2014: 92).

[5] Acaulescent or shortly caulescent, usually in groups, with **Ros** lying almost on their sides; **L** ±20, densely rosulate, lanceolate-acuminate, usually falcate, ±30 × 7 cm, tip usually a spine, grey-green to glaucous, surface rough, lower face with slight keel near the tip with ±6 prickles, **marginal teeth** 5 mm, horny, reddish-brown, 10 mm apart; **Inf** to 60 cm, with up to 10 **Br**, lower ones sometimes rebranched; racemes usually cylindrical-acuminate, to 30 (–40) × 7 cm, shorter and denser to longer and more lax; **Bra** deltoid-acuminate, 18 mm or slightly longer; **Ped** ±18 mm; **Fl** dull reddish to pale scarlet, rarely yellow, 40 mm, base shortly attenuate, 7 mm Ø across the ovary, scarcely narrowed above; **OTep** free for 10 mm; **St** exerted 8 mm; **Sty** exerted 10 mm.

**A. ferox** Miller (Gard. Dict., Ed. 8, no. 22, 1768). **Type**: [lecto — icono]: Munting, Phytogr. Curios., fig. 95, 1727. — **Lit**: Viljoen & al. (1996: as *A. candelabrum*); Smith & al. (2016: vs. *A. candelabrum*); Kuiper & al. (2015: pollination ecology). **Dist**: SW Lesotho, RSA (Western



**Fig. 23** *Aloe ferox*. (Copyright: G. F. Smith)

Cape, Eastern Cape, SE Free State); mountain slopes to flat open areas in arid bushland, 0–1500 m. **I**: Reynolds (1950: 460–465); Carter & al. (2011: 665); Wyk & Smith (2014: 62–63). — **Fig. 23**.

≡ *Pachidendron ferox* (Miller) Haworth (1821); **incl.** *Aloe perfoliata* var. *ε* Linné (1753); **incl.** *Aloe perfoliata* var. *γ* Linné (1753); **incl.** *Aloe socotorina* Masson (1773); **incl.** *Aloe perfoliata* Thunberg (1785) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe perfoliata* var. *ferox* Aiton (1789); **incl.** *Aloe perfoliata* var. *ζ* Willdenow (1799); **incl.** *Aloe supralaevis* Haworth (1804) ≡ *Pachidendron supralaevae* (Haworth) Haworth (1821); **incl.** *Aloe pseudoferox* Salm-Dyck (1817) ≡ *Pachidendron pseudoferox* (Salm-Dyck) Haworth (1821); **incl.** *Aloe subferox* Sprengel (1826) ≡ *Aloe ferox* var. *subferox* (Sprengel) Baker (1880); **incl.** *Aloe ferox* var. *incurvata* Baker (1880); **incl.** *Aloe ferox* var. *hanburyi* Baker (1896); **incl.** *Aloe galpinii* Baker (1901) ≡ *Aloe ferox* var. *galpinii* (Baker) Reynolds (1937); **incl.** *Aloe candelabrum* A. Berger (1906); **incl.** *Aloe ferox* var. *erythrocarpa* A. Berger (1908).

[9] Caulescent, simple; stem to 3 (–5) m, with dead leaf remains; **L** 50–60, densely rosulate, lanceolate-ensiform, to 100 × 15 cm, dull green, sometimes reddish-tinged, surface glabrous or with few to many irregular prickles, **marginal teeth** ±6 mm, reddish to reddish-brown, 10–20 mm apart; **Inf** with 5–8 **Br**; racemes cylindrical, slightly acuminate, 50–80 × 9–12 cm, narrowing

to  $\pm 6$  cm at the tip, very dense, buds horizontal; **Bra** ovate-acute,  $8\text{--}10 \times 3\text{--}5$  mm; **Ped** 4–5 mm; **Fl** scarlet, sometimes orange, sometimes also white, 33 mm, slightly ventricose-clavate, base rounded, enlarging above the ovary, slightly narrowed at the mouth; **OTep** free for 22 mm; **St** and **Sty** exerted 20–25 mm. — **Cytology**:  $2n = 14$  (Fernandes 1930, Vosa 1982: as *A. candelabrum*).

A very variable species, but Reynolds (1950) did not accept the varieties that have been described. According to Reynolds (1950) *A. horrida* Haworth possibly belongs here. Natural hybrids with other species have been reported by the same author. The lectotype cited above has been designated by Smith & Figueiredo (2018a), who also designated the specimen *E. E. Campbell* 2737 (PEU), from the Eastern Cape, RSA, as epitype.

One of the most utilised species, with a long history of indigenous use and now a lucrative crop plant for the export market (Newton & Vaughan 1996). It is one of the few plants appearing in ancient San rock paintings (Reynolds 1950). Export to Europe of the bitter leaf exudate, called “Cape aloes”, started in 1761 (Wyk 2008). Products prepared from the leaf exudate and more recently from the gel of the inner parenchyma, range from laxative medicine to skin creams and tonic drinks. Chemically, there are considerable differences from the more widely used *A. vera*, with more variation between plants (O’Brien & al. 2011). Wild plants are still exploited, apparently without causing great harm to the natural populations (Newton & Vaughan 1996). In an investigation of the sustainability of wild-harvesting, Shackleton & Gambiza (2007) reported an annual growth of  $\pm 2$  cm in plants over 2 m tall, with 1.24–3.71 leaves per rosette added each year. The tallest plants, at 2.65 m, were estimated to be 95 years old. Pollination is almost exclusively by nectar-feeding birds (Hargreaves & al. 2012), which arrive at the *Aloe* locality in large numbers in the flowering season (Kuiper & al. 2015). Field studies by Stokes & Yeaton (1995: as *A. candelabrum*) confirm that birds are most important for pollination, with greater seed production in denser populations

and at times when many plants are in flower. Seeds are dispersed over distances up to three times the height of the parent plant.

**A. fibrosa** Lavranos & L. E. Newton (Cact. Succ. J. (US) 48(6): 273–275, ill., 1976). **Type**: Kenya, Eastern Prov. (*Archer* 410 [EA, K]). — **Distr**: S Kenya, N Tanzania; rocky slopes with dense scrub, 1500–2000 m. **I**: Carter & al. (2011: 567).

[16] Caulescent, branching at the base; stem erect to  $2 \text{ m} \times 3 \text{ cm}$ , when longer supported by surrounding vegetation or decumbent to 2.5 m, with dead leaf remains; **L** scattered along the stem, lanceolate-acute,  $30\text{--}35 \times 3\text{--}6$  cm, bright green, tinged brownish in exposed situations, with a few spots on young shoots, interior leaf tissue with internal fibres, esp. at the base and in the sheath, **marginal teeth** 3–4 mm, firm, brown-tipped, 15–17 mm apart; **Inf** to 1 m, simple or with 1–2 **Br**; racemes conical-cylindrical,  $10\text{--}20 \times 10$  cm, dense; **Bra** ovate,  $12\text{--}18 \times 7$  mm, whitish, imbricate in bud stage; **Ped** 20–25 mm; **Fl** orange-red, yellowish at the mouth, 30–35 mm, base truncate, 8–9 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, enlarging to 9–10 mm at the mouth; **OTep** free for  $\pm 10\text{--}11$  mm; **St** and **Sty** exerted  $\pm 1$  mm. — **Cytology**:  $2n = 14$  (Cutler & al. 1980).

**A. fievetii** Reynolds (J. South Afr. Bot. 31(4): 279–281, ill., 1965). **Type**: Madagascar, Fianarantsoa (*Rauh* 10332 [PRE, K, P, TAN]). — **Distr**: SE Madagascar (Fianarantsoa).

**A. fievetii** ssp. **fievetii** — **Lit**: Castillon (2010). **Distr**: SE Madagascar (Fianarantsoa); grass soil pockets on rocky granite hills in full sun, 1200 m; known only from the type locality. **I**: Reynolds (1966: 464–465); Castillon & Castillon (2010: 140–141); Carter & al. (2011: 255).

[4] Acaulescent or shortly caulescent, usually simple; **L** 12–16, densely rosulate, lanceolate-attenuate, tip slightly twisted and with 3–4 small teeth,  $35 \times 5\text{--}6$  cm, green with slight reddish tinge, with pinkish-red margin, **marginal teeth** 2–3 mm, pinkish-red, 7–10 mm apart; **Inf** to 50 cm, simple or with 1 **Br**; racemes corymbose-



capitate,  $\pm 9 \times 4$  cm, dense; **Bra** ovate-acute,  $5 \times 5$  mm, reddish-brown with membranous edge; **Ped** 30 mm; **Fl** orange, 27–30 mm, slightly clavate, base rounded,  $5\text{--}6$  mm  $\varnothing$  across the ovary, enlarging above; **OTep** free for 14 mm; **St** and **Sty** exserted 0–1 mm.

**A. fievetii** ssp. **johannis-baptistei** J.-B. Castillon (CactusWorld 31(1): 47–48, ills., 2013). **Type:** Madagascar, Fianarantsoa (*Castillon* 56 [TAN]). — **Distr:** SE Madagascar (Fianarantsoa); on granite rocks, 2000 m.

[4] Differs from ssp. *fievetii*: **Ros** more open; **L**  $60 \times 8$  cm; **Inf** shorter, with up to 10 **Br**.

**A. fievetii** var. **altimatsiatrae** (J.-B. Castillon) J.-B. Castillon (Cact.-Avent. Int. 84: 32, 2009). **Type:** Madagascar, Fianarantsoa (*Castillon* 35 [TAN]). — **Distr:** SE Madagascar (Fianarantsoa); shaded granite outcrops, 1200 m. **I:** Castillon & Castillon (2010: 142).

≡ *Aloe altimatsiatrae* J.-B. Castillon (2008).

[4] Differs from ssp. *fievetii*: Suckering to form small groups; stem to 50 cm, decumbent; **L** 15–30, laxly rosulate,  $30\text{--}55 \times 4\text{--}6$  cm; **Inf** 70–110 cm, usually with 2 **Br**; **Fl** yellow (orange in bud).

Includes also *A. estevei* (see there) according to Castillon & Castillon (2010).

**A. fievetii** var. **ambatofinandrahanensis** J.-B. Castillon (Cact.-Avent. Int. 85: 6–7, ills., 2010). **Type:** Madagascar, Fianarantsoa (*Castillon* 46 [TAN, P]). — **Distr:** SE Madagascar (Fianarantsoa); mountains, 1900 m.

[4] Differs from ssp. *fievetii*: Smaller, with fewer suckers; **L** shorter, thicker, glaucous-reddish, **marginal teeth** more robust with black tip and closer together; **Inf** shorter, 30–50 cm.

**A. fimbrialis** S. Carter (Kew Bull. 51(4): 779–781, ills., 1996). **Type:** Zambia, Northwest Prov. (*Fanshawe* 8938 [K, SRGH]). — **Lit:** Williamson (2003b); Williamson (2005). **Distr:** W Zambia, SW Tanzania; Miombo woodland, often on ant hills, 900–1250 m.

[2] Acaulescent; **R** fibrous plus 7–10 thickened **R** to 12 mm  $\varnothing$ ; **L** to 7, rosulate, spreading flat on

the ground with tips upturned, bases expanded to form a bulb 7–8 cm  $\varnothing$ , lamina ovate to broadly ovate, to  $24 \times 12$  cm, pea-green merging to green-brown, both surfaces scabrid, exudate honey-coloured to orange, **marginal teeth** 1–1.5 mm, soft, white, densely crowded; **Inf** 90 cm, simple; raceme cylindrical,  $20\text{--}30 \times 6$  cm, lax to subdense; **Bra** linear-lanceolate, attenuate,  $10\text{--}14 \times 2\text{--}2.3$  mm, imbricate in bud stage; **Ped** 8–10 mm; **Fl** coral-pink, lobe apices white with dark central nerves, 30–35 mm, base flat, 5 mm  $\varnothing$  across the ovary; **OTep** free for 10–15 mm.

**A. fleurentinorum** Lavranos & L. E. Newton (Cact. Succ. J. (US) 49(3): 113–114, ills., 1977). **Type:** Yemen, Sana'a Prov. (*Lavranos* 11386 [E]). — **Lit:** McCoy & Lavranos (2010). **Distr:** SW Saudi Arabia (Asir), Yemen; rocky slopes, 1500–2350 m. **I:** Collenette (1999: 22); Carter & al. (2011: 308).

**Incl.** *Aloe edentata* Lavranos & Collenette (2000).

[3] Acaulescent, simple; **L** 8–12, rosulate, lanceolate,  $20\text{--}30 \times 6\text{--}7$  cm, dark green, tinged brownish in exposed situations, surface rough, **marginal teeth** 1–1.5 mm, firm, whitish; **Inf** 35–40 cm, with 3–6 **Br**; racemes cylindrical, lax, with 10–20 flowers; **Bra** acute, 6–8 mm; **Ped** 11 mm; **Fl** bright red, yellow at the mouth, 31–33 mm, base very shortly attenuate, 8 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for 9–10 mm; **St** exserted 0–1 mm; **Sty** not exserted. — **Cytology:**  $2n = 14$  (protologue).

**A. fleuretteana** Rauh & Gerold (Kakt. and Sukk. 51(5): 121–123, ills., 2000). **Type:** Madagascar, Toliara (*Gerold* s.n. in *BG Heidelberg* 75706 [HEID]). — **Distr:** SW Madagascar (Toliara); bushland on granite. **I:** Castillon & Castillon (2010: 207); Carter & al. (2011: 535).

[14] Caulescent, suckering at the base forming dense groups; stems to 5 cm; **L**  $\pm 10$ , loosely rosulate, lanceolate-attenuate,  $13 \times 8$  cm, green with fine white striations and white flecks, **marginal teeth** pungent, deltoid, 2 mm; **Inf** to 35 cm, erect, simple; racemes cylindrical with 10–12 flowers, lax; **Bra** 10–15 mm; **Fl** shiny cinnabarred, whitish with green mid-stripe above, 28 mm,

base flat, scarcely constricted above the ovary, then widening to 7 mm  $\emptyset$ ; **OTep** free for  $\pm 5$  mm; **St** and **Sty** exerted 0–1 mm.

The type locality is uncertain. Possibly a hybrid with *A. bakeri* as one parent.

**A. flexilifolia** Christian (J. South Afr. Bot. 8(2): 167–169, ills., 1942). **Type:** Tanzania, Lushoto Distr. (*Boscawen* s.n. in Christian 897 [SRGH, EA, K, PRE]). — **Distr:** Tanzania (Usambara Mts.); rocky slopes and cliff faces, 1000–1220 m; known only from the region of the type locality. **I:** Reynolds (1966: 363–364); Carter & al. (2011: 511).

[13,15] Caulescent, much branched at the base, forming groups to 2 m  $\emptyset$ ; stem in deep soil to 1 m  $\times$  6–7 cm, erect or ascending, in shallow soil and overhanging rock faces to 2 m  $\times$  5 cm, sprawling and pendulous; **L** rosulate and persistent for 30 cm below, ensiform-attenuate, becoming recurved or falcately decurved when stems pendulous, 50  $\times$  6–7 cm, glaucous-green tinged bluish, with narrow pale cartilaginous margin, exudate drying brownish, **marginal teeth** 1–2 mm, brownish, 10–20 mm apart; **Inf** 50–65 cm, usually sub-oblique or basally curving downwards with racemes erect, with 6–8 **Br**; racemes cylindrical, to 12  $\times$  7–8 cm, subdense; **Bra** ovate-deltoid, 5–6  $\times$  3 mm; **Ped** 12–14 mm; **Fl** scarlet or brownish-red, paler at the mouth, 33–35 mm, base rounded, 9 mm  $\emptyset$  across the ovary, slightly narrowed above, slightly enlarging towards the mouth; **OTep** free for  $\pm 11$ –12 mm; **St** and **Sty** exerted 2–4 mm.

The specific epithet was chosen because the type plant developed transverse folds in the leaves when they became deflexed, but this is not a constant character.

**A. florenceae** Lavranos & T. A. McCoy (Kakt. and. Sukk. 55(10): 284, ills., 2004). **Type:** Madagascar, Antananarivo (*Razafindratsira* s.n. in Lavranos 31860 [TAN, P, Z]). — **Distr:** Madagascar (Antananarivo: SW of Antsirabe); quartzitic mountains. **I:** Castillon & Castillon (2010: 77);

[4] Acaulescent, suckering to form small clumps with up to 5 **Ros**; **L** to 40, triangular,

acute, 3–4  $\times$  0.9–1.1 cm, dark green to brownish, surface with warts 0.75 mm long in 2–4 rows, each with a soft papilla, **marginal teeth** soft, 1 mm, 1.2 mm apart; **Inf** 30 cm, erect, simple; racemes shortly conical, with 8–22 flowers; **Bra** lanceolate, 22  $\times$  10 mm; **Ped** extremely short; **Fl** cream to pinkish-brown, 27–30 mm, 5 mm  $\emptyset$  across the ovary; **OTep** free for 10–12 mm; **St** shortly exerted; **Sty** exerted 6 mm.

When not in flower, confusion with *A. haworthioides* is possible. Castillon & Castillon (2010: 77) suggest that this could be the hybrid *A. parvula*  $\times$  *A. compressa*.

**A. fontainei** Rebmann (Cact.-Avent. Int. 82: 2–5, ills., 2009). **Type:** Madagascar, Antananarivo (*Rebmann* 18 [BR]). — **Distr:** Madagascar (Antananarivo); granite domes and cliffs, 1300 m.

[13] Caulescent, branching from the base and along the stems; stem to 1 m, prostrate, erect and to 1.5 m when growing from rock clefts; **L** 16–20, rosulate, lanceolate-attenuate, 30  $\times$  8–9 cm, greenish to reddish, **marginal teeth** deltoid, 1.5 mm, hyaline; **Inf** to 90 cm, erect, with 3–5 **Br**; racemes cylindrical, 30–50 cm, lax; **Bra** 12–16 mm, scarious; **Ped** 12–20 mm; **Fl** red, lobes white-tipped, 20–25 mm.

Possibly conspecific with *A. mandatoensis* (Castillon & Castillon 2010: 27, 395, Carter & al. 2011).

**A. forbesii** Balfour *fil.* (in Forbes & Ogilvie-Grant, Nat. Hist. Socotra, 511–512, t. 26B, 1903). **Type:** [icono]: l.c. t. 26B. — **Distr:** Yemen (Socotra); rocky embankments, 900 m. **I:** Reynolds (1966: 193–195); Carter & al. (2011: 213).

[5] Acaulescent or shortly caulescent, simple or in small groups; **L** 16–20, densely rosulate, lanceolate-attenuate, 25  $\times$  6–7 cm, dull green, **marginal teeth** 0.5–1 mm, pale, 4–8 mm apart; **Inf** 60–80 cm, with 5 or more **Br**; racemes cylindrical, to 10–25  $\times$  5 cm, lax; **Bra** 3–4  $\times$  1.5 mm; **Ped** 10–12 mm; **Fl** pale scarlet in the lower  $\frac{1}{2}$ , becoming yellowish above, 22–24 mm, base shortly attenuate, narrowed above the ovary, enlarging towards the mouth; **OTep** free for 6–7 mm; **St** and **Sty** exerted 2 mm. — **Cytology:** 2n = 14 (Brandham 1971).

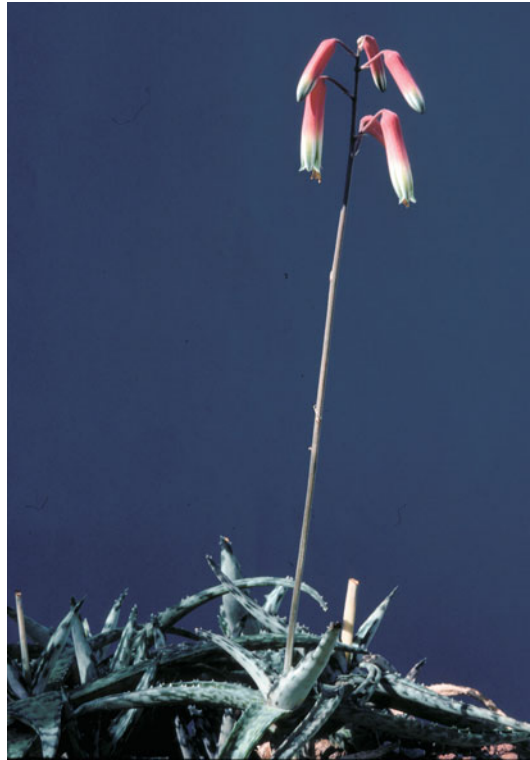
**A. fosteri** Pillans (South Afr. Gard. 23: 140, 1933). **Type:** RSA, Mpumalanga (*Pillans* s.n. [BOL 20447]). — **Distr:** RSA (Limpopo, Mpumalanga: Lydenburg Distr.); stony soils in subtropical bushland, 200–1220 m. **I:** Reynolds (1950: 253–254); Carter & al. (2011: 187); Wyk & Smith (2014: 228–229).

[5] Acaulescent or with stem to 20 cm, usually suckering to form small groups, sometimes simple; **L**  $\pm 20$ , rosulate, lanceolate-attenuate,  $\pm 40 \times 8$ –10 cm, upper face pale dull green, obscurely lineate and with obscure dull white oval spots in  $\pm$  transverse bands, lower face usually unspotted, exudate drying purplish, **marginal teeth** 3–4 mm, pungent, slightly deflexed, 10–15 mm apart; **Inf** to 2 m, with  $\pm 8$  **Br**, lower ones rebranched; racemes narrowly cylindrical-acuminate, to  $40 \times 6$ –7 cm, lax; **Bra** lanceolate-acuminate, usually a little longer than the pedicels; **Ped** 6–9 mm; **Fl** pale dull brick-red, somewhat pruinose, 30 mm, base truncate, 9 mm  $\varnothing$  across the ovary, abruptly narrowed to 5.5 mm above, enlarging towards the mouth; **OTep** free for 8 mm; **St** and **Sty** exserted 0–1 mm. — **Cytology:**  $2n = 14$  (Müller 1945).

**A. fouriei** D. S. Hardy & Glen (Flow. Pl. Afr. 49(3–4): t. 1941 + text, 1987). **Type:** RSA, Mpumalanga (*Fourie* 3070 [PRE]). — **Distr:** RSA (Mpumalanga: Lydenburg Distr.: Pilgrim's Rest); steep grassy slopes usually on dolomite, 1000–1800 m. **I:** Craib (2006: 53–56); Carter & al. (2011: 135); Wyk & Smith (2014: 314–315).

[10] Caulescent, simple or forming small groups; stem  $\pm 15$  cm, with dead leaf bases on the apical 1 cm; **L** distichous, triangular,  $27.5$ – $35 \times 1$ – $2.5$  cm, grass-green, **marginal teeth**  $\pm 0.4$  mm, 2.5 mm apart; **Inf**  $\pm 40$  cm, simple; raceme capitate, subdense, with  $\pm 20$  flowers; **Bra**  $\pm 16 \times 8$  mm; **Ped** 23–45 mm; **Fl** orange, becoming green towards the tip, 35–40 mm, base rounded, 11–13 mm  $\varnothing$  across the ovary, narrowing above to 6–8 mm at the mouth; **OTep** free to the base; **St** and **Sty** exserted 0–1 mm.

Craib (2006) considers that *A. fourieri*, *A. verecunda* and *A. vossii* might be mere ecotypes of one species. Further fieldwork is required.



**Fig. 24** *Aloe fragilis*. (Copyright: U. Eggli)

**A. fragilis** Lavranos & Rösli (Cact. Succ. J. (US) 66(1): 4–5, ills., 1994). **Type:** Madagascar, Antsiranana (*Lavranos & al.* 28737 [ZSS, P]). — **Lit:** Lüthy (2006: 37–38, conservation, with ill.). **Distr:** N Madagascar (Antsiranana: Cap Manambato); crystalline basement rocks by the sea-shore; known only from the type locality. **I:** Castillon & Castillon (2010: 326–327); Carter & al. (2011: 396); Castillon & Nusbaumer (2014: 79). — Figs. 24 and 25.

[11] Acaulescent or shortly caulescent, caespitose forming large groups, branches procumbent; **L** rosulate, deltoid-acute,  $3$ – $5$  (– $10$ )  $\times 1.5$ – $2$  cm, glossy, dark glaucous-green, with many whitish-green spots, with narrow greenish-white margin, **marginal teeth** 1–1.5 mm, firm, greenish-white, often coalescent; **Inf** 20–60 cm, usually simple, rarely with 1 **Br**; racemes cylindrical, 10–15 cm, lax, with up to 25 flowers; **Bra** lanceolate,  $\pm 2 \times 1$  mm; **Ped** 8–9 mm; **Fl** with carmine-red base, becoming creamy-white with green midrib towards the mouth, 20–25 mm, base shortly



**Fig. 25** *Aloe fragilis*. (Copyright: U. Eggli)

attenuate, 4 mm  $\varnothing$  across the ovary, very slightly narrowed above, then enlarging slightly above and narrowing at the mouth; **OTep** free for 3.5–4 mm; **St** and **Sty** exerted 0–1 mm.

The recently described *A. gautieri* is closely similar but has paler flowers, a more elongated raceme, and a less well-defined rosette.

**A. framesii** L. Bolus (South Afr. Gard. 1933: 140 (June), 1933). **Type:** RSA, Northern Cape (*Frames* s.n. [BOL 19186]). — **Distr:** RSA (W Northern Cape, NW Western Cape); coastal sand flats, to 100 m. **I:** Reynolds (1950: 403–404); Carter & al. (2011: 569); Wyk & Smith (2014: 196–197). — Fig. 26.

≡ *Aloe microstigma* ssp. *framesii* (L. Bolus) Glen & D. S. Hardy (2000); **incl.** *Aloe amoena* Pillans (1933).

[12] Caulescent, branching freely forming dense groups of up to 20 **Ros** and to 3 m  $\varnothing$ ; stem decumbent; **L** densely rosulate, lanceolate-attenuate, 30–35  $\times$  7–8 cm, dull grey-green to

slightly bluish-green, with or without scattered white spots, **marginal teeth**  $\pm$ 3 mm, pungent, reddish-brown, 10 mm apart; **Inf** to 70 cm, sometimes simple, mostly with 2–3 **Br**; racemes conical to cylindrical-acuminate, to 25  $\times$  10 cm, subdense; **Bra** ovate-acute, 20  $\times$  9 mm, reddish; **Ped** 25–30 mm; **Fl** dull scarlet, sometimes greenish-tipped, 35 mm, base rounded, not narrowed above the ovary; **OTep** free to the base; **St** and **Sty** exerted 5–6 mm. — **Cytology:**  $2n = 14$  (Riley 1959).

Close to *A. microstigma*, and sometimes treated as mere coastal subspecies.

**A. francombei** L. E. Newton (Brit. Cact. Succ. J. 12(2): 54–55, ills., 1994). **Type:** Kenya, Rift Valley Prov. (Newton & al. 4130 [K, EA]). — **Distr:** Kenya (Rift Valley Prov.: Laikipia Distr.); shade of shrubs on rocky slopes, 1520–1650 m; known only from the area of the type locality. **I:** Carter & al. (2011: 598).

[15] Caulescent, branching at the base; stem erect or ascending, to 40 cm; **L** 15–20, rosulate, triangular, to 31  $\times$  7 cm, dull green with few or many white elliptic spots, mostly on the lower face, becoming red-tinged in exposed situations, surface rough, exudate yellow, **marginal teeth** to 4 mm, firm, brown-tipped, 7–9 mm apart; **Inf** to 60 cm, with up to 8 **Br**; racemes cylindrical, 6–20 cm, subdense; **Bra** triangular, 10–12  $\times$  3 mm, imbricate in bud stage; **Ped** 8–13 mm; **Fl** pale pink with minutely pustulate surface, lobes with white margins, 25 mm, base rounded, 5.5 mm  $\varnothing$  across the ovary, enlarging to 7 mm above, then narrowing to 6 mm at the mouth, lobes spreading to 8–9 mm; **OTep** free for 12–14 mm; **St** and **Sty** exerted 2–5 mm.

**A. friisii** Sebsebe & M. G. Gilbert (Kew Bull. 55(3): 683–686, ills., 2000). **Type:** Ethiopia, Gamo Gofa Region (*Friis* & al. 8931 [ETH, C, K]). — **Distr:** S Ethiopia (Gamo Gofa Region); under thickets on a rocky slope in deciduous woodland, 600–1600 m; known only from the type locality. **I:** Sebsebe Demissew & Nordal (2010: 103–104); Carter & al. (2011: 499).

[13] Caulescent; stem erect or sprawling, to 20 cm, 2–4 cm  $\varnothing$ , simple or with up to 2 branches; **L**



**Fig. 26** *Aloe framesii*.  
(Copyright: L. E. Newton)



lax, narrowly elliptic, 25–35 × 3.5–5 cm, pale green with sparse whitish, sometimes obscure, spots, **marginal teeth** 1–2 mm, whitish, sometimes with brownish tips, 2–8 mm apart; **Inf** 50–75 cm, ascending, with 8–13 **Br**, lower ones rebranched; racemes cylindrical, 3–14 cm, lax; **Bra** ovate-acuminate, 2–5 × 1–3 mm, scarious with usually 3 reddish-brown veins; **Ped** 8–12 mm; **Fl** yellow with darker longitudinal veins, 22–25 × 7–10 mm, base rounded, slightly narrowed above the ovary; **OTep** free for 7.3–8.3 mm; **St** and **Sty** not exerted.

**A. fullerii** Lavranos (Cact. Succ. J. (US) 39(4): 125–127, ill., 1967). **Type:** Yemen (*Fuller* s.n. in *Lavranos* 4206 [PRE]). — **Lit:** Lavranos & McCoy (2002). **Distr:** Yemen; *Acacia* scrub on sandy soil, 500–900 m. **I:** Carter & al. (2011: 269).

**Incl.** *Aloe rigens* var. *mortimeri* Lavranos (1967).

[3] Caulescent, simple; stem short; **L** ±12, rosulate, ensiform, 45 × 8 cm, glaucous green, at times tinged yellowish, with reddish-brown cartilaginous margin, **marginal teeth** 1–2 mm, pungent, brown, 12–25 mm apart; **Inf** 40–70 cm, with 1–2 **Br**; racemes cylindrical-acuminate, 30–35 cm, lax; **Bra** 12–15 mm, pink at the base; **Ped** 5–6 mm; **Fl** coral-red, tips of the lobes pinkish-cream, outside densely but minutely papillate, esp. on the lobes, 35 mm, base attenuate,

7 mm Ø across the ovary, narrowed to 5 mm above, then enlarging to the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 0–1 mm.

Yellow-flowered plants have also been seen at the type locality.

**A. gariensis** Pillans (South Afr. Gard. 23: 213, 1933). **Type:** Namibia, Karas (*Pillans* 6557 [PRE]). — **Distr:** S Namibia, N RSA (NW Northern Cape): lower reaches of the Gariiep (Orange) river; rocky slopes. **I:** Reynolds (1950: 401–402); Carter & al. (2011: 259); Wyk & Smith (2014: 198–199). – Fig. 27.

**Incl.** *Aloe gariusiana* Dinter (1928) (*nom. inval.*, ICN Art. 32.1c).

[4] Acaulescent or shortly caulescent, usually simple, sometimes branching to form small groups; stem erect or procumbent, to 1 m when simple, with dead leaf remains; **L** densely rosulate, lanceolate-attenuate, 30–40 × 5–8 cm, dull green to reddish-brown, somewhat lineate, with or without white spots, with horny margin, **marginal teeth** 2–3 mm, pungent, reddish-brown, ±10 mm apart; **Inf** 80–120 cm, simple; racemes narrowly cylindrical-acuminate, 35–50 × 7 cm, dense; **Bra** lanceolate, ±25 × 8 mm, imbricate in bud stage; **Ped** 15–20 mm; **Fl** mostly yellow or greenish-yellow, sometimes reddish in bud, 23–27 mm, base rounded, enlarging towards the mouth; **OTep** free to the base; **St** and **Sty** exerted 5–6 mm.





**Fig. 27** *Aloe gariopensis*. (Copyright: D. J. Supthut)

A very variable species. Natural hybrids with other species have been reported (Reynolds 1950). The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984).

**A. gautieri** J.-P. Castillon & Nusbaumer (Candollea 69(1): 76–78, ills., 2014). **Type:** Madagascar, Antsiranana (*Gautier & al.* 4272 [G, MO, P, PRE, TAN, Herb. Daraina]). — **Distr:** N Madagascar (Antsiranana); dry forest or on granite ridges with little soil, 350–550 m.

[11] Caulescent, suckering from the base, with bulbils on the lower part of the stem; stem to 35 × 0.4 cm, 8–15 per tuft; **L** to 13, dispersed along the stem, narrowly linear-lanceolate, 5–14 × 0.5 cm, tip obtuse with 2–4 white teeth, green with many irregular white spots, sheath 1 cm, with reddish veins, exudate straw-yellow drying darker yellow, **marginal teeth** 1 mm, white, 1–5 mm apart; **Inf** 25–45 cm, erect, simple; raceme cylindrical, 10–18 cm, lax; **Bra** triangular, 5 × 3 mm, white, scarious, with central greenish to maroon nerve;

**Ped** 7–10 mm, pink at the base, becoming greenish-white; **Fl** pink at the base, becoming white with central green nerve towards the mouth, 25 × 4 mm Ø; **OTep** free for 12.5 mm; **St** and **Sty** not exerted.

Compared with *A. fragilis* in the protologue.

**A. gerstneri** Reynolds (J. South Afr. Bot. 3: 133, 1937). **Type:** RSA, KwaZulu-Natal (*Reynolds* 2320 [PRE, BOL]). — **Distr:** RSA (N KwaZulu-Natal: Babanango Distr.); grassland on rocky slopes, 500–900 m. **I:** Reynolds (1950: 455–456, t. 51); Carter & al. (2011: 284); Wyk & Smith (2014: 154–155).

[4,5] Acaulescent or shortly caulescent, usually simple; **L** 20–30, densely rosulate, lanceolate-ensiform, to 60 × 9 cm, dull grey-green, surface smooth, lower face sometimes with a few prickles in a median line near the tip, **marginal teeth** 4 mm, pungent, pale brown with white base, 10–15 mm apart; **Inf** to 1.3 m, simple in young plants, later with 1–2 **Br**; racemes cylindrical, slightly acuminate, to 36 × 6–7 cm, dense; **Bra** lanceolate, 18 × 5 mm; **Ped** 5 mm; **Fl** reddish-orange, 30 mm, slightly ventricose, base very shortly attenuate; **OTep** free for 15–17 mm; **St** and **Sty** exerted 13 mm. — **Cytology:** 2n = 14 (Müller 1945).

The distribution range has been degraded, and the species is now known from only 7 localities. These are threatened by soil erosion caused by extreme overgrazing, and are in some cases close to main roads where they are threatened by illegal collecting and by road maintenance and expansion (Nkuna 2017).

**A. ghibensis** Sebsebe & Friis (Kew Bull. 66 (1): 113–114, fig. 2 (p. 115), 2011). **Type:** Ethiopia, Oromia (*Sebsebe & al.* 6764 [ETH, K]). — **Distr:** SW Ethiopia (Oromia: Ghibe Gorge); woodland of the Kefa floristic region, on the edge of volcanic cliffs, 1365–1760 m; known only from the area of the type locality. **I:** Sebsebe Demissew & Nordal (2010: 99–101).

[12] Caulescent, suckering to form clumps; stem to 100 × 5–7 cm; **L** rosulate, 35–50 × 7–10 cm, dull green, surface smooth, exudate drying yellow, **marginal teeth** 3 mm, white,

**Fig. 28** *Aloe gilbertii* ssp. *gilbertii*. (Copyright: M. G. Gilbert)



7–10 mm apart; **Inf** 45–55 cm, erect, with 7–8 **Br**; racemes cylindrical, with subsecund flowers, 10–22 cm, lax; **Bra** ovate-acuminate, 3–4 × 2.5 mm; **Ped** 5–6 mm; **Fl** scarlet, 28–30 mm, base truncate, 6 mm Ø across the ovary; **OTep** free for 6–8 mm.

The protologue describes the stems as scandent (i.e. climbing), but a habitat photograph shows a low clump of rosettes, with no sign of climbing. Yellow flowers are also reported in the protologue.

**A. gilbertii** T. Reynolds *ex* Sebsebe & Brandham (Kew Bull. 47(3): 509, 512, *ills.*, 1992). **Type:** Ethiopia, Sidamo Region (*Gilbert & al.* 9307 [K, ETH, UPS]). — **Lit:** Gilbert & Sebsebe Demissew (1997). **Distr:** Ethiopia.

**A. gilbertii** ssp. *gilbertii* — **Distr:** C & S Ethiopia; woodland, hedgerows and sandy mountain slopes, 1300–1800 (–1900) m. **I:** Sebsebe Demissew & Nordal (2010: 98); Carter & al. (2011: 620). — Fig. 28.

[7] Acaulescent or usually shortly caulescent, usually suckering to form dense sprawling clumps, rarely simple; stem ascending, to 1.5 m; **L** densely rosulate, ascending with tips gently recurved, 40–60 × 9–11 cm, dark green or grey-green, often tinged brown or mauve, surface smooth, **marginal teeth** 3–5 mm, brown-tipped, 0.7–1.4 mm apart; **Inf** to 1.2 m, with 5–20 **Br**, lower ones sometimes rebranched; racemes

cylindrical, 6–15 cm, lax; **Bra** ovate-acute, 4–6 × 2–3 mm; **Ped** 9–10 mm; **Fl** orange to red, 23–27 mm, cylindrical to somewhat clavate, 4.5–8 mm Ø when pressed; **OTep** free for 8–11 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (protologue, Fentaw & al. (2013)).

Fikre Dessalegn (2013) investigated the population biology and found small percentages of seedlings and juveniles. He also reports that the taxon is used for the rehabilitation of degraded land and soil conservation locally.

**A. gilbertii** ssp. *megalacanthoides* M. G. Gilbert & Sebsebe (Kew Bull. 52(1): 151, 1997). **Type:** Ethiopia, Gamo Gofa Region (*Gilbert & Phillips* 9135 [K, ETH, UPS]). — **Distr:** SW Ethiopia (Gamo Gofa Region); *Acacia*–*Commiphora* woodland on rocky slopes, 1200–1350 m. **I:** Carter & al. (2011: 620).

[7] Differs from ssp. *gilbertii*: **L** spreading and deeply canaliculate, strongly recurved; **Fl** 27–28 mm.

**A. gillettii** S. Carter (Kew Bull. 49(3): 417, 1994). **Type:** Somalia, Bari Region (*Gillett* 23457 [K, EA, MOG]). — **Distr:** NE Somalia (Bari Region: Al Muskat Mts.); bushland on rocky limestone slopes, 1340–1650 m. **I:** Carter & al. (2011: 478).

[13] Caulescent, sparsely branched; stem decumbent, 0.5–1 cm Ø; **L** laxly rosulate, linear-lanceolate, to ±15 × 1.5 cm, dark grey-

green, with many whitish spots, exudate drying purplish, **marginal teeth** 1 mm, cartilaginous, 3–5 mm apart; **Inf** to 25 cm, simple; raceme 3–5 cm, lax, with 8–12 flowers; **Bra** ovate-acuminate, 4–5 × 2 mm, white; **Ped** to ±10 mm; **Fl** coral-red, green-tipped, 20–26 mm, 7 mm Ø across the ovary; **OTep** free for 6–8 mm; **St** and **Sty** exerted 2.5 mm. — **Cytology**: 2n = 14 (Brandham & al. 1994).

**A. glabrescens** (Reynolds & P. R. O. Bally) S. Carter & Brandham (Bradleya 1: 23–24, ill., 1983). **Type**: Somalia (Reynolds 8390 [PRE, EA, K]). — **Distr**: NE Somalia; arid plains and gypsum hills, 800–1000 m. **I**: Reynolds (1966: 126, as *A. rigens* var. *glabrescens*); Carter & al. (2011: 452).

≡ *Aloe rigens* var. *glabrescens* Reynolds & P. R. O. Bally (1958).

[7] Acaulescent or caulescent, suckering to form small to large groups; stem decumbent, to 50 cm; **L** 18–24, densely rosulate, triangular, 40–50 × 10–12 cm, grey-green tinged reddish, **marginal teeth** 3 mm, pungent, reddish-brown, 10–20 mm apart; **Inf** 75–100 cm, with 3–4 **Br**; racemes cylindrical-acuminate, 25 × 5–6 cm; **Bra** ovate-acute, 9 × 4 mm; **Ped** 5 mm; **Fl** strawberry-pink, paler to greenish at the mouth, glabrous or minutely pubescent under a lens, 32 mm, base rounded, very slightly narrowed above the ovary; **OTep** free for 9 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Carter & Brandham 1983).

**A. glauca** Miller (Gard. Dict., Ed. 8, *Aloe* no. 16, 1768). **Type** [lecto – icono]: Commelin, Praeludia Bot., t. 24, 1703. — **Distr**: RSA. **I**: Carter & al. (2011: 264–265); Wyk & Smith (2014: 156).

This name has been proposed for conservation against *A. rhodacantha* De Candolle by Smith (2018), with a Commelin plate from 1703 as lectotype, correcting the unnecessary neotype designation as shown above.

**A. glauca** var. *glauca* — **Distr**: RSA (Northern Cape, Western Cape); rocky hills and slopes, dry scrub, 200–1300 m **I**: Reynolds (1950: 197–202); Carter & al. (2011: 264).

**Incl.** *Aloe perfoliata* var. *κ* Linné (1753); **incl.** *Aloe perfoliata* var. *glauca* Aiton (1789); **incl.** *Aloe rhodacantha* De Candolle (1800); **incl.** *Aloe glauca* var. *major* Haworth (1812); **incl.** *Aloe glauca* var. *minor* Haworth (1812); **incl.** *Aloe glauca* var. *elatior* Salm-Dyck (1817); **incl.** *Aloe glauca* var. *humilior* Salm-Dyck (1817).

[2] Shortly caulescent; **L** 30–40, densely rosulate, lanceolate, to 30–40 × 10–15 cm, very glaucous, obscurely lineate, lower face sparingly tuberculate-aculeate near the tip, **marginal teeth** 4–5 mm, pungent, reddish-brown; **Inf** ±60–80 cm, simple; raceme cylindrical-acuminate, 15–20 × 8–9 cm, dense; **Bra** ovate-deltoid, ±30 × 10 mm, white, basally subamplexicaul; **Ped** 30–35 mm; **Fl** pink, greenish-tipped, ±40 mm, base rounded, slightly narrowed above the ovary, then enlarging and narrowing again to the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Resende 1937).

Leaf characters are variable, and distinct variants are found in different localities. Natural hybrids with *A. arborescens* have been reported (Reynolds 1950).

**A. glauca** var. *spinosior* Haworth (Revis. Pl. Succ., 40, 1821). **Type**: [neo – icono]: Commelin, Praeludia Bot., t. 24, 1703. — **Distr**: RSA (Western Cape); quartzite slopes. **I**: Carter & al. (2011: 265).

**Incl.** *Aloe muricata* Schultes (1809) ≡ *Aloe glauca* var. *muricata* (Schultes) Baker (1880).

[2] Differs from var. *glauca*: **L** more spreading, less glaucous, lower face more tuberculate-aculeate, **marginal teeth** larger.

Regarded by Smith & Figueiredo (2019) as a synonym of *A. glauca*, with the same newly designated type.

**A. globuligemma** Pole-Evans (Trans. Roy. Soc. South Africa 5: 30, 1915). **Type**: RSA, Limpopo (Pole-Evans s.n. in *Govt. Herb.* 20 [PRE]). — **Distr**: E Botswana, Zimbabwe, RSA (Limpopo, Mpumalanga); dry bushland, 460–1325 m. **I**: Reynolds (1950: 444–447, t. 45); Reynolds (1966: 223–224); Carter & al. (2011: 459); Wyk & Smith (2014: 158–159). – Fig. 29.

[7] Shortly caulescent, suckering and branching forming large dense groups; stem



**Fig. 29** *Aloe globuligemma*.  
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decumbent, to 50 cm; **L**  $\pm$ 20, densely rosulate, lanceolate-attenuate, 45–50  $\times$  8–9 cm, glaucous, with narrow dull white to pale pink cartilaginous margin, **marginal teeth** 2 mm, dull white, pale brown-tipped, mostly curved towards the tip, to 10 mm apart; **Inf** to 1 m, with 8–18 **Br**, lower ones sometimes rebranched; racemes oblique with secund flowers, 30–40 cm, subdense; **Bra** ovate-acute, 6 mm; **Ped** 3–4 mm; **Fl** yellow to ivory, reddish-tinged near the base, with a bloom, 26 mm, clavate, base rounded, 5 mm  $\varnothing$  across the ovary, enlarging to 10 mm above, narrowing slightly at the mouth; **OTep** free for  $\pm$ 18 mm; **St** exerted 12 mm; **Sty** exerted 12–14 mm. — **Cytology**:  $2n = 14$  (Müller 1941).

The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984), and local use in herbal medicine has caused deaths (Drummond & al. 1975). Natural hybrids with *A. aculeata*, *A. angelica*, *A. burgersfortensis*, *A. castanea*, *A. chabaudii* and *A. marlothii* have been reported (Reynolds 1950, Craib 2003).

**A. gneissicola** (H. Perrier) J.-B. Castillon & J.-P. Castillon (Aloe Madagascar, 28, 2010). **Type**: Madagascar, Mahajanga (Perrier 13499 [P]). — **Distr**: Madagascar (Mahajanga, Fianarantsoa); gneissic rocks, 600–1440 m. **I**: Reynolds (1966: 468–469); Carter & al. (2011: 337–338); both as *A. capitata* var.; Castillon & Castillon (2010: 310–311).

$\equiv$  *Aloe capitata* var. *gneissicola* H. Perrier (1926).

[3] Acaulescent or with a stem to 20 cm; **L** to 25, rosulate, lanceolate to falcate, apex with 3–5 short teeth, 40  $\times$  3.5–5 cm, grey-green to glaucous tinged red-brown; **Inf** 80 cm, erect, with 3 **Br**; racemes capitate, 70 cm, dense; **Bra** ovate-acute, 10  $\times$  5 mm; **Ped** 5 mm for the lowest flowers, 35 mm for upper flowers; **Fl** yellow, 35 mm, 5 mm  $\varnothing$  across the ovary, widening above to 15 mm at the mouth; **OTep** free to the base; **St** and **Sty** exerted 15 mm.

**A. gossweileri** Reynolds (J. South Afr. Bot. 28 (3): 205–207, ills., 1962). **Type**: Angola, Cuanza Sul (Reynolds 9760 [PRE, K, LISC]). — **Distr**: W-C Angola (Benguela, Cuanza Sul); rocky hills, 850–1100 m; known only from the region of the type locality. **I**: Reynolds (1966: 372); Carter & al. (2011: 631).

[16] Caulescent, branching at the base, forming thickets to several m  $\varnothing$ ; stem ascending or divergent, 1–1.5 m  $\times$  3–4 cm  $\varnothing$ ; **L**  $\pm$ 16, rosulate, persistent for 10–20 cm below, lanceolate-attenuate, 30  $\times$  5 cm, green, sometimes with spots, **marginal teeth** 3–4 mm, 15 mm apart; **Inf** 40–50 cm, with 6–8 **Br**; racemes with secund flowers, 10–15  $\times$  5–6 cm, subdense; **Bra** ovate-acute, 3  $\times$  2 mm; **Ped** 10 mm; **Fl** scarlet, paler at the mouth, 30 mm, base rounded, 6 mm  $\varnothing$  across the ovary, slightly narrowed

above, then enlarging slightly to the mouth; **OTep** free for 10–12 mm; **St** and **Sty** exerted 1–3 mm.

**A. gracilicaulis** Reynolds & P. R. O. Bally (J. South Afr. Bot. 24(4): 184–186, tt. 27–28, 1958). **Type:** Somalia, Sanaag (*Reynolds* 8428 [PRE, EA, K]). — **Distr:** N Somalia (Sanaag); dry bushland, 1065–1600 m. **I:** Reynolds (1966: 309–310); Carter & al. (2011: 670).

[9] Caulescent, simple or branching at the base; stem to 4 m, 8–10 cm  $\varnothing$  at the base,  $\pm 6$  cm  $\varnothing$  above, with dead leaf remains for 30–50 cm below the tip; **L**  $\pm 20$ , rosulate, ensiform-acute, 50–60  $\times$  8 cm, grey-green, with 1 mm white cartilaginous margin, **marginal teeth** 1 mm, blunt, white, 2–10 mm apart; **Inf** 60 cm, with  $\pm 10$  **Br**, lower ones rebranched; racemes cylindrical, 5–6  $\times$  5 cm, subdense; **Bra** ovate-acute, 3  $\times$  2 mm; **Ped** 5–6 mm; **Fl** yellow, 18 mm, base rounded, 5 mm  $\varnothing$  across the ovary, enlarging slightly to the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 3–5 mm.

Carter (2007) argues that this species is probably only a colour variant of *A. medishiana*. The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984).

**A. graciliflora** Groenewald (Tydskr. Wetensk. Kuns 14: 137–139, 1936). **Type** [neo]: RSA, Mpumalanga (*van der Merwe* s.n. in *PRE* 24089 [PRE]). — **Lit:** Klopper & al. (2011: with ill.). **Distr:** RSA (Mpumalanga); grassland on rocky outcrops and sandstone ridges, 1600–2100 m.

[5] Acaulescent or with short stem to 20 cm, solitary or suckering to form small groups; **L** 15–20, densely rosulate, lanceolate-deltoid, to 23  $\times$  10 cm, bright green with oblong whitish spots, scattered or in undulating transverse bands, lower face paler, obscurely lineate or rarely copiously spotted in undulating transverse bands, exudate honey-coloured, drying yellowish, **marginal teeth** deltoid, 5 mm, brown, 10 mm apart; **Inf** 60–80 cm, erect, simple or mostly with 3 **Br**; racemes cylindrical-acuminate, to 30 cm, subdense; **Bra** deltoid-acuminate, 30 mm, scarious, with 5–7 nerves; **Ped** 25–30 mm; **Fl** deep pink to dull orange-red, with a bloom, to 52 mm, 9–10 mm  $\varnothing$  across the ovary, narrowed to 5

mm above, enlarging to 7 mm at the mouth; **OTep** free for 12–15 mm; **St** and **Sty** exerted 1–2 mm.

Formerly included in the synonymy of *A. greatheadii* var. *davyana*.

**A. gracilis** Haworth (Philos. Mag. J. 66: 279, 1825). **Type:** RSA, Eastern Cape (*Bowie* s.n. [K [lecto — icono: plate by F. Bauer, reproduced in Reynolds, *Aloes S. Afr.*, 357, 1950]]). — **Distr:** RSA (S Eastern Cape: Port Elizabeth & Uitenhage Distr.); thickets on rocky slopes, 100–1000 m. **I:** Reynolds (1950: 357–359); Carter & al. (2011: 553); Wyk & Smith (2014: 114–115).

$\equiv$  *Aloiampelos gracilis* (Haworth) Klopper & Gideon F. Smith (2013); **incl.** *Aloe laxiflora* N. E. Brown (1906).

[16] Caulescent, branching at the base; stem erect, to 2 m  $\times$   $\pm 2$  cm  $\varnothing$ ; **L** scattered along the stem for 30–60 cm, lanceolate, 25  $\times$  2.5 cm, dull green, **marginal teeth** 1 mm, firm, white, 2–5 mm apart, leaf sheath 10–15 mm, pale green, striate; **Inf** 20–30 cm, simple or with 1–2 **Br**; racemes cylindrical to slightly conical,  $\pm 10$  cm, subdense, with 20–30 flowers; **Bra** deltoid-acuminate, 5  $\times$  2–3 mm; **Ped** 8 mm; **Fl** bright red to scarlet, yellowish at the mouth, 40–45 mm, base rounded, scarcely narrowed above the ovary; **OTep** free for  $\pm 10$ –12 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Müller 1941: as *A. laxiflora*).

The total distribution is uncertain, as Germishuizen & Meyer (2003) and Carter & al. (2011) also give Western Cape, but this is not included by Wyk & Smith (2014).

**A. grandidentata** Salm-Dyck (Observ. Bot. Hort. Dyck., 3, 1822). **Type:** not typified. — **Distr:** S Botswana, RSA (E Northern Cape, North-West Prov., W Free State); stony plains and ironstone slopes, frequently in the shade of low bushes, 1000–1800 m. **I:** Reynolds (1950: 285–287); Carter & al. (2011: 160); Wyk & Smith (2014: 232–233). — Figs. 30 and 31.

[7] Acaulescent or shortly caulescent, suckering to form dense groups; **L** 10–20, densely rosulate, lanceolate,  $\pm 15$ –20  $\times$  6–7 cm, apical 5 cm soon drying, brownish-green with many dull white oblong spots, usually in transverse bands,



**Fig. 30** *Aloe grandidentata*.  
(Copyright: G. F. Smith)



usually more prominent on the lower face, with horny reddish-brown margin, **marginal teeth** 3–5 mm, pungent, reddish-brown, 8–10 mm apart; **Inf** ±90 cm, with 4–7 **Br**; racemes cylindrical, slightly acuminate, to 20 cm, lax, with 20–30 flowers, sometimes shorter and denser; **Bra** deltoid-acuminate, 10–15 mm, white; **Ped** 10–15 mm; **Fl** dull reddish, rarely pink, lobes with a 1.5 mm white border, 28–30 mm, clavate, base rounded, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for ±8–10 mm; **St** and **Sty** exerted 5 mm. — **Cytology**:  $2n = 14$  (Resende 1937).

Germishuizen & Meyer (2003) also include Eastern Cape and Western Cape in the distribution, but these provinces are not shown by Wyk & Smith (2014). — Natural hybrids with other species have been reported (Reynolds 1950).

**A. granitica** Rebmann (Cact. Succ. 5(2): 55–57, ills., 2013). **Type**: Madagascar, Antananarivo (Rebmann 24 [BR]). — **Distr**: C Madagascar (Antananarivo: Antsirabé); vertical granite cliffs, 1750 m.

[8] Caulescent, unbranched; stem 1.5–2.2 m, with dried leaves persistent; **L** 35–55, rosulate, lanceolate, apex acute with 3 teeth, 45–47 × 7 cm, green with red tint, lower surface green with grey bloom, **marginal teeth** deltoid, 2 mm, red to brown, 2–14 mm apart; **Inf** 1.2–1.5 m, erect, with 4–5 **Br**; racemes densely capitate, 6–7 cm; **Ped**

20–30 mm; **Fl** said to be yellow-orange, otherwise unknown.

Flower details are not known, because the species was described without the author having seen the plants in flower, the flower colour having been given by nearby villagers.

**A. grata** Reynolds (J. South Afr. Bot. 26(2): 87–89, tt. 8–9, 1960). **Type**: Angola, Bié (Reynolds 9246 [PRE, K, LUA]). — **Distr**: W-C Angola (Benguela, Bié, Huambo); hillsides, mostly on rocks, 1770 m; known only from the area of the type locality. **I**: Reynolds (1966: 117–118); Carter & al. (2011: 415).

[7] Acaulescent or shortly caulescent, suckering to form dense groups; **L** 16–20, densely rosulate, lanceolate-attenuate, ±20–25 × 7–8 cm, upper face green tinged reddish-brown, lower face paler glaucous-green with many crowded pale green 1 mm  $\varnothing$  spots in the lower  $\frac{1}{4}$ , exudate drying pale yellow, **marginal teeth** 2–3 mm, 5–8 mm apart; **Inf** 70–90 cm, with 2–3 **Br**; racemes capitate or subcapitate, 8–10 × 8 cm; **Bra** ovate-acute, 2 × 1.5 mm; **Ped** 20 mm; **Fl** scarlet, 25–28 mm, base shortly attenuate, 6 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, then enlarging, narrowing slightly at the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 1–3 mm.

**A. greatheadii** Schönland (Rec. Albany Mus. 1: 121, 1904). **Type**: Botswana (Schönland 1616

[GRA, PRE]). — **Distr:** Botswana, Malawi, Moçambique, Zimbabwe, RSA, Swaziland, Zambia.

**A. greatheadii** var. **davyana** (Schönland) Glen & D. S. Hardy (South Afr. J. Bot. 53(6): 490–491, 1987). **Type:** RSA, Transvaal (*Burt Davy* 1855 [GRA]). — **Distr:** RSA (Free State, Gauteng, KwaZulu-Natal, Mpumalanga, Limpopo, North-West Prov.), Swaziland; grassland on rocky slopes, (600–) 725–2100 m. **I:** Reynolds (1950: 234–236, t. 13, as *A. davyana*); Carter & al. (2011: 177); Wyk & Smith (2014: 222–223, as *A. davyana*, & 256–257, as *A. mutans*).

≡ *Aloe davyana* Schönland (1904); **incl.** *Aloe comosibracteata* Reynolds (1936); **incl.** *Aloe labiaflava* Groenewald (1936); **incl.** *Aloe mutans* Reynolds (1936); **incl.** *Aloe verdoorniae* Reynolds (1936); **incl.** *Aloe davyana* var. *subolifera* Groenewald (1939).

[4] Differs from var. *greatheadii*: Sometimes suckering to form dense groups; **L** to 30 × 6–8 cm; **Inf** 50–120 cm, with 3–5 **Br**; racemes conical to subcapitate; **Bra** 20–25 mm; **Ped** 20–25 mm; **Fl** dull brick-red to pink, lobes with a white border, 30–37 mm. — **Cytology:** 2n = 14 (Kondo & Megata 1943).

Treated at species rank by Wyk & Smith (2014), though they state that this and *A. greatheadii* (var. *greatheadii*) gradually merge and are almost impossible to distinguish. Natural

hybrids with other species have been reported (Reynolds 1950). Nepi & al. (2006) report that bees collect both pollen and nectar, and that flowers are also visited by sunbirds. Human & Nicolson (2008) consider the taxon as an important source of nectar and pollen for bees, and migratory bee-keepers take advantage of this winter source. Smith & Correia (1992) (cited from Symes (2012)) report that a seed bank is present, and that seeds of the seed bank are viable for longer than two seasons.

**A. greatheadii** var. **greatheadii** — **Distr:** SE Botswana, Malawi, Moçambique, Zambia, Zimbabwe, RSA (Limpopo, Gauteng, Mpumalanga); stony grassland and open woodland, 700–1890 m. **I:** Reynolds (1950: 232–233); Carter & al. (2011: 176); Klopper & al. (2012: 78, 85–86, incl. distribution map); Wyk & Smith (2014: 234–235).

**Incl.** *Aloe pallidiflora* A. Berger (1905).

[3] Acaulescent or shortly caulescent, simple; **L** densely rosulate, attenuate, ±47 × 12 cm, upper face dark glossy green with many elongated whitish spots, near the base usually confluent and forming transverse bands, lower face pale green, lineate, without spots, usually with brown cartilaginous margin, **marginal teeth** ±5 mm, pungent, brown, to 20 mm apart; **Inf** to 175 cm, with ±4–6 **Br**; racemes cylindrical, 9–30 cm, lax when long, usually short and dense; **Bra** acuminate, ±32 × 5 mm; **Ped** 12 mm; **Fl** white with broad

**Fig. 31** *Aloe grandidentata*.  
(Copyright: G. F. Smith)



red midrib, 32 mm, base rounded, 7 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, then enlarged to 8 mm; **OTep** free for 7–9 mm; **St** and **Sty** exerted 0–1 mm.

Different authors have reported different distribution ranges for the species, partly because of different views on recognition of infraspecific taxa. The comments of Klopper & al. (2012) are based on their recognition of var. *davyana* as a separate species. Lane (2004) feels that plants in Malawi reported as this taxon are likely to be *A. swynnertonii*. All reported distribution records are included here, but further work is needed to clarify the situation.

**A. grisea** S. Carter & Brandham (Bradleya 1: 19–20, ills., 1983). **Type:** Somalia, Hargeisa Region (*Bally* 9662 [K]). — **Distr:** NW Somalia, Djibouti; stony ground or rocks on mountain slopes in *Juniperus-Buxus* forest or scrub, 1200–1700 m. **I:** Carter & al. (2011: 169).

[5] Acaulescent, simple or suckering sparsely; **L** rosulate, triangular, to 25  $\times$  15 cm, very glaucous with many white spots in irregular transverse bands, with 1 mm horny brown margin, **marginal teeth** 1–3 mm, 2–8 mm apart; **Inf** to 60 cm, with 2–3 **Br**, lower ones sometimes rebranched; racemes conical to subcapitate,  $\pm 10 \times 6$  cm; **Bra** ovate-aristate, to 20  $\times$  5 mm; **Ped** to 30 mm; **Fl** bright orange-scarlet, yellow at the mouth, 23 mm, base rounded, 6 mm  $\varnothing$  across the ovary, abruptly narrowed to 3.5 mm above, enlarging to the mouth; **OTep** free for 5 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (protologue).

**A. guerrae** Reynolds (J. South Afr. Bot. 26(2): 85–87, tt. 6–7, 1960). **Type:** Angola, Bié (*Reynolds* 9218 [PRE, K, LUAI]). — **Distr:** Angola (Benguela, Bié, Huambo: C highlands); grassland with scattered bushes, 1220–1670 m. **I:** Reynolds (1966: 228–229); Carter & al. (2011: 327).

[3] Acaulescent or shortly caulescent, simple, **Ros** usually tilted slightly to one side; **L**  $\pm 24$ , densely rosulate, lanceolate-attenuate, 40  $\times$  6–7 cm, dull green, obscurely lineate, exudate drying yellow, **marginal teeth** 4–5 mm, pungent, pale brown or reddish-brown, 10–15 mm apart; **Inf**

90–100 cm, with 8–10 **Br**, lower ones sometimes rebranched; racemes with secund flowers, oblique to almost horizontal, 20 cm, subdense; **Bra** ovate-acute, 6–8  $\times$  4 mm; **Ped** 5 mm; **Fl** scarlet with a bloom, 40 mm, base truncate, 8 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for 10–12 mm; **St** exerted 2 mm; **Sty** exerted 3 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. guillaumetii** Cremers (Adansonia, n.s. [sér. 2], 15(4): 498–501, ills., 1976). **Type:** Madagascar, Antsiranana (*Cremers* 2670 [P]). — **Distr:** Madagascar (Antsiranana: Ambilobe region); eroded sandstone outcrops; known only from the type locality. **I:** Glen & al. (1992); Castillon & Castillon (2010: 324–325); Carter & al. (2011: 422). — Fig. 32.

[6] Acaulescent, suckering to form large mats; **L** 6–12, rosulate, triangular, 38–40  $\times$  2–5 cm, bright green tinged red, with scattered small white spots, **marginal teeth** 1 mm, whitish, 2–5 mm apart; **Inf** 80–110 cm, simple; raceme cylindrical, 25–30 cm, lax; **Bra** lanceolate-acute, 4  $\times$  2 mm; **Ped** 15–20 mm; **Fl** red at the base becoming pink then green above, 25 mm, base shortly attenuate, 5 mm  $\varnothing$  across the ovary, narrowed slightly above, then enlarged to 6 mm at the mouth; **OTep** free for 9 mm; **St** and **Sty** exerted 1–2 mm.

**A. haemanthifolia** A. Berger & Marloth (Bot. Jahrb. Syst. 38: 85, 1905). **Type:** RSA, Western Cape (*Marloth* 3786 [BOL, GRA, PRE]). — **Distr:** RSA (SW Western Cape); in grass on steep usually S-facing rocky slopes in damp climate, 500–1675 m. **I:** Reynolds (1950: 156–157); Carter & al. (2011: 407); Wyk & Smith (2014: 160–161).

$\equiv$  *Kumara haemanthifolia* (A. Berger & Marloth) Boatwright & J. C. Manning (2014).

[6] Acaulescent, usually suckering to form dense groups, rarely simple; **L** 10–16, distichous, lorate, tip obtuse to rounded and minutely crenate, to 18  $\times$  8 cm, dull glaucous green with reddish margin, surface smooth, exudate colourless, **marginal teeth** absent; **Inf** to 45 cm, simple; raceme capitate, 4–5 cm, with  $\pm 30$  flowers; **Bra** lanceolate-acuminate, to 25  $\times$  6–7 mm, fleshy; **Ped** 25–35 mm; **Fl** scarlet, 38 mm, slightly

**Fig. 32** *Aloe guillaumetii*.  
(Copyright: U. Eggli)



clavate, base attenuate, above the ovary gradually enlarging to the mouth; **OTep** free almost to the base; **St** not exerted; **Sty** exerted 0–1 mm.

**A. haggeherensis** T. A. McCoy & Lavranos (Kakt. and. Sukk. 58(11): 297–298, ills., 2007). **Type:** Yemen, Socotra (*Lavranos* s.n. [FT]). — **Distr:** Yemen (Socotra: Haggeher Mts.); on granite, 950 m. **I:** Carter & al. (2011: 328).

[5] Acaulescent, solitary or suckering to form small groups with stem to 20 cm; **L** 15–20, rosulate, 30–45 × 6 cm, bright green, exudate yellow, drying light yellow, **marginal teeth** 3 mm, reddish, 3 mm apart; **Inf** 70 cm, erect, with up to 5 **Br**; racemes cylindrical, to 20 cm, lax; **Bra** lanceolate, acute, 3 mm; **Ped** 10 mm; **Fl** orange-red, yellow at the mouth, 25 mm, 5 mm  $\varnothing$  across the ovary; **OTep** free for 6–8 mm; **St** exerted 3 mm; **Sty** exerted 4–5 mm.

**A. hahnii** Gideon F. Smith & Klopper (Bothalia 39(1): 98–99, ills., 2009). **Type:** RSA, Limpopo (*Hahn* 2172 [PRE]). — **Distr:** RSA (N-C Limpopo: Blouberg, Soutpansberg); mist belt, sandy soils, 1000–2050 m. **I:** Wyk & Smith (2014: 238–239).

[3] Acaulescent or rarely with a short prostrate stem to 12 cm, solitary; **L**  $\pm$ 12, laxly rosulate, attenuate, 13–40 × 4–6 cm, dull pale green to brown, with pale milky green to whitish spots in transverse bands, lower surface pale to milky

green, with dense whitish to milky green spots in transverse bands, exudate drying opaquely yellow, **marginal teeth** 2–4 mm, brownish-orange, 7–14 mm apart; **Inf** 26–100 cm, erect, with 4–8 (–10) **Br**; racemes cylindrical to capitate, 4–6 cm, lax; **Bra** 5–15 × 2–3 mm, scarious, brownish-white with many nerves; **Ped** 10–20 mm, red; **Fl** red, sometimes with green, creamy-white and reddish tips, 25–28 mm, 5–7 mm  $\varnothing$  across the ovary, abruptly narrowed to 3–4 mm above, widening to 5 mm at the middle; **OTep** free for 12–14 mm; **St** hardly exerted; **Sty** not exerted.

Formerly regarded as a disjunct population of *A. swynnertonii*.

**A. hardyi** Glen (Flow. Pl. Afr. 49(3–4): t. 1942 + 3 pp. of text, 1987). **Type:** RSA, Mpumalanga (*Fourie* 3252 [PRE]). — **Distr:** RSA (Mpumalanga/Limpopo border area: Lydenburg Distr.); steep rocky cliff faces, 900–1400 m. **I:** Carter & al. (2011: 522); Wyk & Smith (2014: 94–95); Walker (2014).

[13] Caulescent, branching; stem pendulous; **L** 12–20, rosulate, pendulous, lanceolate, 40–70 × 5–8 cm, glaucous blue-green, **marginal teeth** small, scattered; **Inf** 50–70 cm, simple; raceme conical to subcapitate, subdense; **Bra** obovate-acute, 14–17 × 10–15 mm; **Ped** 15–30 mm; **Fl** pink to red, 25–35 mm, base rounded, slightly narrowed above the ovary, then enlarging to the mouth; **St** and **Sty** exerted 3–4 mm.



**A. harlana** Reynolds (J. South Afr. Bot. 23(1): 9–10, t. 9, 1957). **Type:** Ethiopia, Harerge Prov. (Reynolds 8158 [PRE, K]). — **Distr:** E Ethiopia (Harerge Region); in low bush on stony (often limestone) slopes, 1650–2000 m. **I:** Reynolds (1966: 276); Sebsebe Demissew & Nordal (2010: 75–76); Carter & al. (2011: 353).

[5] Acaulescent or shortly caulescent, simple or dividing into 2–4 rosettes; **L** ±24, densely rosulate, lanceolate-attenuate, 50 × 12–15 cm, pale to dark olive-green, sometimes glossy, lower face sometimes with a few dull elongated pale green blotches near the base, usually with horny reddish-brown margin, exudate drying deep brown, **marginal teeth** 3–4 mm, pungent, reddish-brown, 10–15 mm apart; **Inf** ±70–90 cm, with 6–8 **Br**; racemes conical-capitate or cylindrical-acuminate, to 20 cm; **Bra** ovate-acute, 10 × 5–7 mm, densely imbricate in bud stage; **Ped** 15 mm; **Fl** deep red, sometimes yellow, 33 mm, base shortly attenuate, 11 mm Ø across the ovary, not narrowed above; **OTep** free for 10 mm; **St** and **Sty** exerted 3–5 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. haroniensis** T. A. McCoy & al. (Cact. Succ. J. (US) 86(4): 155–157, ill., 2014). **Type:** Zimbabwe, Manicaland Prov. (McCoy 4012 [FT]). — **Distr:** E Zimbabwe (Manicaland Prov.); rock faces or outcrops in forest, 310 m. **I:** McCoy (2014).

[3] Acaulescent, solitary; **L** densely rosulate, narrowly lanceolate, 60 × 10 cm, green, lower face with dark green striations, **marginal teeth** deltoid, 3–5 mm, reddish-brown, 10–20 mm apart; **Inf** 65–80 cm, erect, with 3–6 **Br**; racemes capitate, 25–40 cm, with 20–30 flowers; **Bra** narrowly deltoid-acuminate, 12–14 mm; **Ped** 18 mm; **Fl** dull reddish-pink with pruinose waxy bloom, 24–27 mm, 5.5 mm Ø across the ovary, narrowed to 3.5 mm above, enlarging to the mouth; **OTep** free for 6–7 mm; **St** and **Sty** exerted 0–1 mm.

**A. haworthioides** Baker (J. Linn. Soc., Bot. 22: 259, 1886). **Type:** Madagascar, Fianarantsoa (Baron 3424 [K]). — **Lit:** Lüthy (2006: 39–40, conservation, with ill.). **Distr:** Madagascar (Fianarantsoa).

≡ *Aloinella haworthioides* (Baker) Lemée (1939) (*nom. inval.*, Art. 43.1) ≡ *Lemeea haworthioides* (Baker) P. V. Heath (1993).

**A. haworthioides** var. **aurantiaca** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 50, 1926). **Type:** Madagascar, Fianarantsoa (Perrier 14582 [P]). — **Distr:** Madagascar (Fianarantsoa: N Andringitra Massif); on granite, 2000 m; known only from the type locality. **I:** Reynolds (1966: 397–398); Castillon & Castillon (2010: 143); Carter & al. (2011: 394).

[4] Differs from var. *haworthioides*: **Inf** racemes bright orange-red, including axis, **Bra** and **Fl**.

**A. haworthioides** var. **haworthioides** — **Distr:** Madagascar (Fianarantsoa: Betsileo Country); gneiss and quartzite rocks, in tufts of grass, 1200–1800 m. **I:** Reynolds (1966: 395–396); Castillon & Castillon (2010: 143); Carter & al. (2011: 395).

[4] Acaulescent, simple or suckering to form dense groups; **R** fusiform; **L** ±30, densely rosulate, narrowly lanceolate-deltoid, 3–4 cm, dark grey-green, with many white pustules sometimes tipped with a short white hair, the tip a short pellucid point, **marginal teeth** 1–2 mm, narrowly deltoid, soft to firm, white, crowded; **Inf** 20–30 cm, simple; raceme cylindrical, slightly acuminate, 4–6 × 1.2 cm, subdense, with 20–30 flowers; **Bra** suborbicular, obtuse, shortly mucronate, 5 mm; **Ped** none or negligible; **Fl** white to pale pink, 6–8 mm, slightly campanulate; **OTep** free to the base; **St** and **Sty** exerted 5 mm.

**A. hazeliana** Reynolds (J. South Afr. Bot. 25 (4): 279–281, tt. 25–26, 1959). **Type:** Zimbabwe, Melssetter Distr. (*Munch* s.n. in Reynolds 9031 [PRE, K]). — **Distr:** W Moçambique, E Zimbabwe.

**A. hazeliana** var. **hazeliana** — **Distr:** W Moçambique, E Zimbabwe: Chimanimani Mts.; montane grassland, soil pockets and rock fissures, 1200–2135 m. **I:** Reynolds (1966: 25–26); Carter & al. (2011: 132).



[10] Caulescent, branching sparsely at the base; stem to 50 × 1.5 cm; **L** ±12, distichous, scattered along the stem for 15 cm, linear, tip obtuse, cuspidate and minutely dentate, to 20 × 1–1.5 cm, green, sometimes with a few small scattered pale green elliptic spots, lower face with many crowded pale green elliptic spots near the base, with narrow hyaline margin, **marginal teeth** 0.5 mm, firm, white, 5 mm apart, leaf sheath 10–15 mm, with many spots; **Inf** 30–40 cm, simple; raceme cylindrical, 8–10 × 4 cm, lax, with ±18 flowers; **Bra** ovate-acute, 4 × 3 mm, slightly fleshy; **Ped** to 13 mm; **Fl** scarlet, green-tipped, 25 mm, base shortly attenuate, 6 mm Ø across the ovary, not enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. hazeliana** var. **howmanii** (Reynolds) S. Carter (in Exell & al., *Fl. Zambes.* 12(3): 61, 2001). **Type:** Zimbabwe, Eastern Prov. (*Ball* 646 [PRE, SRGH]). — **Distr:** W Moçambique, E Zimbabwe: Chimanimani Mts.; cliff faces, shaded quartzite rocks, 1500–2300 m. **I:** Reynolds (1966: 17–18, as *A. howmanii*).

≡ *Aloe howmanii* Reynolds (1961).

[10] Differs from var. *hazeliana*: Stem pendulous, to 75 cm; **L** mostly falcately decurved; **Inf** 20–25 cm, descending, with the raceme upturned.

**A. helenae** Danguy (Bull. Mus. Nation. Hist. Nat., Sér. 2, 1: 433, 1929). **Type:** Madagascar, Toliara (*Decary* 3325 [P]). — **Lit:** Lüthy (2006: 41–42, conservation, with ills.). **Distr:** Madagascar (SW Toliara: Tolanaro region); dense bush and coastal forest on littoral sand and limestone. **I:** Reynolds (1966: 513–514); Castillon & Castillon (2010: 230–231); Carter & al. (2011: 669). — Fig. 33.

[9] Caulescent, simple; stem to 4 m, to 20 cm Ø, with dead leaf remains; **L** ±40, densely rosulate, ensiform, greatly recurved, to 140 × 12–15 cm, green, **marginal teeth** 2–3 mm, pungent, pale green, 15 mm apart; **Inf** 40–60 cm, simple; raceme cylindrical-claviform, 15 × 9 cm, dense, with 300–400 flowers; **Bra** lanceolate-deltoid, acute, 12 × 6 mm, red-tipped, thick and fleshy; **Ped** 2–3 mm; **Fl** yellowish, reddish at the mouth, 24–27 mm, cylindrical at



**Fig. 33** *Aloe helenae*. (Copyright: K. Grantham)

the base becoming widely campanulate above, base obtuse, 4 mm Ø across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 12–15 mm; **St** and **Sty** exerted 9–10 mm.

A hybrid with *A. divaricata* ssp. *vaotsohy* has recently been described as *A. ×anosyana* (Castillon 2012).

**A. heliderana** Lavranos (Cact. Succ. J. (US) 45(3): 114–115, ills., 1973). **Type:** Somalia, Bari Region (*Lavranos & Bavazzano* 8456 [FI]). — **Distr:** NE Somalia (Bari Region); semidesert on limestone hills, ±500 m. **I:** Carter & al. (2011: 618).

[15] Caulescent, branching sparingly at the base; stem erect, to 1 m × 4 cm Ø, covered by dried leaf bases; **L** ±20, rosulate, deltoid-acute, ±20 × 6 cm, grey-green with few or many white spots, with white cartilaginous margin, **marginal teeth** to 2 mm, white, 5–10 mm apart; **Inf** to 60 cm, with ±8 **Br**, lower ones rebranched; racemes

capitate or shortly cylindrical, flowers sometimes slightly secund, lax; **Bra** deltoid-acute, brownish, brittle, 3–5 mm; **Ped** 7 mm; **Fl** red or yellow, 20–22 mm, base rounded, 5–6 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to 5–6 mm at the mouth; **OTep** free for 5–7 mm; **St** and **Sty** exerted 2–6 mm.

**A. hemmingii** Reynolds & P. R. O. Bally (J. South Afr. Bot. 30(4): 221–222, ill., 1964). **Type:** Somalia, Sanaag Region (*Bally* 7146 [EA]). — **Lit:** Carter & al. (1984). **Distr:** N Somalia (Sanaag Region); limestone rocky soil with sparse scrub, 700–1200 m. **I:** Reynolds (1966: 51–52); Carter & al. (2011: 215).

[4] Acaulescent or very shortly caulescent, simple or in small groups; **L**  $\pm$ 10, densely rosulate, ovate or lanceolate-attenuate, 10–12  $\times$  3–3.5 cm, brownish-green with many dull white elongated streaks, lower face with white streaks smaller and more numerous, **marginal teeth** 2 mm, pungent, whitish and brown-tipped, 4–6 mm apart; **Inf** 30–35 cm, simple; raceme cylindrical, 10–15  $\times$  5 cm, lax, with  $\pm$ 18 flowers; **Bra** ovate-acuminate, 8  $\times$  3 mm; **Ped** 6–8 mm; **Fl** flamingo-pink or pale rose-red, minutely spotted, 24 mm, base truncate, 8 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Carter & al. 1984).

Carter & al. (1984) concluded that this is conspecific with *A. somaliensis*, but it is still recognized as distinct by Lavranos (1995) and Carter & al. (2011).

**A. hendrickxii** Reynolds (J. South Afr. Bot. 21 (2): 51–53, ill., 1955). **Type:** Democratic Republic of the Congo [Zaire], Prov. Orientale (*Hendrickx* 6401 in *Reynolds* 6300 [PRE, BR]). — **Distr:** E Democratic Republic of the Congo [Zaire]: E-facing escarpment of the Great Rift Valley; granite outcrops, 2450 m. **I:** Reynolds (1966: 336–337).

[7] Acaulescent or shortly caulescent, branching freely to form dense groups; **L**  $\pm$ 16, rosulate, lanceolate-attenuate, 22  $\times$  4 cm, upper face dull green with greyish bloom, lower face grey-green sometimes with a few obscure dull

greyish elongated spots, exudate drying yellow, **marginal teeth** 3 mm, firm, greenish-white in the lower  $\frac{1}{2}$  of the leaf, brownish-tipped above, 5–8 mm apart; **Inf** 40–50 cm, with 4–5 **Br**; racemes cylindrical-conical, 12–15 cm, laterals shorter, subdense; **Bra** deltoid, 14  $\times$  3–4 mm; **Ped** 13 mm; **Fl** dull scarlet, 30 mm, base rounded, 4.5 mm  $\varnothing$  across the ovary, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 3 mm.

**A. hereroensis** Engler (Bot. Jahrb. Syst. 10: 2, 1888). **Type:** Namibia (*Marloth* 1438 [B, NBG, PRE]). — **Distr:** SW Angola (Huambo, Namibe), Botswana, Namibia, RSA (NE Northern Cape, W Free State); arid stony deserts and dry rocky slopes, 800–1400 m. **I:** Reynolds (1950: 324–325); Reynolds (1966: 101); Carter & al. (2011: 321); Wyk & Smith (2014: 162–163).

**Incl.** *Aloe hereroensis* var. *hereroensis*; **incl.** *Aloe orpeniae* Schönland (1905)  $\equiv$  *Aloe hereroensis* var. *orpeniae* (Schönland) A. Berger (1908); **incl.** *Aloe hereroensis* var. *lutea* A. Berger (1908).

[5] Acaulescent or usually very shortly caulescent, sometimes in age with decumbent stem to 1 m, simple or in small groups; **L**  $\pm$ 30, densely rosulate, lanceolate-deltoid, 30–50  $\times$  6–9 cm, very glaucous, obscurely lineate to sulcate, lower face sometimes with few or many irregularly scattered whitish spots, **marginal teeth** 3–4 mm, pungent, sometimes bifid, reddish-brown to brownish, 8–15 mm apart; **Inf**  $\pm$ 1 m, with 4–8 **Br**, lower ones sometimes rebranched; racemes capitate, corymbose, 6–8  $\times$  8–10 cm, dense; **Bra** lanceolate-deltoid, attenuate, 15–30 mm; **Ped** 30–50 mm; **Fl** usually orange, but also various shades of red and yellow, 25–35 mm, base rounded, enlarged slightly above the ovary, narrowing at the mouth; **OTep** free for 14–16 mm; **St** exerted 2–4 mm; **Sty** exerted 5 mm. — **Cytology:**  $2n = 14$  (Müller 1941).

Natural hybrids with other species have been reported (Reynolds 1950).

**A. heybensis** Lavranos (Cact. Succ. J. (US) 71 (3): 159–160, ill., 1999). **Type:** Somalia, Bay Region (*Lavranos & Bauer* 27847 [UPS]). —

**Distr:** S Somalia (Bay Region: Buur Heybe); granite inselberg,  $\pm 700$  m; known only from the type collection. **I:** Carter & al. (2011: 607).

[11] Caulescent, branching at the base; stem to 45 cm, weak and becoming decumbent; **L**  $\pm 12$ , rosulate, triangular, to  $35 \times 7$  cm, glaucous to brownish-green, often with pale spots, surface glossy, smooth, exudate pale yellow, drying pale yellow, **marginal teeth** deltoid, 4 mm, brown-tipped, 5–12 mm apart; **Inf** 45 cm, erect, with up to 5 **Br**; racemes cylindrical, lax below, subcapitate towards the tip; **Bra** triangular-acuminate,  $10 \times 2$  mm, reddish-brown; **Ped** 14 mm; **Fl** dull red, glossy, becoming dull green towards the tip, 25 mm, base very shortly attenuate, 9 mm  $\varnothing$  across the ovary, not narrowing above; **OTep** free for 10–12 mm; **St** and **Sty** exerted 2–5 mm.

**A. hildebrandtii** Baker (Curtis's Bot. Mag. 144: t. 6981 + text, 1888). **Type:** Somalia (Hildebrandt s.n. [K]). — **Lit:** Brandham & al. (1994). **Distr:** Somalia (N Somali escarpment); rocky (mainly limestone) slopes and dry bush, 1095–1615 m. **I:** Reynolds (1966: 341–343); Carter & al. (2011: 495).

**Incl.** *Aloe gloveri* Reynolds & P. R. O. Bally (1958).

[13] Caulescent, branching at the base; stem decumbent, to  $1 \text{ m} \times 3\text{--}4$  cm  $\varnothing$ ; **L** scattered along the stem for 30 cm below the tip, lanceolate-attenuate,  $20\text{--}30 \times 4\text{--}6$  cm, dull green, sometimes with a few white lenticular spots, exudate drying orange-brown, **marginal teeth** 2–3 mm, pungent, reddish-brown, 8–10 mm apart; **Inf**  $\pm 50$  cm, usually oblique, with 8–12 **Br**, lower ones sometimes rebranched; racemes cylindrical, slightly conical, flowers subsecund in oblique racemes,  $10\text{--}18 \times 5$  cm, lax; **Bra** ovate-acute,  $3 \times 2$  mm; **Ped** 10–15 mm; **Fl** yellow, orange or dull scarlet with a bloom, 26–30 mm, base rounded, 8 mm  $\varnothing$  across the ovary, above narrowing slightly to the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 3–4 mm. — **Cytology:**  $2n = 14$  (Brandham & al. 1994).

Natural hybrids with *A. megalacantha* have been reported (Reynolds 1966).

**A. hlangapies** Groenewald (Tydskr. Wetensk. Kuns 14: 60–63, 1936). **Type** [lecto]: RSA, Mpumalanga (*van der Merwe* 102 [PRE]). — **Distr:** RSA (N KwaZulu-Natal, S Mpumalanga); grassland, 1100–1600 m; reduced to highly fragmented populations due to afforestations. **I:** Reynolds (1950: 138–139); Craib (2006: 57–61); Carter & al. (2011: 142); Wyk & Smith (2014: 316–317).

**Incl.** *Aloe hlangapitis* Groenewald (1936) (*nom. inval.*, ICN Art. 61.1); **incl.** *Aloe hlangapensis* Groenewald (1937) (*nom. inval.*, ICN Art. 61.1).

[4] Acaulescent or shortly caulescent, simple or branching at the base to form small groups; stem to 15 cm; **L** 10–14, distichous, lorate-acuminate,  $35\text{--}45 \times 5\text{--}6$  cm, dull green, sometimes with few white spots, lower face usually with many white spots near the base, **marginal teeth**  $\pm 0.5$  mm, soft, white, 5–15 mm apart; **Inf** 50 cm, simple; raceme capitate, to  $7 \times 9\text{--}10$  cm, dense, with  $\pm 50$  flowers; **Bra** ovate-acuminate,  $15 \times 7$  mm; **Ped** 25 mm; **Fl** apricot-yellow, greenish-tipped, 28–30 mm, base rounded, enlarged slightly above the ovary, narrowing at the mouth; **OTep** free for 23–25 mm; **St** and **Sty** exerted 0–1 mm.

Groenewald later changed the name to *A. hlangapitis* and then to *A. hlangapensis*, but these changes are illegitimate under the ICN, and are here treated as orthographical variants. Included in *A. ecklonis* by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011) and Wyk & Smith (2014). Craib (2006: 60) illustrates hybrids with *A. ecklonis*, which are notable because of the different flowering season of the latter.

**A. hoffmannii** Lavranos (Cact. Succ. J. (US) 74(3): 116–118, ill., 2002). **Type:** Madagascar, Fianarantsoa (*Röösli & Hoffmann* 43/95 [P]). — **Distr:** Madagascar (Fianarantsoa: Itremo pass); rocky slabs, 1700 m. **I:** Castillon & Castillon (2010: 106–107); Carter & al. (2011: 538).

[11] Caulescent, branching sparingly from the base; stem to 25 cm, erect; **L** 3–6, rosulate, strap-shaped with rounded denticulate apex,  $6\text{--}15 \times 0.7\text{--}1$  cm, olive-green or grey-green, exudate colourless, drying pale brownish-yellow,



**Fig. 34** *Aloe humilis*.  
(Copyright: L. E. Newton)



**marginal teeth** pungent, 1.5–2 mm, reddish, 4–10 mm apart; **Inf** 25–30 cm, erect, simple; raceme capitate, dense; **Bra** ovate, 2–3 mm, brownish; **Ped** 20 mm, red; **Fl** red, becoming cream at the mouth, 20–22 mm, 4 mm  $\varnothing$  across the ovary, widening to 7–8 mm at the mouth; **OTep** free for 12–14 mm; **St** and **Sty** exserted 1 mm.

Close to *A. parallelifolia*.

**A. humbertii** H. Perrier (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 692, 1931). **Type:** Madagascar, Toliara (*Humbert* 6211 [P]). — **Lit:** Castillon & Castillon (2010: 227); Carter & al. (2011: 249). **Distr:** S Madagascar (Toliara: Andohahela Masif); siliceous rocks, 1800–1980 m.

[2] Acaulescent or shortly caulescent, simple; **L** 7–12, rosulate, triangular with the tip rounded and dentate, 25–30  $\times$  5–6 cm, green with horny margin, **marginal teeth** yellow, 3–6 mm apart; **Inf** 35–40 (–80) cm, simple or with 1–2 **Br**; racemes 8 cm, lax or dense; **Bra** lanceolate, shortly cuspidate, 11  $\times$  5 mm; **Ped** absent; **Fl** red or yellow tinged-red,  $\pm$ 20 mm; **OTep** free for 10 mm; **St** and **Sty** exserted 0–1 mm.

Not found again since its first discovery.

**A. humilis** (Linné) Miller (Gard. Diet. Abr. ed. 6, no. 10, 1771). **Type:** RSA, “Cape Prov.” (*Oldenland* s.n. [[lecto — icono]: Commelin, Horti Med. Amstelod., t. 46, 1706]). — **Distr:**

RSA (SE Western Cape, W Eastern Cape); karroid vegetation, in shade or in the open, 0–1600 m. **I:** Reynolds (1950: 174–175); Carter & al. (2011: 401); Wyk & Smith (2014: 290–291). — Fig. 34.

$\equiv$  *Aloe perfoliata* var. *humilis* Linné (1753)  $\equiv$  *Catevala humilis* (Linné) Medikus (1786); **incl.** *Aloe humilis* var. *humilis*; **incl.** *Aloe verrucosospinosa* Allioni (1773); **incl.** *Aloe humilis* var. *incurva* Haworth (1804)  $\equiv$  *Aloe incurva* (Haworth) Haworth (1812); **incl.** *Aloe suberecta* Haworth (1804)  $\equiv$  *Aloe humilis* var. *suberecta* (Haworth) Baker (1896); **incl.** *Aloe suberecta* var. *acuminata* Haworth (1804)  $\equiv$  *Aloe acuminata* (Haworth) Haworth (1812)  $\equiv$  *Aloe humilis* var. *acuminata* (Haworth) Baker (1880); **incl.** *Aloe tuberculata* Haworth (1804); **incl.** *Aloe humilis* Ker Gawler (1804) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe echinata* Willdenow (1809)  $\equiv$  *Aloe humilis* var. *echinata* (Willdenow) Baker (1896); **incl.** *Aloe acuminata* var. *major* Salm-Dyck (1817); **incl.** *Aloe humilis* subvar. *semiguttata* Haworth (1821); **incl.** *Aloe humilis* var. *semiguttata* Haworth (1821); **incl.** *Aloe subtuberculata* Haworth (1825)  $\equiv$  *Aloe humilis* var. *subtuberculata* (Haworth) Baker (1896); **incl.** *Aloe humilis* subvar. *minor* Salm-Dyck (1837); **incl.** *Aloe humilis* var. *candollei* Baker (1880).

[6] Acaulescent, suckering to form dense groups; **L** 20–30, rosulate, ovate-lanceolate, very acuminate,  $\pm$ 10  $\times$  1.2–1.8 cm, glaucous-green

with a dewy bloom, obscurely lineate, upper face with few tubercles, lower face more copiously tuberculate and with a few irregular soft white prickles, **marginal teeth** 2–3 mm, soft, white; **Inf** 25–35 cm, simple; raceme cylindrical, to 10 cm, subdense, with  $\pm 20$  flowers; **Bra** lanceolate-acuminate, 25–35 mm; **Ped** 25–35 mm; **Fl** scarlet, sometimes orange, 35–42 mm, ventricose, base rounded, enlarged above the ovary, narrowing at the mouth; **OTep** free for 23–28 mm; **St** and **Sty** exerted to 1 mm. — **Cytology**:  $2n = 14$  (Satô 1937).

A very variable species. The published varieties were based on material cultivated in Europe. Reynolds (1950) suggested that there are only 2 distinct varieties but he did not change the classification. The varieties were not documented by Carter & al. (2011) or Wyk & Smith (2014) and hence are not recognized here.

Natural hybrids with other species have been reported (Reynolds 1950), and Kemble (2005) and Kemble (2014) reports a wide array of species that were successfully crossed with *A. humilis* in cultivation.

**A. huntleyana** Van Jaarsveld & Swanepoel (Bradleya 30: 3–6, ills., 2012). **Type**: Namibia, Kunene (Van Jaarsveld & al. 18805 [WIND]). — **Lit**: Jaarsveld & Condy (2015: with ills.). **Distr**: NW Namibia (Kunene: Omavanda); E-facing sandstone cliffs, 1800–2000 m.

[13] Caulescent, branching from the base, forming clumps to 2 m wide; stem spreading or pendulous; **L** in apical **Ros**, linear-lanceolate, acuminate, slightly falcate, 16–18  $\times$  2–3 cm, greyish-green, lower face sparingly spotted near the base, **marginal teeth** pungent, 3–5 mm, yellowish-green, 8–12 mm apart, leaf sheath 15–20 mm, striate; **Inf** 30–40 cm, descending at the base and curving upwards again with a U-bend, simple or with up to 3 **Br**; racemes conical-triangular, terminal 13–15 cm, laterals 8–11 cm, subdense, with subsecund flowers; **Bra** ovate-acuminate, to 5  $\times$  3 mm; **Ped** 8–10 mm; **Fl** red, whitish and yellowish towards the mouth, 28–29 mm, base obtuse, shortly stipitate, 6 mm  $\varnothing$  across the ovary; **OTep** free for 10 mm; **St** and **Sty** exerted 2 mm.

**A. ibitiensis** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 30, 1926). **Type**: Madagascar, Antananarivo (Perrier 13980 [P]). — **Distr**: C Madagascar (Antananarivo: Mt. Ibity); quartzite cliffs and ledges, 1450–2000 m. **I**: Castillon & Castillon (2010: 82–83); Carter & al. (2011: 252).

**Incl.** *Aloe ibityensis* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1); **incl.** *Aloe cremersii* Lavranos (1974); **incl.** *Aloe cyrillei* J.-B. Castillon (2004); **incl.** *Aloe saronarae* Lavranos & T. A. McCoy (2006).

[5] Acaulescent, usually simple; **L** 12–16, densely rosulate, lanceolate-acute, 25–30  $\times$  7 cm, yellowish- to olive-green, prominently lineate-striate, **marginal teeth** 1–2 mm, firm, pale yellowish, 3–5 mm apart; **Inf**  $\pm 80$  cm, with 2–4 **Br**; racemes cylindrical-acuminate, 25  $\times$  5 cm, subdense; **Bra** ovate-acute, 4–7  $\times$  2–3 mm; **Ped** 14 mm; **Fl** scarlet, 26 mm, base attenuate, 4–5 mm  $\varnothing$  across the ovary, enlarging above; **OTep** free for 9 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

Castillon (2005) reports that there are 2 distinguishable local forms of this rare species, that can easily be confused with *A. deltoideodonta*. Castillon & Castillon (2008a) placed several other species here as synonyms. According to Castillon & Castillon (2008b) Reynolds misidentified *A. ibitiensis*, and Reynolds' plants were named *A. manandonae*. The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984).

**A. ifanadianae** J.-B. Castillon (CactusWorld 26(4): 238, ills. (pp. 239–242), 2008). **Type**: Madagascar, Fianarantsoa (Castillon 41 [TAN, HBG, P]). — **Distr**: C-E Madagascar (Fianarantsoa); steep quartzitic cliffs; known only from the type locality. **I**: Castillon & Castillon (2010: 368); Carter & al. (2011: 519).

[13] Caulescent, suckering to form large sprawling groups; stem to 2 m, with dried leaves persistent for 50 cm; **L** 25–40, laxly rosulate, linear-lanceolate, 40–65  $\times$  4 cm, green, **marginal teeth** 1 mm, whitish, 3–10 mm apart; **Inf** 1 m, spreading but racemes erect, simple or mostly with 1 **Br**; racemes cylindrical, 25–35 cm, subdense to lax; **Bra** 10  $\times$  7 mm, fleshy; **Ped** 25–30



mm; **Fl** yellow, 27–32 mm, 4 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exserted 5–7 mm.

**A. ikiorum** Dioli (Cact. Succ. J. (US) 83(6): 271–274, ill., 2012). **Type:** Uganda, Karamoja Region (*Dioli* 116 [ABH, EA [photo], FT [photo]]). — **Distr:** NE Uganda (Rift Valley Escarpment); among tall grasses, 1900 m; known only from the type locality. **I:** Cole & Forrest (2017: 62–67).

[13] Caulescent, solitary, rarely branched; stem to 30 cm, decumbent; **L** 12–24, rosulate, lanceolate, 20–40  $\times$  4–6 cm, bright green, striate, surface smooth, exudate pale yellow, drying to chestnut-brown, **marginal teeth** 2 mm, brown-tipped, 4–16 mm apart; **Inf** 85–155 cm, erect, with 4–5 **Br**; racemes capitate, 3–8 cm, dense; **Bra** linear-lanceolate, 18  $\times$  2 mm; **Ped** 10–13 mm; **Fl** pinkish-red, pale yellow in the upper  $\frac{1}{3}$ , 24 mm, 6 mm  $\varnothing$  across the ovary, narrowed above to 4 mm, widening to the mouth; **OTep** free for 8–10 mm; **St** and **Sty** exserted 0–1 mm.

**A. imalotensis** Reynolds (J. South Afr. Bot. 23: 68, 1957). **Type:** Madagascar, Fianarantsoa (*Perrier* 11022 [P]). — **Distr:** Madagascar. **I:** Castillon & Castillon (2010: 180–183); Carter & al. (2011: 315).

**A. imalotensis** var. **imalotensis** — **Distr:** Madagascar (Fianarantsoa: E Horombe Plateau); rock outcrops of sandstone and shale, 600–1000 m. **I:** Reynolds (1966: 445–447); Castillon & Castillon (2010: 180–181); Carter & al. (2011: 315).

**Incl.** *Aloe deltoideodonta* var. *contigua* H. Perrier (1926)  $\equiv$  *Aloe contigua* (H. Perrier) Reynolds (1958); **incl.** *Aloe deltoideodonta* fa. *latifolia* H. Perrier (1938) (*nom. inval.*, ICN Art. 39.1); **incl.** *Aloe deltoideodonta* fa. *longifolia* H. Perrier (1938) (*nom. inval.*, ICN Art. 39.1); **incl.** *Aloe deltoideodonta* subfa. *variegata* Boiteau ex H. Jacobsen (1954) (*nom. inval.*, ICN Art. 39.1).

[5] Acaulescent or shortly caulescent, simple or branching to form small groups; stem decumbent, to 20  $\times$  3 cm; **L** 20–24, densely rosulate,

ovate-acute, to 30  $\times$  12–15 cm, very fleshy, dull bluish-green tinged reddish, obscurely lineate, with 1 mm pink to reddish cartilaginous margin, exudate drying yellow, **marginal teeth** 1–1.5 mm, deltoid or obtuse, pink, 1–4 mm apart, sometimes contiguous; **Inf** 50–60 cm, with 2–4 **Br**; racemes cylindrical, slightly acuminate, 10–20  $\times$  7 cm, subdense; **Bra** ovate-acute, 7–10  $\times$  3–4 mm; **Ped** 15–18 mm; **Fl** coral-red, 30–34 mm, base shortly attenuate, 6 mm  $\varnothing$  across the ovary, very slightly narrowed above, then enlarging slightly to the mouth; **OTep** free almost to the base; **St** and **Sty** exserted 2 mm.

**A. imalotensis** var. **longiracemosa** J.-B. Castillon (Kakt. and. Sukk. 56(10): 270–271, ill., 2005). **Type:** Madagascar, Toliara (*Castillon* 17 [HBG]). — **Distr:** Madagascar (Toliara: near Mahaboboka); sandstone rocks and gravel, 355 m; known only from the type locality. **I:** Castillon & Castillon (2010: 182–183; 254–255, incl. a form referred to as '*variegata*'); Carter & al. (2011: 315).

[5] Differs from var. *imalotensis*: Acaulescent, forming small groups; **L** 25  $\times$  15 cm, thinner, light green to pale brownish, usually with small round pale spots; **Inf** racemes longer, lax.

**A.  $\times$ imerinensis** Bosser (*Adansonia*, n.s. [sér. 2], 8(4): 510–512, ill., 1968). **Type:** Madagascar, Centre (*Bosser* 17043 [P]). — **Distr:** Madagascar. = *Aloe capitata*  $\times$  *A. macroclada*.

**A. immaculata** Pillans (South Afr. Gard. 24: 25, 1934). **Type:** RSA, Limpopo (*Stellenbosch Univ. Gard.* 6774 [BOL]). — **Distr:** RSA (S Limpopo); warm river valleys, open grassland or shade of bushes, 900–1800 m. **I:** Reynolds (1950: 239–240); Carter & al. (2011: 185); Wyk & Smith (2014: 240–241).

[3] Acaulescent or shortly caulescent, simple; stem to 10 cm; **L** 16–20, densely rosulate, lanceolate-attenuate, to 40  $\times$  6–8 cm, apical 5–10 cm soon drying, upper face dull green to brownish-green, with distinct darker longitudinal striations, sometimes with a few scattered white spots, lower face greyish-green, sometimes obscurely finely striate, with horny brownish to

reddish-brown margin, exudate drying purple, **marginal teeth** 4–5 mm, pungent, brownish to reddish-brown, 10–15 mm apart; **Inf** to 1 m, with 6–10 **Br**, lower ones sometimes rebranched; racemes subcapitate, 10–20 × 8–9 cm, dense; **Bra** lanceolate-deltoid, 10–15 mm; **Ped** 12–15 mm; **Fl** coral-red, 30–33 mm, base truncate, 7 mm  $\varnothing$  across the ovary, abruptly narrowed to 4 mm above, then enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

Included in *A. affinis* by Glen & Hardy (2000).

**A. inamara** L. C. Leach (J. South Afr. Bot. 37 (4): 259–266, ills., 1971). **Type**: Angola, Cuanza-Sul (Leach & Cannell 14608 [LISC, PRE]). — **Distr**: W Angola (Cuanza-Sul: mouth of the Quimbo River); almost vertical cliff faces; known only from the type locality. **I**: Carter & al. (2011: 518).

[13] Caulescent, branching at the base and more sparingly above, sometimes forming dense mats to 3 m; stem pendulous, to 2 m × 2 cm  $\varnothing$ , covered by dried leaf bases; **L**  $\pm 9$ , rosulate, falcate, pointing downwards, 45–60 (–90) × 4–5 cm, pale yellowish-green, brown when exposed to sun, obscurely lineate with few to many small  $\pm$  H-shaped whitish spots, lower face with more spots in  $\pm$  transverse bands, with whitish or faint pink margin, exudate yellow, not bitter, **marginal teeth** 0.3–1 mm, whitish, often brown-tipped, 4–20 mm apart; **Inf** 40–55 cm, descending and upturned towards the tip, with 4–6 **Br**; racemes cylindrical-conical to almost capitate, to 7.5 × 7.5 cm, subdax; **Bra** triangular-attenuate, 7.5–9 ×  $\pm 3$  mm; **Ped** 22–27 mm; **Fl** dull red with greenish tip, 26–29 mm, base truncate, 8 mm  $\varnothing$  across the ovary, abruptly narrowed to  $\pm 7$  mm above, then enlarging and narrowing again to  $\pm 6$  mm at the mouth; **OTep** free for 6.5–8 mm; **St** exerted 0–1 mm.

**A. inconspicua** Plowes (Aloe 23(2): 32–33, ills., 1986). **Type**: RSA, KwaZulu-Natal (Plowes 7079 [PRE]). — **Lit**: Hargreaves & al. (2008: pollination ecology). **Distr**: RSA (C-W KwaZulu-Natal: Bushmans River catchment); grassy glades among acacias on shale and sandstone,

1000–1200 m. **I**: Carter & al. (2011: 107); Wyk & Smith (2014: 360–361).

[1] Acaulescent, simple, with persistent leaf bases forming an ovoid bulb to 50 × 25 mm; **R** fleshy; **L** rosulate, linear-acuminate, 3 × 0.3–0.4 cm, green, lower face with elongated white spots on the basal  $\frac{1}{2}$ , with translucent margin, **marginal teeth** 0.5 mm, soft, translucent, 2–4 mm apart; **Inf**  $\pm 1.5$  m, simple; raceme cylindrical,  $\pm 7 \times 2$  cm, with  $\pm 30$  flowers; **Bra** 13 mm; **Ped** absent; **Fl** green with semitranslucent whitish tepal margins, 15 mm, narrowing slightly at the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

Hargreaves & al. (2008) found this taxon to be exclusively pollinated by bees, esp. females of the solitary bee *Amegilla fallax*.

**A. inermis** Forsskål (Fl. Aegypt.-Arab., 74, 1775). **Type**: Yemen (Forsskål s.n. [C †]). — **Lit**: Wood (1983); Lavranos (1992). **Distr**: Yemen; rocky slopes, 760 m. **I**: Reynolds (1966: 221); Carter & al. (2011: 599).

[13] Caulescent, suckering and forming small to large groups; stem decumbent or ascending to erect, to 50 cm; **L**  $\pm 12$ –16, rosulate and persistent for 20 cm, lanceolate or ensiform, attenuate, spreading and becoming decurved, 25–30 (–45) × 5–7 cm, grey-green or dull pale olive-green, sometimes with few or many scattered small dull white lenticular spots towards the base, with whitish cartilaginous margin, surface rough, **marginal teeth** absent; **Inf**  $\pm 70$  cm, oblique, with 6–9 **Br**, lower ones sometimes rebranched; racemes with flowers secund on more oblique branches, to 15 cm, subdense; **Bra** ovate-acute, 4 × 2–3 mm, white; **Ped** 5–9 mm; **Fl** dull scarlet or yellow, 28–30 mm, base rounded, 7–8 mm  $\varnothing$  across the ovary, slightly narrowed above the ovary, then slightly enlarging to the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology**:  $2n = 14$  (Wood 1983).

A natural hybrid with *A. vacillans* has been reported (Wood 1983).

**A. inexpectata** Lavranos & T. A. McCoy (Cact. Succ. J. (US) 75(6): 258–261, ills., 2003). **Type**: Madagascar, Fianarantsoa (Lavranos & McCoy 31681 [MO, P, TAN]). — **Distr**:

Madagascar (Fianarantsoa: Ambatofinandrahana); limestone cliff face, 1400 m; known only from the type locality. **I**: Castillon & Castillon (2010: 116–117); Carter & al. (2011: 530).

[11] Caulescent, branching at the base, forming groups; stems up to 12, decumbent or ascending and then 3–12 cm; **L** 5–9, distichous, 3–5 × 0.6–0.9 cm, grey-green, **marginal teeth** deltoid, soft, 2–3 mm, white, 2 mm apart; **Inf** 20–25 cm, erect, simple; racemes cylindrical, 5–7 cm, lax; **Bra** 5 mm; **Ped** 12–15 mm; **Fl** coral-red, almost white towards the mouth, 20 mm; **OTep** free for 6 mm; **St** and **Sty** exerted 0–1 mm.

**A. ×inopinata** Gideon F. Smith & al. (Haseltonia 22: 60–61, ill. (pp. 57, 59–60), 2016). **Type**: RSA, Mpumalanga (*Oosthuizen* 1960 [BNRH]). — **Distr**: RSA (Mpumalanga); montane grassland, in the mist belt in shallow soils amongst rocks and shrubs, 1500 m.

[15] Shrub, branching at or near the base; stem erect, to 60 × 3.5–4 cm, with persistent dry leaves to 7 cm; **L** densely rosulate, lanceolate-attenuate, 20–40 × 0.8–2.5 cm, light to mid-green, rarely with scattered white spots on both faces, surface smooth, exudate pale creamy-beige, drying purplish, **marginal teeth** 0.8–1.2 mm, white, 5–9 mm apart; **Inf** 40–60 cm, erect, simple; raceme subconical to conical or conical-cylindrical, 8–10 cm, dense; **Bra** ovate-elongated, 12–15 × 6 mm, straw-coloured to brownish-white, scarious, many-nerved; **Ped** 20–22 mm; **Fl** orange-red, 30 mm, 3–5 mm Ø across the ovary, slightly narrowed above, widening slightly to the mouth; **OTep** free to the base; **St** not or slightly exerted; **Sty** exerted 5–8 mm.

This is the naturally occurring hybrid *A. arborescens* × *A. chortolirioides* var. *chortolirioides*.

**A. integra** Reynolds (Flow. Pl. South Afr. 16: t. 607 + text, 1936). **Type**: RSA, Mpumalanga (*Reynolds* 1650 [PRE]). — **Distr**: N Swaziland, RSA (E Mpumalanga); montane grassland on rocky slopes, 1400–1600 m. **I**: Reynolds (1950: 141–142); Carter & al. (2011: 143); Wyk & Smith (2014: 318–319).

[4] Caulescent, usually simple, sometimes in groups of up to 6 **Ros**; **R** fusiform; stem to 20 × 4–6 cm Ø; **L** 15–30, rosulate, triangular-attenuate, 10–12 × 4–5 cm, apical 5 cm soon drying, glossy deep green, obscurely lineate, **marginal teeth** usually absent, sometimes very minute and 2–5 mm apart; **Inf** to 50 cm, simple; raceme pyramidal, 8–12 × 7–9 cm, subdense, terminating in a dense tuft of reflexed purple bracts; **Bra** deltoid-acuminate, 15–20 mm, purple; **Ped** to 30 mm; **Fl** lemon-yellow to rich canary-yellow, 15–18 mm, base attenuate, enlarged above the ovary, narrowing at the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Müller 1945).

**A. inyangensis** Christian (Flow. Pl. South Afr. 16: t. 640 + text, 1936). **Type**: Zimbabwe (*Piers* s.n. in *Christian* 518 [PRE 28428]). — **Distr**: Zimbabwe.

**A. inyangensis** var. **inyangensis** — **Distr**: Zimbabwe (Nyanga Mts. and border to Moçambique); in peaty soil and in cracks and crevices on rocks, 1825–2560 m. **I**: Reynolds (1966: 23–24); Carter & al. (2011: 137).

[10] Caulescent, branching near the base to form dense clumps to 2 m Ø; stem ±20 × 1.5–2 cm, **L** ±8–10, laxly distichous, 15–20 × 1.5 cm, dark green, with or without a few scattered spots near the base, lower face usually with many very pale green lenticular spots near the base, spots sometimes tuberculate, with white cartilaginous margin, exudate yellow, **marginal teeth** 0.5 mm, 1–2 mm apart; **Inf** 30–35 cm, simple; raceme cylindrical-acuminate, 6–8 cm, sublax, with ±16 flowers; **Bra** lanceolate-attenuate, 25 × 9 mm, imbricate in bud stage; **Ped** 30 mm; **Fl** bright scarlet, greenish at the mouth, 35–40 mm, base rounded, 7 mm Ø across the ovary, not narrowed above; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. inyangensis** var. **kimberleyana** S. Carter (Kew Bull. 51(4): 777–779, ill., 1996). **Type**: Zimbabwe, Eastern Prov. (*Carter & al.* 2702 [K, SRGH]). — **Distr**: Zimbabwe (Nyanga Mts.);

damp places on rocks and pendulous on cliffs, 1220–1900 m. **I:** Carter & al. (2011: 138).

[10] Differs from var. *inyangensis*: Stem to 1 m; **Br** more robust; **L** to 40 × 2.5 cm, thick and fleshy.

**A. irafensis** Lavranos & al. (Cact. Succ. J. (US) 80(1): 41, 2008). **Type:** Yemen (*McCoy* 2669 [FT, UPS]). — **Lit:** Lavranos & al. (2004: with ills.). **Distr:** Yemen (Jabal Iraf); in forests of *Juniperus excelsa*, 1200–1250 m. **I:** Carter & al. (2011: 485).

[13] Caulescent, branching sparingly at the base; stem to 1 m, decumbent; **L** 10–16, distichous, narrowly strap-shaped, apex acute, 20 × 3–3.5 cm, blackish- or dark jade-green, sometimes with numerous small white spots, exudate greenish-yellow, drying brownish-yellow, **marginal teeth** absent or occasionally small, white; **Inf** to 45 cm, with 3–9 **Br**; racemes oblique or suberect, lax, flowers subsecund; **Bra** ovate, acute, 3–7 × 1.5–3 mm; **Ped** 7 mm; **Fl** dull red with waxy bloom, yellowish-green at the mouth, 20 mm, 4 mm Ø across the ovary; **OTep** free for 5 mm; **St** and **Sty** exerted 3–3.5 mm.

The name was first published invalidly (Lavranos & al. 2004), and was only subsequently validated.

**A. isaloensis** H. Perrier (Bull. Acad. Malgache, n.s. 10: 20, 1927). **Type:** Madagascar, Fianarantsoa (*Perrier* 17232 [P, K]). — **Distr:** Madagascar (Fianarantsoa: Isalo Massif); bush on sandstone slopes, 600–1200 m. **I:** Reynolds (1966: 493–495); Castillon & Castillon (2010: 185–187); Carter & al. (2011: 592). — Fig. 35.

[10] Caulescent, branching at the base; stem erect, divergent or decumbent, to 30 (–50) × 0.8–1 (–1.2) cm; **L** 10–14, sublax and persistent for up to 10 cm, linear-attenuate, 13–20 × 1–1.3 cm, grey-green, exudate yellow-orange, very abundant, **marginal teeth** 1–1.5 mm, firm, greenish to pale brown, 5–10 mm apart, leaf sheath 0.5 cm, obscurely striate; **Inf** 30–50 cm, simple or with up to 5 **Br**; racemes cylindrical, slightly acuminate, 10–14 × 4–5 cm, lax, with 20–30 flowers; **Bra** deltoid, 3 × 1.5 mm; **Ped** 6–7 mm; **Fl** scarlet, 22 mm, base shortly attenuate, 6 mm Ø



**Fig. 35** *Aloe isaloensis*. (Copyright: U. Eggli)

across the ovary, narrowed to 5 mm above, then enlarging slightly to the mouth; **OTep** free for 11 mm; **St** exerted 0–1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. ithya** T. A. McCoy & L. E. Newton (Haseltonia 19: 64–65, ills., 2014). **Type:** South Sudan, Eastern Equatoria (*Idriss* s.n. in *McCoy* 2892 [EA, FT]). — **Distr:** SE South Sudan; rocky cliffs.

[12] Caulescent, branching at the base; stem to 2 m, erect, with persistent dead leaves; **L** loosely rosulate and to 15 cm below the stem tip, lanceolate, apex acute, 30 × 3.5 cm, mid-green, lower face with few whitish spots near the base, surface smooth, exudate pale yellow, **marginal teeth** uncinuate, firm, 3 mm, red-tipped, 10 mm apart, leaf sheath 10 mm, green with whitish spots; **Inf** to 50 cm, erect, simple or with 1 **Br**; racemes cylindrical, 18 cm, dense; **Bra** ovate, shortly attenuate, 2 × 2 mm; **Ped** 12–14 mm; **Fl** coral-red, 30 mm, base stipitate, 5 mm Ø across the ovary, slightly

narrowed above, to 5 mm at the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 5 mm.

**A. ivakoanyensis** Letsara & al. (Malagasy Nat. 6: 52, ills. (pp. 50, 53), 2012). **Type:** Madagascar, Toliara (*Letsara & Andriamihajarivo* 624 [TAN]). — **Distr:** Madagascar (Toliara), rocky slopes in humid forest, 925 m.

[4] Acaulescent or shortly caulescent, solitary or suckering and forming groups with up to 5 rosettes; **L** 14–23, rosulate, spreading, lanceolate-triangular, 39–45 × 3–4 cm, green, surface smooth, exudate green-yellowish, **marginal teeth** 3.5 mm, pale, 8–20 mm apart; **Inf** 30 cm, erect or ascending, simple or with 1 **Br**; racemes cylindrical to laxly conical, 10 cm; **Bra** narrowly lanceolate, 4–4.5 mm, scarious, pale tan, with 1 nerve; **Ped** 9 mm, orange-red; **Fl** orange-red, paler towards the mouth, 28 mm, 7 mm Ø across the ovary, narrowed above; **OTep** free only at the mouth; **St** exerted 5 mm; **Sty** exerted 3 mm; **Fr** a globose berry, 18–19 mm.

**A. jacksonii** Reynolds (J. South Afr. Bot. 21 (2): 59–61, t. 5, 1955). **Type:** Ethiopia, Bale Region (*Jackson* s.n. in *Reynolds* 6224 [PRE]). — **Lit:** Brandham & al. (1994). **Distr:** E Ethiopia (Bale Region); limestone rock outcrops, 1050 m; known only from the type collection. **I:** Reynolds (1966: 54–55); Carter & al. (2011: 477).

[11] Caulescent, suckering to form groups to 50 cm Ø; stem erect or sprawling, to 20 × 0.8–1 cm; **L** 5–7, laxly rosulate, subulate-attenuate, 10–15 × 1–1.4 cm, upper face dull green with several scattered dull pale green lenticular spots towards the base, lower face greyish-green with many dull pale green lenticular spots, scattered or sometimes in broken transverse bands, surface very slightly rough, exudate drying yellow, **marginal teeth** 1 mm, firm, white, reddish-tipped, 3–6 mm apart; **Inf** 30 cm, simple; raceme cylindrical, 6–8 cm, lax, with 16–20 flowers; **Bra** ovate-acuminate, 4 × 2.5 mm; **Ped** 5–7 mm; **Fl** bright scarlet, paler to almost white towards the mouth, 27 mm, base truncate, 8–9 mm Ø across the ovary, narrowing slightly towards the mouth; **OTep** free for 6–7 mm; **St** and **Sty** exerted 2–3 mm. — **Cytology:** 2n = 28 (Brandham 1971).

In 2000, when searching for this at the stated type locality (El Kerré), M. Dioli did not find it, but found instead a different species, which he named as *A. elkerriana* (Dioli 2008). The exact origin of *A. jacksonii* is as yet unresolved.

**A. jawiyon** Christie & al. (in A. G. Miller & M. Morris, Ethnopl. Soqotra Archip., 723, 2004). **Type:** Yemen, Socotra (*Miller & al.* 20022 [E]). — **Lit:** Christie & al. (2005). **Distr:** Yemen (W Socotra); on limestone in low scrub, 500–800 m. **I:** Carter & al. (2011: 549).

[11] Caulescent, suckering to form small clumps; stem to 20 cm, erect or prostrate; **L** densely rosulate, lanceolate-acuminate, to 20 × 3.5 cm, yellowish-green tinged bronze, surface finely glabrous, **marginal teeth** 2 mm, green, 6 mm apart; **Inf** to 20 cm, erect, simple; racemes cylindrical, 10–20 cm, dense; **Bra** lanceolate-deltoid, 4–6 mm; **Ped** 8 mm; **Fl** bright orange, green at the mouth, 10–20 mm, slightly narrowed above the ovary, widening to the mouth; **OTep** free for 8 mm; **St** and **Sty** exerted 0–1 mm.

Occurs sympatric with *A. perryi*, but no hybrids were observed (Christie & al. 2005).

**A. jeppeae** Klopper & Gideon F. Smith (Phytotaxa 76(1): 12, 2013). **Type:** RSA, Free State (*Fritz* 1025 [PRE]). — **Distr:** RSA (C Free State, Gauteng, SE North-West); grassland on sandy soil. **I:** Craib (2006: 131, as *Chortolirion angolense*); Zonneveld & Fritz (2010: 33, as *C. latifolium*); Wyk & Smith (2014: 362–363). — Fig. 36.

≡ *Chortolirion latifolium* Zonneveld & G. Fritz (2010); ≡ *Aloe aestivalis* Boatwright & J. C. Manning (2013) (*nom. illeg.*, ICN Art. 52.1).

[4] Acaulescent, with short subterranean bulb 4 × 1.5–3 cm, suckering to form clumps; **L** rosulate, linear, 5–12 × 0.4–0.5 cm, glaucous greyish-green, with white spots on the lower face, **marginal teeth** minute; **Inf** 20–40 cm, erect, simple; racemes cylindrical, lax; **Bra** deltoid, 9 × 2 mm, with 1 light brown nerve; **Ped** 10–20 mm; **Fl** pinkish-white with greenish keels, 14–17 mm, base obtuse, **Tep** free almost to the base.





**Fig. 36** *Aloe jeppaea*. (Copyright: G. Fritz)

**A. jibisana** L. E. Newton (*Haseltonia* 12: 20, ills. (pp. 19–20), 2007). **Type:** Kenya, Eastern Prov. (*Brown* s.n. in *Newton* 5573 [K, EA]). — **Distr:** Kenya (Eastern Prov.: Marsabit Distr., Jibisa Mtn.); rock ledges, 1370 m. **I:** Carter & al. (2011: 476).

[13] Caulescent, branching freely at and near the base; stem erect to 45 cm, then decumbent to 150 cm, rooting where they touch the ground; **L** scattered along the stem for 60 cm or more, lanceolate, 14 × 2.5 cm, dull green with light waxy bloom, lower face with scattered white spots, surface smooth, exudate yellow, **marginal teeth** pungent, forward-pointing, 2 mm, whitish with dark red tip, 6–8 mm apart; **Inf** 25 cm, erect, simple or with 1 **Br**; racemes cylindrical, terminal to 8 cm with 20–25 flowers, lateral ones 3 cm, subdense; **Bra** triangular, long-attenuate, 5 × 2 mm; **Ped** 10–11 mm; **Fl** yellow, reddish at the mouth, 20 mm, base shortly attenuate, 7 mm Ø across the ovary, narrowing to 6 mm above; **OTep** free for 10 mm; **St** and **Sty** exerted 1–2 mm.

**A. johannis** J.-B. Castillon (*Succulent* 2006 (1): 18–19, ills., 2006). **Type:** Madagascar, Antananarivo (*Castillon* 18 [HBG, P]). — **Distr:** Madagascar (Antananarivo); on quartzite rocks, 1930–2000 m; known only from the area of the type locality. **I:** Castillon & Castillon (2010: 86–87); Carter & al. (2011: 562).

[13] Caulescent, branching at the base and above; stem to 50 cm, decumbent; **L** 7–12, elongate-deltoid, apex aculeate, 15–30 × 2.5–4.5 cm, lustrous dark green, **marginal teeth** 1 mm, white or reddish, 5 mm apart; **Inf** 30–60 cm, erect, with up to 2 **Br**; racemes capitate to subcapitate, dense, with 15–30 flowers; **Bra** ovate-acute, 5 × 4 mm; **Ped** 25 mm; **Fl** yellow, 25 mm, 4 mm Ø across the ovary, 7 mm at the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 2–3 mm.

**A. johannis-bernardii** J.-P. Castillon (*Cact.-Avent. Int.* 80: 12–13, ills. (pp. 13–16), 2008). **Type:** Madagascar, Antananarivo (*Castillon* 40 [TAN, P]). — **Distr:** Madagascar (Antananarivo: near Antsirabe); quartzite hill in degraded forest, 100–200 m. **I:** Castillon & Castillon (2010: 344); Carter & al. (2011: 274).

[7,11] Acaulescent or caulescent, suckering to form small groups; stem absent or to 20 cm; **L** 11–15, rosulate, lanceolate-attenuate, with red-toothed tip, 50 × 3–4 cm, green, **marginal teeth** pungent, 2 mm, yellow, 15 mm apart; **Inf** 50–70 cm, with 1–2 **Br**; racemes capitate to shortly cylindrical, 6–8 cm, dense, flowers opening from the top downwards; **Bra** 3 × 2–4 mm, white; **Ped** 24 mm; **Fl** yellowish-green to cream, 25–27 mm, 4 mm Ø across the ovary, widening to 8 mm at the mouth; **OTep** free to the base; **St** and **Sty** exerted 1–2 mm.

Possibly identical to *A. capitata* var. *silvicola* (*Castillon & Castillon* 2010: 344).

**A. johannis-philippeii** J.-B. Castillon (*CactusWorld* 27(1): 52–55, ills., 2009). **Type:** Madagascar, Fianarantsoa (*Castillon* 42 [TAN]). — **Distr:** Madagascar (Fianarantsoa: Andringitra); granite crevices on cliffs, 2500 m. **I:** Castillon & Castillon (2010: 156–157).

[2] Acaulescent, solitary; **L** 40, rosulate, triangular, 80 × 15 cm, green, reddish-tinged, **marginal teeth** 3 mm, whitish-yellow, 5–10 mm apart; **Inf** 85 cm, erect, simple; raceme cylindrical, 25 cm, dense; **Bra** rectangular, tip acute, 10 × 1.5 mm, fleshy; **Ped** absent; **Fl** reddish-brown with whitish margins, 25 mm, campanulate, 5 mm Ø across the ovary, 15 mm Ø at the mouth; **OTep** free to the base; **St** exerted 15 mm; **Sty** exerted 5 mm.

**A. jucunda** Reynolds (J. South Afr. Bot. 19 (1): 21–23, t. 11, 1953). **Type:** Somalia, Hargeisa (*Bally* 7157 in *Reynolds* 6223 [PRE]). — **Distr:** NW Somalia (Hargeisa: Gaan Libah plateau); on limestone, usually in the shade of residual juniper forest, 1060–1680 m. **I:** Reynolds (1966: 49–50); Carter & al. (2011: 397).

[11] Acaulescent or shortly caulescent, suckering to form dense groups to 50 cm Ø; **L** ±12, densely rosulate, ovate-acuminate, 4 × 2–5 cm, dark green with many pale green to dull white spots, more numerous on the lower face, surface smooth, exudate yellow, **marginal teeth** 2 mm, pungent, reddish-brown, 3–4 mm apart; **Inf** 33 cm, simple; raceme cylindrical, 13 × 5 cm, subdense, with ±20 flowers; **Bra** ovate-acute, 5 × 3 mm; **Ped** 7 mm; **Fl** pale rose-pink, 20 mm, base shortly attenuate, 7 mm Ø across the ovary, slightly narrowed above, enlarging slightly to the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 2–3 mm. — **Cytology:** 2n = 14, 21 (Brandham 1971).

Many artificial hybrids have been obtained with *A. jucunda* as one parent (Jonkers 2014).

**A. juddii** Van Jaarsveld (Aloe 45(1): 4–6, ill., 2008). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 18295 [NBG]). — **Lit:** Molteno (2017). **Distr:** RSA (Western Cape: Overberg Mts.); Fynbos vegetation on sandstone ridge, 300–500 m. **I:** Carter & al. (2011: 531); Wyk & Smith (2014: 116–117).

≡ *Aloiampelos juddii* (Van Jaarsveld) Klopper & Gideon F. Smith (2013).

[13] Caulescent, solitary; stem to 60 cm, decumbent with age; **L** densely packed along the

stem, triangular-ovate to triangular-lanceolate, 5.5–7.5 × 1.5–2.5 cm, dark green, faintly striate, exudate clear, **marginal teeth** 1 mm, white, 1–1.5 mm apart; **Inf** 35–48 cm, erect, simple; racemes cylindrical, 5.5–8 cm, sublux; **Bra** ovate-acuminate, 7 × 3 mm; **Ped** 10–12 mm; **Fl** orange-red, yellowish-green at the mouth, 40 mm, 8 mm Ø across the ovary; **OTep** free for 20 mm; **St** and **Sty** not exerted.

**A. juvenna** Brandham & S. Carter (Cact. Succ. J. Gr. Brit. 41(2): 27–29, ill., 1979). **Type:** Kenya (*Carter & Stannard* 5 [K]). — **Distr:** S Kenya, N Tanzania: W side of the Rift Valley; in grass on rocky ridge, 2300 m. **I:** Carter & al. (2011: 529).

[11] Caulescent, freely branching and suckering at the base; stem erect to 25 × 0.7 cm, or decumbent to 45 × 1.2 cm, densely leafy; **L** persistent below the stem tip, to 35 per 10 cm of stem, deltoid, to 4 × 2 cm, bright green with many elongated pale green spots, many raised into small prickles, **marginal teeth** 2–4 mm, cartilaginous, 4–6 mm apart; **Inf** 25 cm, simple or with 1 **Br**; racemes conical, to 8 × 6 cm, subdense; **Bra** ovate, ±5 × 4 mm; **Ped** 13–18 mm; **Fl** coral-pink, greenish-yellow tipped, 27 mm, base attenuate, 8 mm Ø across the ovary, very slightly narrowed above, enlarging slightly to the mouth; **OTep** free for 9 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 28 (Brandham 1971).

First described from cultivated material of undocumented origin, and later rediscovered in its natural habitat.

**A. kahinii** T. A. McCoy & Lavranos (Haseltonia 13: 32–33, ill., (pp. 29–30), 2008). **Type:** Somalia, Northern Region (*McCoy* 2992 [FT]). — **Distr:** N Somalia (Northern Region: near Las Anod); on gypsum hills, 750 m. **I:** Carter & al. (2011: 437).

[13] Caulescent, suckering, forming groups with up to 15 **Ros**; stem to 15 cm, procumbent; **L** 9–12, rosulate, lanceolate, acute, 20–30 × 4–5 cm, olive or greyish-green, exudate dark orange, drying brown, **marginal teeth** absent, or occasionally small near the leaf apex; **Inf** 45 cm, oblique, with 6–12 **Br**; racemes cylindrical, to

15 cm, lax; **Bra** ovate, acute,  $3 \times 1$  mm; **Ped** 5 mm; **Fl** pink, yellow at the mouth, 20–25 mm, 4–5 mm  $\varnothing$  across the ovary, slightly narrowed above; **OTep** free for 5 mm; **St** and **Sty** exerted 6–7 mm.

**A. kammellii** Van Jaarsveld (Aloe 46(2): 38–39, ills., 2009). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 22166 [NBG, PRE]). — **Distr:** RSA (Western Cape); steep N-facing shale slope, 250–300 m. **I:** Wyk & Smith (2014: 96–97).

[12] Caulescent, branching from the base forming a dense shrub with up to 25 **Ros**, rarely solitary; stem to 1.5 m, erect; **L** rosulate, linear-lanceolate,  $39\text{--}40 \times 5\text{--}8$  cm, glossy grass-green, striate, exudate drying faintly orange-yellow, **marginal teeth** 6–7 mm, dark brown, 10–20 mm apart; **Inf** 80–100 cm, ascending, simple; raceme cylindrical-acuminate, 45–51 cm, dense; **Bra**  $35 \times 15$  mm, yellow; **Ped** 20–22 mm; **Fl** yellow, 45 mm, 8–10 mm  $\varnothing$  across the ovary, narrowing to 5–6 mm at the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

The altitude 600–800 m given on p. 40 of the protologue is an error (Van Jaarsveld, pers. comm.).

**A. kaokoensis** Van Jaarsveld & al. (Bothalia 36 (1): 75–76, ills., 2006). **Type:** Namibia, Kunene (*Van Jaarsveld & Swanepoel* 19504 [WIND]). — **Distr:** NW Namibia (Kunene: Kaokoveld: Otjihipa Mts.); arid Mopane woodland on granitic soil, 700–2000 m. **I:** Carter & al. (2011: 645).

[9] Caulescent, solitary; stem to 1 m, erect, becoming decumbent, with dead leaves persistent; **L** rosulate, lanceolate,  $38\text{--}67 \times 4\text{--}14$  cm, pale glaucous, upper face sparsely white-spotted at the base, lower face densely spotted in transverse bands, surface slightly rough, exudate yellowish, drying dark brown, **marginal teeth** 3–4 mm, black, 7–15 mm apart; **Inf** 123–142 cm, erect, with up to 15 **Br**; racemes cylindrical-acuminate, 33–47 cm, lax; **Bra** linear-lanceolate,  $10\text{--}12 \times 3$  mm; **Ped** 11–14 mm; **Fl** orange-red to yellowish, 35 mm, 6–6.5 mm  $\varnothing$  across the ovary; **OTep** free for 17–18 mm; **St** and **Sty** exerted 1 mm.

**A. karasbergensis** Pillans (J. Bot. 66: 233, 1928). **Type:** RSA, Northern Cape (*Pillans* 5848

[BOL]). — **Lit:** Lavranos (2004); Klopper & al. (2008). **Distr:** Namibia, RSA (Northern Cape). **I:** Reynolds (1950: 297–299); Carter & al. (2011: 352).

≡ *Aloe striata* ssp. *karasbergensis* (Pillans) Glen & D. S. Hardy (1987).

**A. karasbergensis** ssp. **hunsbergensis** Van Jaarsveld & Swanepoel (Aloe 48(3): 64–66, ills., 2011). **Type:** Namibia, Oranjemund (*Van Jaarsveld & Swanepoel* 21018 [WIND]). — **Distr:** Namibia (Oranjemund: Rosh Pinah); sandstone, 1300–1500 m.

[5] Differs from ssp. *karasbergensis*: Stoloni-ferous; **Ros** 30–40 cm  $\varnothing$ ; **L**  $15\text{--}20 \times 5\text{--}8$  cm.

**A. karasbergensis** ssp. **karasbergensis** — **Distr:** S Namibia, RSA (Northern Cape); arid sandy areas and stony mountain slopes, to 1200 m. **I:** Reynolds (1950: 297–299); Carter & al. (2011: 352); Wyk & Smith (2014: 164–165).

[5] Caulescent, solitary or branching; stem very short; **Ros** to 1 m  $\varnothing$ ; **L** 15–20, rosulate, ovate-lanceolate, acuminate,  $40\text{--}50 \times 15\text{--}20$  cm, pale glaucous, with dark green striations, **marginal teeth** absent; **Inf** 50–60 cm, with up to 50 **Br**; racemes conical, lax; **Bra** narrowly deltoid, 3–6 mm; **Ped** 8–12 mm; **Fl** dull red, 25–27 mm, 7 mm  $\varnothing$  across the ovary, narrowed to 4 mm above; **OTep** free for 6 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:**  $2n = 14$  (Riley 1959).

**A. ×keayi** Reynolds (*pro sp.*) (J. South Afr. Bot. 29(2): 43–44, t. 6–7, 1963). **Type:** Ghana (*Keay & Adams* FHI-37757A [K, GC]). — **Distr:** Ghana (Accra Plains).

[5] Shortly caulescent, simple or with a few suckers from the base; stem to 25 cm, decumbent; **L** 20–30, densely rosulate, lanceolate,  $60 \times 10\text{--}12$  cm, pale green with scattered whitish elliptic spots, surface smooth, exudate yellow, **marginal teeth** deltoid, 5–6 mm, white-tipped, 10–15 mm apart; **Inf** to 100 cm, erect, with 2–3 **Br**; racemes cylindrical, 15–20 cm, semidense; **Bra** deltoid-acute,  $5\text{--}7 \times 2\text{--}4$  mm, white with 3 brownish nerves; **Ped** 10–12 mm; **Fl** pale apricot-scarlet to pinkish-apricot, 35 mm, base rounded, 8 mm  $\varnothing$  across the ovary, narrowed to

6 mm above, widening to 8 mm towards the mouth; **OTep** free for 14–15 mm; **St** and **Sty** exerted 3–4 mm. — **Cytology**:  $2n = 14$  (Newton 1970).

= *A. buettneri* × *A. schweinfurthii* (Newton 1976).

**A. kedongensis** Reynolds (J. South Afr. Bot. 19(1): 4–6, tt. 3–4, 1953). **Type**: Kenya, Rift Valley Prov. (*Reynolds* 6546 [PRE, EA, K]). — **Distr**: Kenya (Rift Valley Prov.: top of the Kedong Escarpment); dense bush, usually on rocky ground, 1825–2300 m. **I**: Reynolds (1966: 375–376); Carter & al. (2011: 563).

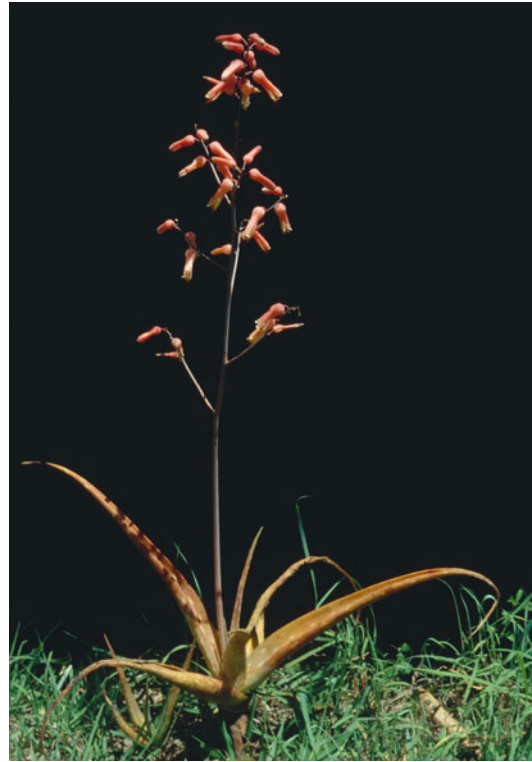
≡ *Aloe nyeriensis* ssp. *kedongensis* (Reynolds) S. Carter (1980).

[16] Caulescent, branching at or near the base, forming dense thickets; **Br** erect or sprawling, to 4 m, 3–7 cm Ø; **L** rosulate and persistent for 30–60 cm, lanceolate, 30 × 4 cm, grey-green to yellowish-green, surface smooth, exudate drying yellowish, **marginal teeth** 2–3 mm, reddish-brown-tipped, 10–15 mm apart; **Inf** to 75 cm, with 2–4 **Br**; racemes cylindrical, 10–20 × 8 cm, dense; **Bra** ovate-acute, 5 × 5 mm; **Ped** 20–25 mm; **Fl** scarlet, 35 mm, base shortly attenuate, 7 mm Ø across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for 14 mm; **St** and **Sty** exerted 3 mm. — **Cytology**:  $2n = 28$  (Cutler & al. 1980).

Natural hybrids with *A. secundiflora* have been reported by Newton (1998a: 142).

**A. kefaensis** M. G. Gilbert & Sebsebe (Kew Bull. 52(1): 140–141, 1997). **Type**: Ethiopia, Kefa Region (*Lissanework* s.n. in *Sebsebe* 2411 [ETH, K, UPS]). — **Distr**: SW Ethiopia (Kefa Region); wooded grassland, ±1800 m. **I**: Carter & al. (2011: 188).

[5?] Acaulescent; **L** rosulate, 35–45 × 8–11 cm, green, obscurely lineate, usually with sparse pale spots, **marginal teeth** 3–4.5 mm, pale, sometimes with minute dark tip, 1.2–1.9 mm apart; **Inf** ±1.5 m, with few **Br**; racemes cylindrical, 30–35 cm, lax; **Bra** 11–14 × 4.5–6 mm; **Ped** 16–22 mm; **Fl** scarlet, 28–32 mm, 6 mm Ø across the ovary, narrowed to 4.5–5 mm above; **OTep** free for 6–7 mm; **St** and **Sty** exerted 0–1 mm.



**Fig. 37** *Aloe ketabrowniorum*. (Copyright: L. E. Newton)

Material from Gonder cited under this species in the Flora of Ethiopia is now considered to be *A. trigonantha* (Sebsebe Demissew & Nordal 2010: 66).

**A. ketabrowniorum** L. E. Newton (Brit. Cact. Succ. J. 12(2): 50–51, ills., 1994). **Type**: Kenya, Eastern Prov. (*Brown* 136 [K, EA]). — **Distr**: N Kenya (Eastern Prov.: Marsabit Distr.); rocky slopes, on lava, 760 m. **I**: Carter & al. (2011: 445). — Fig. 37.

[13] Caulescent, branching at the base; stem decumbent, to 30 cm; **L** 6–10, rosulate, triangular to slightly falcate, to 38 × 4.5 cm, mid-green, often reddish-tinged, with a few scattered elliptical whitish spots, surface smooth, with white hyaline margin, exudate pale yellow, drying brown, **marginal teeth** 1 mm, firm, white or red-tipped, sometimes pointing backwards, 5–10 mm apart; **Inf** to 70 cm, with 7–8 **Br**; racemes with subsecund flowers, 3–14 cm, lax; **Bra** triangular, 4 × 2 mm; **Ped** 5 mm; **Fl** pale red, fading above to



**Fig. 38** *Aloe kilifiensis*.  
(Copyright: L. E. Newton)



white with pale red midstripe on the lobes, 25–28 mm, base rounded, 8–10 mm  $\varnothing$  across the ovary, narrowed to 6–7 mm above, enlarging to the mouth; **OTep** free for 9–12 mm; **St** and **Sty** exerted 5–6 mm.

**A. khamiesensis** Pillans (South Afr. Gard. 1934: 24, 1934). **Type:** RSA, Northern Cape (Pillans 6665 [BOL]). — **Distr:** RSA (W Northern Cape: S Namaqualand); rocky slopes in mountains, on granitoid rocks, 500–1500 m. **I:** Reynolds (1950: 405–406); Carter & al. (2011: 658); Wyk & Smith (2014: 200–201).

[8] Caulescent, simple or branched about the middle; stem to 1.5 m  $\times$  10–15 cm  $\varnothing$ , with persistent dead leaf bases; **L** densely rosulate, lanceolate-attenuate,  $\pm 40 \times 8$  cm, dull green, obscurely lineate, usually with a few scattered elliptic white spots, more numerous on the lower face, **marginal teeth** 2–4 mm, pungent, reddish-brown, 5–10 mm apart; **Inf** to 90 cm, with 4–8 **Br**; racemes long-conical, 25–30  $\times$  9 cm, dense; **Bra** ovate-acute, 18  $\times$  8 mm; **Ped** 25 mm; **Fl** orange-red, greenish-tipped, 30–35 mm, base rounded, very slightly narrowed above the ovary; **OTep** free to the base; **St** and **Sty** exerted 2–4 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

**A. kilifiensis** Christian (J. South Afr. Bot. 8(2): 169–170, t. 3, 1942). **Type:** Kenya, Coast Prov. (Moggridge s.n. in Burt 5554 [SRGH, BM, K]). — **Distr:** SE Kenya, NE Tanzania; coastal coral

cliffs and dry bushland, 3–380 m. **I:** Reynolds (1966: 81); Carter & al. (2011: 190). — Fig. 38.

[5] Acaulescent or shortly caulescent, simple or suckering to form small groups; stem to 30 cm; **L**  $\pm 15$ , rosulate, lanceolate-attenuate,  $27 \times 7$  cm, dull green, usually with many scattered elliptic or H-shaped whitish spots, surface smooth, exudate yellow, **marginal teeth** 3 mm, horny, brown, 4 mm apart; **Inf** to 57 cm, with 4–6 **Br**; racemes capitate, 8  $\times$  8 cm, subdense, with  $\pm 20$  flowers; **Bra** triangular, 14  $\times$  6 mm; **Ped** 16 mm; **Fl** deep wine-red, 30 mm, base truncate, 10 mm  $\varnothing$  across the ovary, abruptly narrowed to 6 mm above, then enlarged to 9 mm and narrowed again to the mouth; **OTep** free for 11 mm; **St** and **Sty** exerted 0–1 mm.

Plants at higher altitude have flowers of a paler red colour. The occurrence in Tanzania was first recorded by Wabuyele (2006b).

**A. knersvlakensis** S. J. Marais (Aloe 47(4): 96–97, ills. (pp. 96–99), 2011). **Type:** RSA, Western Cape (Marais s.n. [NBG]). — **Distr:** RSA (N Western Cape: N Knersvlakte NE of Vanrhynsdorp); N-facing quartzitic sandstone ridges and medium slopes, 270 m. **I:** Wyk & Smith (2014: 202–203).

[12] Caulescent, solitary or usually branching, with 2–3 **Ros**; stem to 1.5 m, erect; **L** densely rosulate, lanceolate-attenuate, 30–40  $\times$  5–8 cm, dull green to reddish-brown, striate, with H-shaped white spots, exudate brownish-yellow,



**marginal teeth** deltoid, pungent, 2 mm, reddish-brown, 12 mm apart; **Inf** to 73 cm, erect, with 3–4 **Br**; racemes long-conical, 33–43 cm, dense; **Bra** ovate-acute, to 13 mm; **Ped** to 27 mm; **Fl** yellow, greenish at the mouth, 28 mm, 5 mm  $\varnothing$  across the ovary; **OTep** not further described; **St** exerted 5 mm; **Sty** exerted 5–6 mm.

Very close to *A. framesii*, differing only in the fewer inflorescence branches (Carter & al. 2011).

**A. kniphofioides** Baker (Hooker's Icon. Pl. 1890: t. 1939, 1890). **Type:** RSA, KwaZulu-Natal (Tyson 2829 [SAM, GRA, BOL]). — **Distr:** RSA (S & N KwaZulu-Natal, Eastern Cape, Free State, Mpumalanga), W Swaziland; grassy slopes, 300–1800 m. **I:** Reynolds (1950: 122–123); Craib (2006: 71–74); Carter & al. (2011: 119); Wyk & Smith (2014: 364–365).

**Incl.** *Aloe marshallii* J. M. Wood & M. S. Evans (1897).

[1] Acaulescent, simple, with ovoid bulb-like underground swelling 6–8  $\times$  5–6 cm; **R** fusiform; **L**  $\pm$ 20, multifarious, linear, 20–30  $\times$  0.6–0.7 cm, green, **marginal teeth** absent or minute, white; **Inf** to 55 cm, simple; raceme cylindrical, 10–15 cm, lax, with  $\pm$ 12–16 flowers; **Bra** ovate-acuminate, to 15 mm; **Ped** to 15 mm; **Fl** scarlet, green-tipped, 35–50 mm, base rounded, not narrowed above the ovary; **OTep** free for 6–8 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Müller 1945: as *A. marshallii*).

Flowering is fire-dependent, but establishment is prevented when fires occur every year (Craib 2006).

**A. koenenii** Lavranos & Kerstin Koch (Cact. Succ. J. (US) 78(5): 222–223, ills., 2006). **Type:** Jordan (*Koenen* 1/82 [FT]). — **Distr:** Jordan (Petra); sandstone rock slopes and ledges. **I:** Carter & al. (2011: 448).

$\equiv$  *Aloe porphyrostachys* ssp. *koenenii* (Lavranos & Kerstin Koch) Lodé (2007).

[11] Caulescent, suckering freely at the base to form dense groups; stem to 50 cm, becoming decumbent; **L** 20–30, rosulate, 40  $\times$  4–9 cm, glaucous-green with purplish tinge, **marginal teeth** pungent, 2–3 mm, brown-tipped, 5–10 mm apart; **Inf** 1.2 m, erect, with up to 4 **Br**; racemes

cylindrical, to 35 cm, dense, buds and flowers reflexed and appressed to the peduncle; **Bra** 5–8 mm; **Ped** 2–3 mm; **Fl** bright carmine-red, 25–28 mm, ventricose, 4 mm  $\varnothing$  across the ovary, 7 mm above, constricted at the mouth; **OTep** free almost to the base; **St** exerted 3 mm; **Sty** exerted 4 mm.

Apparently a single clone, as no fruits were observed on plants that had flowered abundantly. Presumed to have been introduced to the country long ago, but the wild origin remains unknown.

**A. komaggasensis** Kritzing & Van Jaarsveld (South Afr. J. Bot. 51(4): 287, ill., 1985). **Type:** RSA, Northern Cape (*Kritzing* 12 [NBG, PRE]). — **Lit:** Lavranos (2004). **Distr:** RSA (W Northern Cape: Namaqualand around Komaggas): open xerophytic scrub on W-facing quartz slopes, 500–700 m; known from the type locality only. **I:** Carter & al. (2011: 334); Wyk & Smith (2014: 166–167).

$\equiv$  *Aloe striata* ssp. *komaggasensis* (Kritzing & Van Jaarsveld) Glen & D. S. Hardy (1987).

[5] Acaulescent or with short decumbent stem, usually solitary; **L**  $\pm$ 15, rosulate, broadly triangular, acute, 30–45  $\times$  10–13 cm, blue-green, obscurely striate, often with a few pale spots, **marginal teeth** minute; **Inf** to 1 m, erect, with many **Br**; racemes capitate, dense; **Bra** triangular, 8–15  $\times$  2–6 mm; **Ped** 10–15 mm; **Fl** yellow, rarely orange, 20 mm, 4.5 mm  $\varnothing$  across the ovary; **OTep** free for 4 mm; **St** and **Sty** exerted 0–1 mm.

**A. komatiensis** Reynolds (J. South Afr. Bot. 2: 120, 1936). **Type:** RSA, Mpumalanga (*Reynolds* 1543 [PRE, BOL]). — **Lit:** Smith & al. (2012c). **Distr:** NE RSA (Mpumalanga), SW Moçambique; grassland and bushveld in frost-free summer rainfall area, 0–750 m. **I:** Reynolds (1950: 254–256); Wyk & Smith (2014: 244–245).

**Incl.** *Aloe decurvidens* Groenewald (1937); **incl.** *Aloe lusitanica* Groenewald (1937).

[5] Acaulescent, usually suckering to form small groups; **L** rosulate, 40  $\times$  8–10 cm, yellowish-green to dull green, obscurely lineate, upper surface only with whitish spots in irregular transverse bands, **marginal teeth** deltoid, slightly deflexed, 4 mm, brown, 10–12 mm apart; **Inf** to 2

m, erect, with 8 **Br**; racemes cylindrical, lax; **Bra** 7–10 mm; **Ped** 6–9 mm; **Fl** pale dull brick-red, **OTep** with dull white border towards the mouth, lightly covered with grey powdery bloom, overall 30 mm, 9 mm  $\varnothing$  across the ovary, narrowed above to 5.5 mm, then widening to 7 mm; **OTep** free to 7 mm; **St** and **Sty** exserted 1–2 mm.

Included by some authors in *A. parvibracteata* (e.g. Carter & al. (2011)).

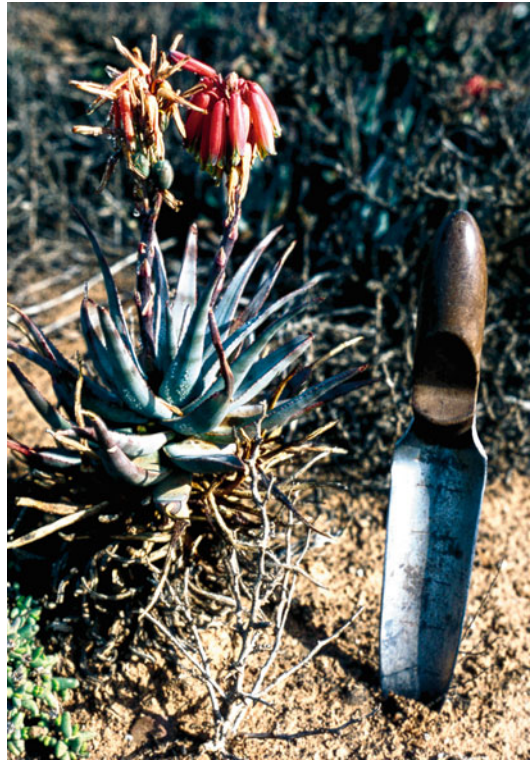
**A. kouebokkeveldensis** Van Jaarsveld & A. B. Low (Aloe 41(2–3): 36–37, ills., 2004). **Type:** RSA, Western Cape (*Van Jaarsveld & Ems* 17744 [PRE]). — **Distr:** RSA (C Western Cape: SW of Citrusdale); on sandstone cliffs and steep slopes, in Fynbos vegetation, 600–800 m. **I:** Carter & al. (2011: 335); Wyk & Smith (2014: 168–169).

[5] Acaulescent, solitary or in small groups of up to 3 **Ros**; **L** rosulate, lanceolate, 40–48  $\times$  10–15 cm, greyish- to bluish-white, obscurely striate, densely spotted, exudate colourless, drying yellow, **marginal teeth** 1 mm, pinkish-white; **Inf** 1–1.4 m, erect, with up to 15 **Br**; racemes capitate, 8–10 cm, dense; **Bra** 5–8 mm; **Ped** 12–15 mm; **Fl** orange-red, 22–23 mm, 4–5 mm  $\varnothing$  across the ovary, narrowed to 3 mm above, widening to 5 mm at the mouth; **OTep** free for 7 mm; **St** and **Sty** exserted 0–1 mm.

**A. krapohlina** Marloth (Trans. Roy. Soc. South Africa 1: 408, 1908). **Type:** RSA, Northern Cape (*Marloth* 4673 [PRE]). — **Distr:** RSA (Northern Cape).

**A. krapohlina** var. **dumoulinii** Lavranos (J. South Afr. Bot. 39(1): 41–43, ills., 1973). **Type:** RSA, Northern Cape (*Lavranos & Butler* 8777 [PRE]). — **Distr:** RSA (NW Northern Cape); exposed quartzite hills on the coastal plain, 0–150 m. **I:** Carter & al. (2011: 237–238).

[6] Differs from var. *krapohlina*: Dividing and suckering to form groups of up to 15 **Ros**; **L** deltoid and strongly incurved, shorter; **Inf** 15 cm; **Ped** 12–15 mm; **Fl** 25–27 mm, ventricose, 6–7 mm  $\varnothing$  across the ovary, enlarged to 8–9 mm above, then narrowing to 4 mm at the mouth.



**Fig. 39** *Aloe krapohlina* var. *krapohlina*. (Copyright: L. E. Newton)

Not recognised as distinct by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011).

**A. krapohlina** var. **krapohlina** — **Distr:** RSA (W Northern Cape, NW Western Cape); sandy flats and arid rocky slopes, 0–1500 m. **I:** Reynolds (1950: 179–181); Carter & al. (2011: 237); Wyk & Smith (2014: 170–171). — Fig. 39.

[4] Acaulescent or shortly caulescent, usually simple, sometimes 2–3 **Ros**; stem to 20 cm; **L** 20–30, rosulate, lanceolate-acuminate, to 20  $\times$  4 cm, glaucous, surface smooth, **marginal teeth** minute, white, 3–5 mm apart; **Inf** to 40 cm, simple or with 1–2 **Br**; racemes cylindrical, 14  $\times$  6 cm, subdense; **Bra** lanceolate-acuminate, to 20  $\times$  5 mm; **Ped** to 20 mm; **Fl** scarlet, greenish at the mouth, 35 mm, base rounded, 7 mm  $\varnothing$  across the ovary, very slightly enlarged above; **OTep** free to the base; **St** and **Sty** exserted 0–1 mm. — **Cytology:** 2n = 14 (Resende 1937).

**Fig. 40** *Aloe kulalensis*.  
(Copyright: L. E. Newton)



The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984).

**A. kraussii** Baker (J. Linn. Soc., Bot. 18(108): 159, 1880). **Type:** RSA, KwaZulu-Natal (*Krauss* 275 [BM]). — **Lit:** Hargreaves & al. (2012: pollination ecology). **Distr:** RSA (C KwaZulu-Natal); in grass on stony slopes, 500–1000 m. **I:** Reynolds (1950: 143–144); Craib (2006: 75–77); Carter & al. (2011: 140); Wyk & Smith (2014: 320–321).

[4] Acaulescent or very shortly caulescent, simple or in small groups; **R** fusiform; **L** 8–10, distichous, becoming rosulate with age, linear-acuminate, 30–40 (–60) × 3.5 (–5) cm, dull green, lower face sometimes with a few white spots near the base, with a narrow white cartilaginous margin, **marginal teeth** minute, obsolescent towards the tip; **Inf** to 40 cm, simple; raceme capitate, dense, with 30–40 flowers; **Bra** lanceolate-deltoid, ±15 mm; **Ped** 35 mm; **Fl** lemon-yellow to yellow, 16–18 mm, base attenuate, narrowed above the ovary to the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 0–1 mm.

Included in *A. ecklonis* by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011) and Wyk & Smith (2014). Hargreaves & al. (2012) found that the taxon is pollinated by Megachilid bees and a species of the bee genus *Amegilla*.

**A. kulalensis** L. E. Newton & Beentje (Cact. Succ. J. (US) 62(5): 251–252, ills., 1990). **Type:** Kenya, Eastern Prov. (*Newton* 3219 [K, EA]). — **Distr:** N Kenya (Eastern Prov.: Marsabit Distr.: Mt. Kulal); steep slopes and rock faces, in the shade of *Olea-Juniperus* woodland, 1585–1890 m. **I:** Carter & al. (2011: 490). – Fig. 40.

[13] Caulescent, branching at the base; stem sprawling or pendulous, to 2 m, to 2.15 cm Ø; **L** 20–25, lax, ±1 cm apart, triangular, 18–25 × 1.8–3 cm, mid-green, surface smooth, exudate drying yellow, **marginal teeth** 1 mm, colourless, 2–13 mm apart; **Inf** to 32 cm, ascending, with 2–4 **Br**; racemes cylindrical, 2.5–15 cm, lax; **Bra** triangular, 5–6 × 1 mm; **Ped** 8–10 mm; **Fl** scarlet with yellow tip, 25 mm, base rounded, 7 mm Ø across the ovary, narrowed gradually to 5 mm above, enlarging to 6 mm at the mouth; **OTep** free for 10–13 mm; **St** and **Sty** exerted 1.5–2.5 mm.

**A. kwasimbana** T. A. McCoy & Lavranos (*Aloe* 44(1): 50–51, ills., 2007). **Type:** Tanzania, Arusha Prov. (*McCoy* 1149 [FT]). — **Distr:** N Tanzania (Arusha Prov.: Lossogoni Plateau); steppe, on granite outcrops, 830 m; known only from the type collection. **I:** Carter & al. (2011: 506).

[12] Caulescent, branching at the base to form a shrub; stems to 1.5 m, with dead leaves persistent; **L** 12–15, rosulate, deltoid-acute, 45 × 3 cm,

dark green, exudate brownish-yellow, drying brown, **marginal teeth** deltoid, 2 mm, red, 10 mm apart; **Inf** 30–40 cm, erect, with 10 or more **Br**; racemes capitate, 10 cm, dense; **Bra** deltoid, 5–8 mm; **Ped** 10–12 mm; **Fl** glossy orange with many white translucent spots, 25–28 mm, 8 mm  $\varnothing$  across the ovary; **OTep** free for 7 mm; **St** and **Sty** exerted 5 mm.

**A. labworana** (Reynolds) S. Carter (Fl. Trop. East Afr., Aloaceae, 28, 1994). **Type:** Uganda, Karamoja Distr. (*Jackson* s.n. in *Reynolds* 7980 [PRE, EA, K]). — **Distr:** South Sudan, N Uganda.

≡ *Aloe schweinfurthii* var. *labworana* Reynolds (1956).

**A. labworana** ssp. *labworana* — **Distr:** South Sudan, N Uganda; rocky outcrops, 1300–1500 m. **I:** Reynolds (1966: 292–293, as *A. schweinfurthii* var.); Carter & al. (2011: 463); Cole & Forrest (2017: 68).

[7] Acaulescent, suckering to form groups; **L** 12–16, rosulate, lanceolate-attenuate, 60–80 × 7–8 cm, bluish-green with grey bloom, with many pale greenish lenticular spots, exudate drying yellowish, **marginal teeth** 5–6 mm, pungent, reddish-tipped, 12–20 mm apart; **Inf** to 90 cm, with 10–12 **Br**; racemes cylindrical, slightly conical, 8–9 × 5 cm, subdense; **Bra** ovate-acute, ±2 mm; **Ped** 10 mm; **Fl** yellow, 28 mm, base rounded, 6–7 mm  $\varnothing$  across the ovary, very slightly narrowed above, then slightly enlarging to the mouth; **OTep** free for 9 mm; **St** and **Sty** exerted 4 mm. — **Cytology:** 2n = 14 (Newton 1970: as *A. schweinfurthii* var.).

**A. labworana** ssp. *longifolia* T. C. Cole & T. G. Forrest (Aloes Uganda, 69, ill. (pp. 69–75), 2017). **Type:** Uganda, Kumi Distr. (Cole 1301 [MHU]). — **Distr:** E Uganda; rocky outcrops, 1800 m.

[7] Differs from ssp. *labworana*: **L** erect, to 100 × 8–14 cm, uniformly blue-green, **marginal teeth** 4–8 mm, red-brown; **Fl** yellow or red, 30 mm.

**A. laeta** A. Berger (in Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 256–257, 1908).

**Type:** Madagascar, Antananarivo (*Catart* 1115 [P]). — **Lit:** Lüthy (2006: 43–44, conservation, with ill.). **Distr:** Madagascar (Antananarivo, Fianarantsoa).

**A. laeta** var. *laeta* — **Distr:** Madagascar (Antananarivo: Mt. Ibity and S-wards); on rocks, 1600–2200 m. **I:** Reynolds (1966: 438–439); Castillon & Castillon (2010: 90–93); Carter & al. (2011: 239).

[2] Acaulescent or very shortly caulescent, simple; stem to 5 × 3.5 cm; **L** ±24, densely rosulate, lanceolate-attenuate, to 20 × 7–8 cm, bluish-grey, obscurely lineate, with conspicuous narrow pink cartilaginous margin, surface rough, **marginal teeth** 2 mm, narrowly deltoid, firm, pink, confluent at the leaf base; **Inf** 40–60 cm, usually simple, sometimes with 2–3 **Br**; racemes capitate or subcapitate, 5–7 × 6 cm, dense; **Bra** deltoid-acute, 5 × 2.5 mm; **Ped** 20–25 mm; **Fl** crimson, 15 mm, base attenuate, enlarged above the ovary to 7 mm, then narrowing to the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 0–1 mm.

**A. laeta** var. *maniaensis* H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 30, 1926). **Type:** Madagascar, Fianarantsoa (*Perrier* 11003 [P]). — **Distr:** Madagascar (Fianarantsoa: S Mt. Ibity); quartzite rocks, ±1400 m; known only from the type locality. **I:** Castillon & Castillon (2010: 94).

[2] Differs from var. *laeta*: **L** 8 × 2 cm, tip rounded; **Fl** straight, infundibuliform.

**A. lanata** T. A. McCoy & Lavranos (Kakt. and. Sukk. 58(11): 296–297, ill. (pp. 295–297), 2007). **Type:** Yemen (*McCoy* 2010 [FT]). — **Distr:** Yemen (S end of Yemeni Plateau); granite slopes, 2130 m; known only from the region of the type locality. **I:** Carter & al. (2011: 386).

[5] Acaulescent, solitary or with up to 3 **Ros**; **L** to 30, rosulate, lanceolate, 95 × 15–20 cm, greyish-green, exudate dark yellow, drying light brown, **marginal teeth** deltoid, 5 mm, brown, red-pointed, 10 mm apart; **Inf** 1.95 m, erect, with up to 10 **Br**; racemes conical, 45 cm, dense; **Bra** ovate-acute, 14 mm; **Ped** 10 mm, tomentose; **Fl**



**Fig. 41** *Aloe lateritia* var. *graminicola*. (Copyright: L. E. Newton)



red, yellow at the mouth, covered densely in golden hairs, 40 mm, 15 mm  $\varnothing$  across the ovary; **OTep** free for 20 mm; **St** and **Sty** exerted 4–5 mm.

**A. latens** T. A. McCoy & Lavranos (*Aloe* 44 (2): 52–53, *ills.*, 2007). **Type:** Tanzania, Arusha Prov. (*McCoy* 1714 [FT]). — **Distr:** N Tanzania (Arusha Prov.); steep sides of conglomerate rock gullies, 1500 m. **I:** Carter & al. (2011: 479).

[13] Caulescent, branching; stem to 2.5 m, pendulous or procumbent; **L** 10–20, forming a loose **Ros** at the stem apex, lanceolate, 17  $\times$  3 cm, shiny light green, surface not described, exudate clear, **marginal teeth** 5 mm, reddish-tipped, 10 mm apart; **Inf** 60 cm, erect, simple or rarely with 1 **Br**; racemes cylindrical, 16 cm, dense; **Bra** obovate-acute, 9  $\times$  6 mm; **Ped** 18 mm; **Fl** orange, with numerous white spots, 40 mm, 7 mm  $\varnothing$  across the ovary; **OTep** free for 10 mm; **St** and **Sty** exerted 2–2.5 mm.

**A. lateritia** Engler (*Pfl.-welt Ost-Afr.*, Teil C, 140, 1895). **Type:** Tanzania, Moshi Distr. (*Volkens* 404 [B, BM]). — **Distr:** Kenya, Tanzania. **I:** Carter & al. (2011: 179–181).

**A. lateritia** var. **graminicola** (Reynolds) S. Carter (*Fl. Trop. East Afr.*, *Aloaceae*, 17, 1994). **Type:** Kenya, Central Prov. (*Reynolds* 6576 [PRE, EA, K]). — **Distr:** Kenya; grassland and open bushland, 1675–2530 m. **I:** Reynolds (1966:

79–80, as *A. graminicola*); Carter & al. (2011: 180–181); Laius (2014: 72–73). – Fig. 41.

$\equiv$  *Aloe graminicola* Reynolds (1953); **incl.** *Aloe solaiana* Christian (1940).

[7] Differs from var. *lateritia*: Acaulescent or very shortly caulescent, usually suckering to form dense clumps; stem to 50 cm; **L** with **marginal teeth** more pungent; **Inf** with racemes always capitate. — **Cytology:**  $2n = 14$  (Brandham 1971: as *A. graminicola*).

Not recognized as a distinct variety by Gilbert & Sebsebe Demissew (1997). Sebsebe Demissew & Nordal (2010: 64) also do not recognize the variety since there is continuity of variation and the type of the species has similarly dense inflorescences. Natural hybrids with *A. nyeriensis* have been reported by Carter (1994).

The amount of blotching of the leaf surface has been studied by Kolm & Newton (2011), and only 57% of 204 studied plants showed the typical condition of numerous blotches, while 7% had no blotches at all.

**A. lateritia** var. **lateritia** — **Distr:** SE Kenya, Tanzania; grassland and open bushland, or rocky slopes, 250–2125 m. **I:** Reynolds (1966: 96, Fig. 100); Carter & al. (2011: 179); Klopper & al. (2012: 80, 86–87, *incl.* distribution map).

**Incl.** *Aloe boehmii* Engler (1895); **incl.** *Aloe campylosiphon* A. Berger (1904); **incl.** *Aloe amanensis* A. Berger (1905).



[5] Acaulescent, usually simple, sometimes suckering to form small groups; **L** 16–20, densely rosulate, lanceolate-attenuate, 25–50 × 5–10 cm, bright green, usually with elongated white spots in irregular transverse bands, surface smooth, **marginal teeth** 3–4 mm, pungent, brown, 10–15 mm apart; **Inf** to 1.25 m, with 3–8 **Br**; racemes capitate to subcapitate, 4–12 × 8 cm, dense, sometimes to 20 cm, lax; **Bra** linear-lanceolate, 10–20 (–25) × 4 mm; **Ped** 20–30 mm; **Fl** orange-red, sometimes yellow, usually glossy, 30–38 mm, base truncate, 8–10 mm Ø across the ovary, abruptly narrowed to ±5 mm above, enlarging to the mouth; **OTep** free for 10–13 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Resende 1937).

Included in *A. macrocarpa*, together with var. *graminicola*, by Wabuye (2006a).

This taxon has been seen once or twice in the extreme N of Malawi, but it is suggested that it has been introduced by travellers from Tanzania (Lane 2004). Reynolds (1966) cited specimens in Democratic Republic of the Congo [Zaire], but these are considered by Carter (1994) to be *A. wollastonii*.

**A. lavranosii** Reynolds (J. South Afr. Bot. 30 (4): 225–227, tt. 31–32, 1964). **Type**: Yemen (*Lavranos* 1890 [PRE, K]). — **Lit**: McCoy & Lavranos (2010). **Distr**: Yemen (Aden hinterland); basalt hills and silty flats, 800–1400 m. **I**: Reynolds (1966: 251–252); Carter & al. (2011: 370); Moore (2016: 136).

**Incl.** *Aloe doei* Lavranos (1965); **incl.** *Aloe splendens* Lavranos (1965); **incl.** *Aloe doei* var. *lavranosii* Marnier-Lapostolle (1970).

[5] Acaulescent or shortly caulescent, usually in groups of up to 8 **Ros**, rarely simple; stem decumbent, to 15 cm; **L** 10–14, densely rosulate, deltoid-acute, somewhat falcate, tip with 2–4 small sharp teeth, 28 × 7.5 cm, olive-green tinged brownish, with pinkish-brown horny margin, **marginal teeth** 3 mm, pungent, brownish, 6–12 mm apart; **Inf** 60 cm, ascending to suberect, with 4–9 **Br**; racemes cylindrical-acuminate, 16–20 × 5 cm, subdense; **Bra** ovate-lanceolate, acute, 8 × 3 mm; **Ped** 8 mm; **Fl** bright yellow, 30 mm, base rounded, 7 mm Ø across the ovary, slightly

narrowed above, enlarging slightly to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 3–4 mm.

**A. leachii** Reynolds (J. South Afr. Bot. 31: 275, 1965). **Type**: Tanzania, Morogoro Distr. (*Leach & Brunton* 10178 [PRE, K]). — **Lit**: Carter & al. (2011: 326). **Distr**: E-C Tanzania (Morogoro Distr.); open wooded grassland, 275–500 m. **I**: Reynolds (1966: 227).

**Incl.** *Aloe nordaliae* Wabuye (2006).

[5] Acaulescent or shortly caulescent, simple or with a few suckers forming small groups; **L** ±20, rosulate, lanceolate-attenuate, 35 × 6 cm, dark green tinged red, **marginal teeth** ±5 mm, pungent, reddish-brown, 10–20 mm apart; **Inf** to 1 m, with 7–10 **Br**, lower ones sometimes rebranched; terminal racemes cylindrical, laterals sometimes with ± secund flowers, 15–20 × 7 cm, lax; **Bra** ovate-acute, 5 × 4 mm; **Ped** 6–8 mm; **Fl** scarlet, paler at the mouth, 30 mm, base rounded, 7 mm Ø across the ovary, scarcely narrowed above; **OTep** free for 15 mm; **St** and **Sty** exerted 1–3 mm.

**A. leandrii** Bosser (Adansonia, n.s. [sér. 2], 8 (4): 505–507, ills., 1968). **Type**: Madagascar, Antananarivo (*Bosser* 18550 [P]). — **Distr**: Madagascar; quartz sand at the edge of tropical forests, 900–1200 m; known only from the area of the type locality. **I**: Castillon & Castillon (2010: 366–367); Carter & al. (2011: 232).

[4] Acaulescent or shortly caulescent, simple or branching at the base; **L** 8–15, rosulate, narrowly lanceolate or linear, 14–15 × 1–2 cm, green, **marginal teeth** 1–1.5 mm, 3.5–8 mm apart; **Inf** 70–85 cm, simple; raceme cylindrical, 5–10 cm, lax; **Bra** ovate or oblong, 5–7 mm; **Ped** 15–25 mm; **Fl** yellow, 25–27 mm, base rounded, slightly narrowed above the ovary; **OTep** free for 8–9 mm; **St** and **Sty** not exerted.

**A. leedalii** S. Carter (Fl. Trop. East Afr., Aloaceae, 9–11, ills., 1994). **Type**: Tanzania, Njombe Distr. (*Leedal* 5523 [K]). — **Distr**: W Tanzania (Kipengere Mts. & Ishinga Escarpment); among rocks in crevices and on ledges, 2130–2950 m. **I**: Carter & al. (2011: 123).

[10] Caulescent, suckering to form dense groups; stem ascending, to 5 × 0.5–1 cm, dead leaf sheaths persistent; **L** rosulate, linear, to 30 × ±1 cm, green, **marginal teeth** minute, cartilaginous, white, densely crowded; **Inf** to 30 cm, simple; raceme cylindrical, 5–8 cm, ± dense; **Bra** ovate-acute, 15–20 × 5–7 mm, orange-brown; **Ped** ±25 mm; **Fl** bright orange, green-tipped, 25–30 mm, base obconical, 5–6 mm Ø across the ovary, very slightly narrowed above, slightly enlarging to the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 0–1 mm.

**A. lensayuensis** Lavranos & L. E. Newton (Cact. Succ. J. (US) 48(6): 276–278, ill., 1976). **Type:** Kenya, North Eastern Prov. (*Classen* 92 [EA]). — **Distr:** Kenya (North Eastern Prov.: Lensayu Rocks); dry *Commiphora* bushland on gneiss inselbergs, 700–2000 m; known only from the region of the type locality. **I:** Carter & al. (2011: 594).

[13] Caulescent, suckering sparsely at the base; stem decumbent, to 1 m × 2.5–3 cm Ø; **L** ±10, laxly rosulate, lanceolate-acute, 30 × 5 cm, bluish-grey, sometimes tinged pinkish, sometimes with a few scattered elongated whitish spots, with white or reddish cartilaginous margin, surface slightly rough, exudate yellow, drying brownish, **marginal teeth** 1 mm, soft, white, 2–10 mm apart; **Inf** ±75 cm, with 8–12 **Br**; racemes cylindrical or with secund flowers on oblique branches, lax, with 5–12 flowers; **Bra** ovate-acute, 1–3 × 1.5 mm; **Ped** ±8 mm; **Fl** pinkish-red with pronounced bloom and pinkish-cream margins on the lobes, 20–24 mm, base shortly attenuate, 6–10 mm Ø across the ovary, narrowed slightly above; **OTep** free for 6–7 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology:** 2n = 14 (protologue).

**A. lepida** L. C. Leach (J. South Afr. Bot. 40(2): 102–106, ill., 1974). **Type:** Angola, Huambo (*Baptista de Sousa* s.n. in *Leach* 14538A [LISC, SRGH]). — **Distr:** C-W Angola (Huambo: SSE of Nova Lisboa); rock slopes in the shade of trees; known only from the type locality. **I:** Carter & al. (2011: 555).

[15] Caulescent, branching at the base; stem erect, to 30 cm; **L** rosulate, ovate-attenuate, 20–28

× 7.5–9 cm, bright to dark yellowish deep green, with white spots in wavy transverse bands, smaller and more numerous on the lower face, **marginal teeth** 3–7 mm, pungent, often hooked, brown-tipped, 6–12 mm apart; **Inf** 30–50 cm, with 1–2 **Br**; racemes cylindrical-acuminate, 20 × 7–8 cm, lax; **Bra** ovate-acuminate, 6–7 × 3–3.5 mm; **Ped** 15–20 mm; **Fl** pale orange-scarlet, somewhat yellowish-striped, 25–29 mm, base truncate, ±5.5 mm Ø across the ovary, narrowed to ±4 mm above, then enlarging to ±6 mm at the mouth; **OTep** free for 5–6 mm; **St** and **Sty** exerted 0–1 mm.

**A. leptosiphon** A. Berger (Bot. Jahrb. Syst. 36: 66, 1905). **Type:** Tanzania, Lushoto Distr. (*Engler* 1073a [B]). — **Distr:** NE Tanzania; steep rocky slopes, often in grass, 1200–1675 m. **I:** Reynolds (1966: 74, as *A. greenwayi*); Carter & al. (2011: 257). — Fig. 42.

**Incl.** *Aloe greenwayi* Reynolds (1964).



**Fig. 42** *Aloe leptosiphon*. (Copyright: L. E. Newton)

[4,5] Acaulescent or shortly caulescent, simple or suckering to form small groups; stem to 50 cm; **L**  $\pm 16$ , densely rosulate, ovate-lanceolate, 20–35  $\times$  5–7 cm, glossy green, upper face sometimes with scattered elongated whitish spots, lower face with many spots, exudate yellow, drying brownish, **marginal teeth** 2 mm, pale green, 8–10 mm apart; **Inf** 40–60 cm, simple or usually with 1–2 **Br**; racemes conical-cylindrical, 10–20  $\times$  5–7 cm, dense; **Bra** ovate-acute, 10–11  $\times$  4–5 mm; **Ped** 8–10 mm; **Fl** bright red to orange-scarlet with greenish-yellow mouth, or entirely yellow, 25–30 mm, base shortly attenuate, 5–6 mm  $\varnothing$  across the ovary, slightly narrowed above; **OTep** free for  $\pm 8$ –10 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Brandham 1971: as *A. greenwayi*).

**A. lettyae** Reynolds (J. South Afr. Bot. 3: 137, 1937). **Type**: RSA, Limpopo (*Reynolds* 2339 [PRE, BOL]). — **Lit**: Smith & al. (2012c). **Distr**: RSA (Limpopo); in tall grass or among bushes, on slopes, 945 m. **I**: Reynolds (1950: 259–260); Carter & al. (2011: 193); Wyk & Smith (2014: 246–247).

[3] Acaulescent, simple; **L**  $\pm 20$ , densely rosulate, lanceolate-attenuate, to 45  $\times$  9 cm, dull green with many elongated dull white spots, lower face with larger more obscure spots in transverse bands, **marginal teeth** 3–4 mm, brownish, 10–15 mm apart; **Inf** to 1.75 m, with 8–12 **Br**, lower ones rebranched; racemes cylindrical, slightly acuminate, 20–25  $\times$  8–9 cm; **Bra** deltoid-acuminate, 12–15 mm; **Ped** 12–15 mm; **Fl** rose-red, 38–42 mm, base rounded, 10–11 mm  $\varnothing$  across the ovary, abruptly narrowed to 6 mm above, then enlarging towards the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Müller 1941).

Included in *A. zebrina* by Glen & Hardy (2000).

**A. liliputana** Van Jaarsveld & Harrower (Bradleya 32: 30–32, ills. (pp. 31–34), 2014). **Type**: RSA, Eastern Cape (*Harrower* 4664 [PRE]). — **Distr**: RSA (Eastern Cape); shallow quartzitic sandstone, 150 m.

[1] Acaulescent, usually solitary, sometimes suckering to form a small group; **L** 3–9, rosulate,

linear, subterete, 8–19 cm, dark to purplish green, lower surface with small faint oval white spots, surface smooth, **marginal teeth** cartilaginous, 0.3 mm, white, 1.5 mm apart; **Inf** 10–14.5 (–18) cm, ascending to decumbent, simple; raceme capitate, 1.5 cm, subdense; **Bra** ovate, acuminate, 4  $\times$  2.5 mm, scarious; **Ped** 7–9 mm; **Fl** pink, lobes with greenish tips, 8–11 mm, base shortly stipitate; **OTep** free to the base; **St** and **Sty** not exerted.

**A. lindenii** Lavranos (Cact. Succ. J. (US) 69 (3): 149–151, ills., 1997). **Type**: Somalia, Nugaal Region (*Lavranos & al.* 23377 [UPS]). — **Distr**: C Somalia (Nugaal Region); rocky places on gypsum and limestone hills, 200–700 m. **I**: Carter & al. (2011: 268).

[2] Acaulescent, solitary; **L** to  $\pm 20$ , densely rosulate, lanceolate-attenuate, 40–45  $\times$  7–8 cm, bluish-grey, distinctly striate, sometimes with scattered pale spots, margins cartilaginous, **marginal teeth** 1–2 mm, 15–22 (–60) mm apart; **Inf** to 70 cm, usually simple, sometimes with 1–2 **Br**; racemes elongate-conical, 18–22 cm, dense; **Bra** deltoid-attenuate, 15  $\times$  4 mm; **Ped** 3 mm; **Fl** pale red, minutely pubescent, 30 mm, base very shortly attenuate, 5 mm  $\varnothing$  across the ovary, scarcely narrowed above, then widening towards the mouth; **OTep** free for 6–7 mm; **St** and **Sty** exerted 2 mm.

**A. linearifolia** A. Berger (Bot. Jahrb. Syst. 57 (5): 640, 1922). **Type**: RSA, KwaZulu-Natal (*Rudatis* 1643 [B]). — **Distr**: RSA (S & C KwaZulu-Natal, NE Eastern Cape); in sparse grass on stony slopes, 100–2000 m. **I**: Reynolds (1950: 139–140); Craib (2006: 78–80); Carter & al. (2011: 116); Wyk & Smith (2014: 322–323).

[1] Acaulescent, simple or with 1–2 branches at the base; **R** fusiform, 6 mm  $\varnothing$ ; **L** 6–8, usually distichous, linear,  $\pm 25 \times 0.5$ –0.8 cm, green, lower face with many white and brown spots near the base, **marginal teeth** presumably only near the leaf base, minute, sometimes absent; **Inf** 20–25 cm, simple; raceme capitate, 2 cm, with 16–24 flowers; **Bra** pale brownish, to 10  $\times$  5 mm; **Ped** 12–15 mm; **Fl** greenish-yellow to yellow, 12 mm, base attenuate, not narrowed above the

ovary; **OTep** free almost to the base; **St** and **Sty** exserted 0–1 mm.

**A. lineata** (Aiton) Haworth (Trans. Linn. Soc. London 7: 18, 1804). **Type** [neo]: RSA, Eastern Cape (*Reynolds* 5728 [PRE, SAM]). — **Distr**: RSA.

≡ *Aloe perfoliata* var. *lineata* Aiton (1789).

**A. lineata** var. **lineata** — **Distr**: RSA (Western Cape, Eastern Cape); in dry scrub and grassland, 0–1600 m. **I**: Reynolds (1950: 203–205, t. 11); Carter & al. (2011: 648); Wyk & Smith (2014: 64–65).

**Incl.** *Aloe lineata* var. *glaucescens* Haworth (1821); **incl.** *Aloe lineata* var. *viridis* Haworth (1821).

[8] Caulescent, simple or branched, usually covered with dead leaves; stem erect, to 1.5 m; **L** 30–40, densely rosulate, lanceolate-acuminate, 30–40 × 7–9 cm, dull to bright green, distinctly lineate, with reddish-brown horny margin, **marginal teeth** 4–6 mm, pungent, reddish-brown, 5–15 mm apart; **Inf** 75–100 cm, simple; raceme conical, 20–30 cm, subdense; **Bra** deltoid-acute, ±20 mm; **Ped** 40 mm; **Fl** salmon-pink, 45–50 mm, base truncate, 9 mm Ø across the ovary, narrowed to 8 mm above, then enlarged to 11 mm and narrowing slightly to the mouth; **OTep** free to the base or almost to the base; **St** and **Sty** exserted 0–1 mm. — **Cytology**: 2n = 14 (Müller 1941).

Natural hybrids with *A. humilis* have been reported by Reynolds (1950).

**A. lineata** var. **muirii** (Marloth) Reynolds (Aloes South Afr. [ed. 1], 205, 1950). **Type**: RSA, Western Cape (*Muir* 3627 [PRE]). — **Distr**: RSA (Western Cape, Eastern Cape); quartzite slopes, 185–600 m. **I**: Reynolds (1950: 204); Carter & al. (2011: 648).

≡ *Aloe muirii* Marloth (1929).

[8] Differs from var. *lineata*: **L** bright yellowish-green to somewhat orange-green, more distinctly lineate, **marginal teeth** larger. — **Cytology**: 2n = 14 (Resende 1937: as *A. muirii*).

Natural hybrids with other species have been reported (Reynolds 1950).

**A. littoralis** Baker (Trans. Linn. Soc. London, Bot. 1: 263, 1878). **Type**: Angola, Luanda (*Welwitsch* 3727 [BM, K, LISU, PRE [photo]]). — **Lit**: Hargreaves (2004). **Distr**: Angola, Botswana, W Moçambique, N Namibia, S Zimbabwe, RSA (N & W Limpopo); dry hills, usually on rocky outcrops in open woodland and grassland, or seasonal pans, 200–1700 m. **I**: Reynolds (1966: 317–319); Carter & al. (2011: 675); Wyk & Smith (2014: 66–67).

**Incl.** *Aloe rubrolutea* Schinz (1896); **incl.** *Aloe schinzii* Baker (1898).

[9] Caulescent, simple; stem erect, to 4 m, covered with dead leaves; **L** ±30–40, densely rosulate, lanceolate-ensiform, acute, 60 × 10–13 cm, grey-green, sometimes with white spots, lower facee sometimes with a few small brown prickles in a median line, **marginal teeth** 3–4 mm, pungent, brown, 10–20 mm apart; **Inf** 1.5 m, with 8–10 **Br**, lower ones sometimes rebranched; racemes cylindrical-acuminate, 30 × 6 cm, dense; **Bra** lanceolate, 12–18 × 5–6 mm, white, usually deflexed; **Ped** 6–7 mm; **Fl** rose-pink to deep pink-scarlet, paler at the mouth, 30–34 mm, base rounded, 6 mm Ø across the ovary, enlarging slightly above the middle; **OTep** free for 15–17 mm; **St** and **Sty** exserted 1–4 mm. — **Cytology**: 2n = 14 (Koshy 1937).

A variable species, as noted by Hargreaves (2004). Natural hybrids with *A. zebrina* have been reported (Reynolds 1966). — Carter (1994) also mentions the species for SW Zambia, but later works did not confirm this occurrence.

**A. lolwensis** L. E. Newton (Cact. Succ. J. (US) 73(3): 156–157, ills., 2001). **Type**: Kenya, Nyanza Prov. (*Hartmann & Newton* 28585 [EA]). — **Distr**: W Kenya (mostly islands in Lake Victoria), S Uganda; grassland and rocky-grassy hills, 1220–1550 m. **I**: Carter & al. (2011: 454); Cole & Forrest (2015: 77); Cole & Forrest (2017: 76–79).

[7] Acaulescent, suckering to form dense clumps; **L** ±30, densely rosulate, erect to slightly spreading, lanceolate, to 50 × 11 cm, glossy mid-green, surface smooth, exudate brownish-yellow, drying pale brown, **marginal teeth** 3 mm, pungent with tips pointing forwards, green



with red-brown tips, 12–15 mm apart; **Inf** to 1.3 m, erect, with 7–9 **Br**, lower ones rebranched; racemes cylindrical, terminal raceme to 20 cm, 6 cm  $\varnothing$ , lateral racemes 6–15 cm, subdense; **Bra** ovate-acute, 3  $\times$  2 mm; **Ped** 6–7 mm; **Fl** bright coral-red, 28–33 mm, lobes with pale margins, base rounded and very shortly attenuate, 6 mm  $\varnothing$  across the ovary, constricted to 5 mm above the ovary, enlarging to 7 mm (side view) just below the mouth; **OTep** free for 13–14 mm; **St** and **Sty** exerted 5–10 mm.

**A. lomatophylloides** Balfour *fil.* (J. Linn. Soc., Bot. 16: 22, 1877). **Type:** Mauritius, Rodrigues Island (*Balfour* 1306 [K, E]). — **Distr:** Mauritius (Rodrigues Island: now limited to the Réserve de la Grande Montagne); ecology not recorded. **I:** Castillon & Castillon (2010: 383); Carter & al. (2011: 586).

≡ *Lomatophyllum lomatophylloides* (Balfour *fil.*) Marais (1975).

[3] Caulescent; stem decumbent, short, 3–4 cm  $\varnothing$ ; **L** densely rosulate, lanceolate-attenuate to ensiform, 50–75  $\times$  8 cm, dark green, **marginal teeth** < 1 mm, 16–25 mm apart; **Inf** 10–12 cm, with 2–3 **Br**; racemes cylindrical, subdense; **Bra** lanceolate, 1.5–4 mm; **Ped** 20–23 mm; **Fl** orange-red, 14–21 mm, base attenuate, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for 5–10 mm; **St** and **Sty** not exerted; **Fr** berries.

**A. longibracteata** Pole-Evans (Trans. Roy. Soc. South Africa 5: 25, 1915). **Type:** RSA, Mpumalanga (*Pole-Evans* 56 [PRE]). — **Distr:** RSA (Mpumalanga, S Limpopo); highveld grassland, 1300–1800 m. **I:** Reynolds (1950: 262–264); Carter & al. (2011: 165); Wyk & Smith (2014: 248–249).

[3] Acaulescent, solitary or rarely suckering; **L** 20–26, densely rosulate, triangular-lanceolate, 20–25  $\times$  9–10 cm, upper surface dark green with elongated whitish spots in transverse bands, lower surface pale green without spots, **marginal teeth** 5–7 mm, red-brown, 9–12 mm apart; **Inf** 80–100 cm, erect, with 1–2 **Br**; racemes cylindrical-acuminate, 20–40 cm, subdense; **Bra** linear-lanceolate, 45–50 mm; **Ped** 20–25 mm; **Fl**

dull pink to bright red, yellowish at the mouth, with a slight bloom, 40–45 mm, 9–10 mm  $\varnothing$  across the ovary, abruptly constricted to 5–6 mm above, widening to the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 0–1 mm.

Included in *A. greatheadii* var. *davyana* by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011). Reynolds (1950) records natural hybrids with *A. greatheadii* var. *davyana* (as *A. barbertoniae* and *A. davyana*) and *A. marlothii*.

**A. longistyla** Baker (J. Linn. Soc., Bot. 18 (108): 158, 1880). **Type** [lecto]: RSA, Eastern Cape (*Bolus* 689 [K, PRE [photo]]). — **Distr:** RSA (Western Cape, Eastern Cape); sandy or stony ground, usually on flats and in partial shade, 500–1500 m. **I:** Reynolds (1950: 158–159, t. 6); Carter & al. (2011: 222); Wyk & Smith (2014: 292–293).

[4] Acaulescent, simple or branching at the base forming groups of up to 10 **Ros**; **L** 20–30, densely rosulate, lanceolate, 12–15  $\times$  3 cm, glaucous with a bloom, surface with soft to firm white prickles with tubercular base, **marginal teeth** 3–4 mm, firm, white, 5 mm apart; **Inf** 15–20 cm, simple; raceme conical, 11  $\times$  11 cm, dense, with 40–50 flowers; **Bra** lanceolate-deltoid, acute, sometimes slightly fleshy, 25–30  $\times$  12–15 mm; **Ped** 6–8 mm; **Fl** pale salmon-pink to rose-red, 55 mm, upper  $\frac{1}{3}$  curving upwards, base rounded, 9 mm  $\varnothing$  across the ovary, narrowed slightly at the mouth; **OTep** free for 13 mm; **St** exerted 25 mm; **Sty** exerted 75 mm. — **Cytology:** 2n = 14 (Resende 1937).

**A. luapulana** L. C. Leach (J. South Afr. Bot. 38(3): 185–188, ill., 1972). **Type:** Zambia, Luapula Distr. (*Weeks* 1 in *Leach* 14754 [SRGH, PRE]). — **Distr:** N Zambia (Luapula Escarpment); on termite mounds and among rocks near waterfall, 1150–1280 m. **I:** Carter & al. (2011: 329).

[3] Acaulescent, simple; **L**  $\pm$ 16, rosulate, ovate-attenuate,  $\pm$ 30  $\times$  6–7.5 cm, pale green, obscurely striate, lower face greyish-green, more clearly striate, exudate drying yellow, **marginal teeth** 1–3.5 mm, pungent, whitish at the base, brownish-orange at the tip, 2–5 mm apart near



the base, larger and 15–18 mm apart above; **Inf** 1–1.2 m, with 6 **Br**; racemes cylindrical-acuminate, 16–26 cm, lax; **Bra** ovate-acute, 4–5 × 3.5 mm; **Ped** ±7.5 mm; **Fl** coral-red with a slight bloom, becoming yellowish at the mouth, 29–33 mm, base truncate, 8–9 mm Ø across the ovary, narrowed to ±5 mm above, then enlarging very slightly to the mouth; **OTep** free for 12–16 mm; **St** and **Sty** exerted 6 mm.

**A. lucile-allorgeae** Rauh (Bradleya 16: 97–98, 100, ills., 1998). **Type:** Madagascar, Toliara (Humbert 13738 [P]). — **Distr:** Madagascar (Toliara: mountains around Tolanaro); W slopes of gneiss hills, 800 m. **I:** Castillon & Castillon (2010: 237); Carter & al. (2011: 533).

[6] Caulescent; stems to 35 cm, with thin creeping part and thicker erect fertile part; **L** scattered along the stem, gradually tapering to the tip, 5–8 × 3 cm, **marginal teeth** deltoid, 1 mm, leaf sheath long; **Inf** up to 20 cm, simple; raceme with few flowers; **Bra** ovate, acute, 2–3 mm; **Ped** 7 mm; **Fl** red becoming paler above, with green tip, 20 mm, slightly constricted above the ovary, base rounded; **OTep** free for ±6.5 mm; **St** and **Sty** not exerted.

Considered as insufficiently known by Castillon & Castillon (2010: 237).

**A. lukeana** T. C. Cole (Cact. Succ. J. (US) 87 (4): 156, ills. (pp. 154–157), 2015). **Type:** Uganda, Kaabong Distr. (Cole 1501 [MHU]). — **Distr:** Uganda, South Sudan; montane shrubby grassland on rocky slopes, 1620–2700 m. **I:** Cole & Forrest (2017: 80–87).

[9] Caulescent, solitary or stem branching above with age; stem to 1.5 m × 12–15 (–18) cm Ø, with dead leaves persistent; **L** 20–35, densely rosulate, lanceolate-attenuate, 50–70 (–90) × 12–13 cm, mid-green, surface smooth, exudate yellow drying brownish, **marginal teeth** deltoid, 3–5 mm, white, brown-tipped, 10 mm apart; **Inf** 75 cm, erect or slightly oblique, with 8–15 **Br**, lowermost rebranched; racemes cylindrical, lax; **Bra** ovate-acuminate, 8–10 × 3–4 mm, sometimes longer than the pedicels, whitish with 3–5 brown nerves; **Ped** to 17 mm; **Fl** orange or red, 35 mm, base rounded, 6 mm Ø across the

ovary, narrowing slightly above, widening to the mouth; **OTep** free for 23 mm; **St** exerted 0–1 mm; **Sty** exerted 2 mm.

**A. luntii** Baker (Bull. Misc. Inform. Kew 1894: 342, 1894). **Type:** Yemen (Lunt 225 [K]). — **Lit:** Lavranos (1992). **Distr:** SE Yemen (Hadhramaut); stony hills, 1000–2100 m. **I:** Reynolds (1966: 222, as *A. inermis*); Carter & al. (2011: 593).

[7] Caulescent, suckering to form small groups; stem to 30 cm; **L** 7–8, distichous at first, becoming densely rosulate, ensiform-acute, ±30 × 5 cm, grey to brownish with a bloom, surface smooth, **marginal teeth** absent; **Inf** with 4–5 **Br**; racemes with secund flowers, lax; **Bra** 3–4 mm; **Ped** 4–6 mm; **Fl** dull red to coral-pink with a conspicuous bloom, 26–28 mm, base shortly attenuate, slightly narrowed above the ovary, enlarging again to the mouth; **OTep** free for <½ their length; **St** and **Sty** exerted 4–5 mm.

Reynolds (1966) included this name as a synonym of *A. inermis*, but Lavranos (1992) argued for its recognition as a distinct species.

**A. lutescens** Groenewald (Flow. Pl. South Afr. 18: t. 707 + text, 1938). **Type:** RSA, Limpopo (van der Merwe 1377 [PRE 23301 (= 23005)]). — **Distr:** SE Botswana, S Zimbabwe, Moçambique, RSA (N Limpopo); between trees or shrubs on dry rocky or stony slopes, 200–1200 m. **I:** Reynolds (1950: 338); Carter & al. (2011: 583); Wyk & Smith (2014: 172–173).

[7] Caulescent, usually dividing to form dense groups; stem erect or decumbent, to 80 cm; **L** ±30, densely rosulate, lanceolate-attenuate, 50–60 × 8–9 cm, dull to semi-glossy yellowish-green, **marginal teeth** ±2 mm, pinkish-brown, 3–5 mm apart; **Inf** 1–1.5 m, with 3 **Br** in one vertical plane; racemes cylindrical-acuminate, 35–40 × 7 cm; **Bra** ovate-acuminate, 15 × 15 mm; **Ped** to 15 mm; **Fl** yellow, sometimes with slightly reddish base, opening from scarlet and green-tipped buds, 30–35 mm, base rounded, not narrowed above the ovary; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Close to *A. cryptopoda*, and the two species appear to grade into one another where they meet across the RSA/Zimbabwe border (Hargreaves 2011).

**A. macleayi** Reynolds (J. South Afr. Bot. 21 (2): 55–57, tt. 3–4, 1955). **Type:** South Sudan, Equatoria Prov. (*MacLeay* s.n. in *Reynolds 6773* [PRE, EA, K]). — **Distr:** SE South Sudan (Equatoria Prov.: Imatong Mts.), N Uganda (Kitgum Distr: Agoro Mts.); amongst rocks in grassland, 1250–2440 m. **I:** Reynolds (1966: 299–300); Carter & al. (2011: 348); Cole & Forrest (2015: 80); Cole & Forrest (2017: 88–93).

[3] Acaulescent, simple; **L** ±24, densely rosulate, lanceolate-attenuate, to 50 × 12 cm, deep green to olive-green, obscurely lineate, with yellowish-white margins, exudate drying yellow, **marginal teeth** 4 mm, firm, white, uncinuate, 8–15 mm apart; **Inf** 90 cm, slightly oblique but with racemes erect, with ±9 **Br**; racemes cylindrical-conical, 22 × 5.5 cm, lax; **Bra** ovate-acute, pale brown, 3 × 4 mm; **Ped** 10 mm; **Fl** scarlet at the base, becoming orange to yellowish towards the mouth, 36 mm, base rounded, 7 mm Ø across the ovary, very slightly narrowed above; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. macra** Haworth (Suppl. Pl. Succ., 45, 105, 1819). **Type:** not typified. — **Lit:** Marais (1975). **Distr:** W La Réunion; rocky cliffs and dry forests. **I:** Castillon & Castillon (2010: 378–380); Carter & al. (2011: 566).

≡ *Phylloma macrum* (Haworth) Sweet (1827)  
≡ *Lomatophyllum macrum* (Haworth) Salm-Dyck ex Schultes & Schultes fil. (1829).

[2] Caulescent; stem to 30 cm; **L** 10–12, laxly rosulate, ensiform-attenuate, 30–35 × 3 cm, green with red margin, **marginal teeth** minute, red; **Inf** 30 cm, simple or with 1 **Br**; racemes cylindrical, 10–15 cm, dense; **Bra** lanceolate, ±5 mm; **Ped** ±10 mm; **Fl** reddish-orange, becoming yellow towards the tip, 13–14 mm; **OTep** free to 4 mm; **St** and **Sty** exerted 0–1 mm; **Fr** berries.

**A. macrocarpa** Todaro (Hort. Bot. Panorm. 1: 36, t. 9, 1876). **Type:** Ethiopia, Tigray Region (?)

(*Schimper* s.n. [[icono]: l.c. t. 9]). — **Lit:** Gilbert & Sebsebe Demissew (1997). **Distr:** Benin, Cameroon, Eritrea, Ethiopia, Ghana, Mali, Nigeria, Sudan, Djibouti; rocky grassland and on rock ledges, 400–2200 (–3000) m. **I:** Reynolds (1966: 92–95); Carter & al. (2011: 173).

**Incl.** *Aloe commutata* Engler (1892) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe macrocarpa* var. *major* A. Berger (1908); **incl.** *Aloe edulis* A. Chevalier (1920); **incl.** *Aloe barteri* Schnell (1953) (*nom. illeg.*, ICN Art. 53.1).

[5] Acaulescent or shortly caulescent, simple or suckering to form small groups; stems to 30 cm; **L** 16–20, densely rosulate, lanceolate to lanceolate-attenuate, 20–40 × 6–7 cm, green with many dull white or pale greenish oval spots arranged irregularly or in transverse bands, surface smooth, **marginal teeth** 3 mm, pale brown, 8–10 mm apart; **Inf** 80–100 cm, with 3–5 **Br**; racemes cylindrical, 15–20 × 6 cm, lax; **Bra** 8 × 3 mm; **Ped** 12–15 mm; **Fl** scarlet, 25–35 mm, base truncate, 8 mm Ø across the ovary, abruptly narrowed to 5 mm above, then enlarging to the mouth; **OTep** free for 6–7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Satô 1937).

Some populations, including those in W Africa, have been named as *A. macrocarpa* var. *major*, but there is no discontinuity in characters between this and the typical variety. A natural hybrid with *A. schweinfurthii* has been seen in Nigeria (Newton, unpublished). Figueiredo & Smith (2012) claim that the plant referred to as *A. commutata* by Engler is the same as that described by Todaro. However, Todaro's *A. commutata* is generally regarded as a hybrid between two South African species (thus *A. × commutata*), whereas Engler cited a specimen from Ethiopia.

**A. macroclada** Baker (J. Linn. Soc., Bot. 20: 273, 1883). **Type** [lecto]: Madagascar, Fianarantsoa (*Baron 1656* [K, P]). — **Distr:** SE Madagascar (Fianarantsoa: Angavo Mts.); grassland on dry mountain slopes and high plateaus, 700–1500 m. **I:** Reynolds (1966: 484–486); Castillon & Castillon (2010: 159–161); Carter & al. (2011: 292).

[2] Acaulescent, simple; **L**  $\pm 36$ , densely rosulate, ensiform-attenuate,  $75 \times 15$  cm, green, **marginal teeth** 3 mm, pungent, orange-brown, paler towards the base,  $\pm 10$  mm apart; **Inf** 1.75 (–2.4) m, simple or sometimes with 1 **Br**; racemes cylindrical,  $60\text{--}75$  (–100)  $\times 7$  cm, very dense; **Bra** ovate-acute, shortly cuspidate,  $10 \times 7$  mm, reflexed at the base; **Ped** 4–5 mm; **Fl** pale scarlet, greenish inside the mouth, 20–25 mm, campanulate, base rounded, 6 mm  $\varnothing$  across the ovary, enlarged above to 20 mm across the mouth; **OTep** free to the base; **St** and **Sty** exerted 8–10 mm.

The protologue included two syntypes, from which a lectotype was selected by Castillon (2009a). Natural hybrids with varieties of *A. capitata* have been reported by Reynolds (1966) and Bosser (1968).

**A. macrosiphon** Baker (in Thiselton-Dyer & al., Fl. Trop. Afr. 7: 459, 1898). **Type:** Tanzania, Bukoba Distr. (*Scott-Elliot* 8176 [K, BM]). — **Distr:** SW Kenya, Rwanda, NW & W Tanzania, SW Uganda; usually in the shade of thickets or among rocks, 1125–1585 m. **I:** Reynolds (1966: 177–179); Carter & al. (2011: 462); Cole & Forrest (2017: 94–99).

**Incl.** *Aloe mwanzana* Christian (1940); **incl.** *Aloe compacta* Reynolds (1961).

[7] Acaulescent, suckering to form dense clumps; **L**  $\pm 16$ , densely rosulate, lanceolate-attenuate,  $50\text{--}70 \times 5\text{--}10$  cm, glossy dark green, tinged reddish-brown in the open, with many dull white to pale green elongated spots, spots smaller on the lower face, surface smooth, exudate yellow drying brownish, **marginal teeth** 2–5 mm, pungent, brown-tipped, 8–15 mm apart; **Inf** 1–1.5 m, with 8–10 **Br**; racemes cylindrical-acuminate, to  $20 \times 6$  cm, subdense; **Bra** ovate-acute,  $10\text{--}15 \times 5\text{--}8$  mm, white; **Ped** 10 mm; **Fl** bright rose-pink, pale yellowish at the mouth, 27–33 mm, base shortly attenuate, 7 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 9–11 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

Natural hybrids with *A. bukobana* and *A. secundiflora* have been reported from Tanzania (Reynolds 1966).

**A. maculata** Allioni (Auct. Syn., 5: 65, 1773). **Type:** [lecto — icono]: Commelin, Hort. Med. Amstel. 2: fig. 5, 1701. — **Lit:** Guglielmone & al. (2009: typification); Mottram (2013: typification). **Distr:** Lesotho, RSA, Swaziland; neophyte in Portugal and Spain.

**Incl.** *Aloe saponaria* var. *luteo-striata* Haworth (1821).

A very variable species. Gilbert & Sebsebe Demissew (1997) have suggested that the better known and long-used name *A. saponaria* should be conserved, esp. as it is the type of the well defined sect. *Saponariae* A. Berger. The distribution of the species was discussed by Smith & al. (2012a). Natural hybrids with other species have been reported (Reynolds 1950: as *A. saponaria*).

**A. maculata** ssp. *ficksburgensis* (Reynolds) Gideon F. Smith & Figueiredo (Bradleya 30: 15, ill. (pp. 14, 16), 2012). **Type:** RSA, Free State (Reynolds 2087 [PRE]). — **Distr:** RSA (Free State), Lesotho; rocky grassland and mountain slopes.

$\equiv$  *Aloe saponaria* var. *ficksburgensis* Reynolds (1937)  $\equiv$  *Aloe maculata* var. *ficksburgensis* (Reynolds) Dandy (1999) (*nom. inval.*, ICN Art. 41.5).

[5] Differs from ssp. *maculata*: **Inf** 50 cm, with 1–2 **Br**; racemes 8 cm  $\varnothing$ ; **Ped** 25 mm; **Fl** 30–40 mm.

**A. maculata** ssp. *maculata* — **Distr:** Lesotho, RSA (Western Cape, Eastern Cape, E Free State, KwaZulu-Natal, Mpumalanga), Swaziland; grassland and scrub to rocky slopes, 0–1830 m. **I:** Reynolds (1950: 225–228, t. 12, as *A. saponaria*); Carter & al. (2011: 171); Wyk & Smith (2014: 250–251). — Fig. 43.

$\equiv$  *Aloe saponaria* var. *saponaria*; **incl.** *Aloe perfoliata* var.  $\theta$  Linné (1753); **incl.** *Aloe perfoliata* var.  $\lambda$  Linné (1753); **incl.** *Aloe disticha* Miller (1768) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe maculosa* Lamarck (1783); **incl.** *Aloe maculata* Medikus (1786) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe perfoliata* var. *saponaria* Aiton (1789) (*nomen rejiciendum*, Art. 56.1)  $\equiv$  *Aloe saponaria* (Aiton) Haworth (1804) (*nomen rejiciendum*, Art. 56.1); **incl.** *Aloe picta* var.



**Fig. 43** *Aloe maculata* ssp. *maculata*. (Copyright: L. E. Newton)

*major* Willdenow (1799); **incl.** *Aloe umbellata* De Candolle (1799); **incl.** *Aloe saponaria* var. *latifolia* Haworth (1804); **incl.** *Aloe latifolia* Haworth (1812); **incl.** *Aloe leptophylla* N. E. Brown *ex* Baker (1880); **incl.** *Aloe saponaria* var. *brachyphylla* Baker (1880); **incl.** *Aloe leptophylla* var. *stenophylla* Baker (1896).

[5] Acaulescent or shortly caulescent, simple or suckering to form dense groups; stem to 50 cm; **L** 12–20, densely rosulate, lanceolate, 25–30 × 8–12 cm, green with many oblong dull white spots arranged in wavy transverse bands, lower face lineate, usually without spots, **marginal teeth** 3–5 mm, pungent, brown, ±10 mm apart; **Inf** 40–100 cm, with 3–7 **Br**; racemes capitate-corymbose, sometimes conical or round-topped, 10–12 × (8–) 12–16 cm, dense; **Bra** deltoid-acuminate, ± $\frac{1}{3}$  to  $\frac{1}{2}$  as long as the pedicels; **Ped** (25–) 35–45 mm; **Fl** usually salmon-pink to orange, sometimes yellow or red, 35–45 mm, base truncate, 10 mm  $\varnothing$  across the ovary, abruptly

narrowed to 6 mm above, then enlarging to the mouth; **OTep** free for 10–15 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Taylor 1925: as *A. saponaria*).

The name *A. perfoliata* var. *saponaria* Aiton (1789) has been proposed for rejection under ICN Art. 56 (Klopper & al. 2016). Hargreaves & al. (2010) showed that this ornithophilous species is subject to pollen theft by various bee species. Duffy & Johnson (2011) found complicated male/female fitness interactions due to self-pollen loads that decrease seed set, and late-acting self-incompatibility.

Wyk & Smith (2014) noted that the taxon also occurs in Zimbabwe, but further evidence for this is needed. Smith & al. (2012a) discuss the taxon in the Free State Province.

**A. mahraensis** Lavranos & T. A. McCoy (Cact. Succ. J. (US) 74(5): 238–240, ill., 2002). **Type**: Yemen, Al-Mahra Prov. (Lavranos & al. 31475 [MO, P]). — **Distr**: Yemen; dry washes on coastal plains, 75 m. **I**: Carter & al. (2011: 414).

[7] Acaulescent, suckering to form large groups; **L** 12–20, densely rosulate, narrowly lanceolate-attenuate, 22–25 × 7 cm, grey- or bluish-green, sometimes with spots near the base, exudate yellow, **marginal teeth** absent; **Inf** 50–70 cm, erect, simple or with 1–2 **Br**; racemes cylindrical, ±30 cm, lax; **Bra** 4 × 2 mm; **Ped** 6 mm; **Fl** red, yellow at the mouth, 22–26 mm, 5 mm  $\varnothing$  across the ovary; **OTep** free for 7 mm; **St** and **Sty** exerted 2–3 mm.

**A. makayana** Lavranos & al. (Kakt. and Sukk. 59(7): 190–191, ill., 2008). **Type**: Madagascar, Toliara (Röösli & Hoffmann 14/03 [TAN, Z]). — **Distr**: Madagascar (Toliara); steep to precipitous quartzitic sandstone slopes, 600 m. **I**: Carter & al. (2011: 322).

[3] Acaulescent or with short procumbent or pendulous stem, usually solitary; **L** 15–22, rosulate, deltoid, 30–40 × 6.5–9 cm, grey-green, often tinged reddish or purple, exudate drying brilliant yellow, **marginal teeth** triangular, backward-pointing, <1 mm, white or pink; **Inf** 90 cm, with up to 5 **Br**; racemes shortly conical, lax; **Bra** 2–3 mm; **Ped** 20–28 mm, spreading



horizontally with buds and flowers pendulous; **Fl** very pale pink to whitish, 26–30 mm, 7.5 mm  $\varnothing$  across the ovary; **OTep** free for  $\pm 15$  mm; **St** and **Sty** exerted 4–6 mm.

Castillon & Castillon (2010: 27) regard this as conspecific with *A. imalotensis*.

**A. manandonae** J.-B. Castillon & J.-P. Castillon (Succulentas 2008(2): 6–9, ills., 2008). **Type:** Madagascar, Antananarivo (Castillon 33 [TAN, HBG]). — **Distr:** Madagascar (Antananarivo: Mt. Ibity); quartzitic rocks, 1400 m; known only from the type locality. **I:** Reynolds (1966: 443–444, as *A. ibitiensis*); Castillon & Castillon (2010: 80–81); Carter & al. (2011: 309).

[5] Acaulescent, solitary or forming small groups; **L** 10–15, laxly rosulate, ovate-acute, 20–30  $\times$  5–7 cm, yellowish-green, densely lineate, **marginal teeth** 1–2 mm, 2–5 mm apart; **Inf** 80 cm, erect, with 2–5 **Br**; racemes cylindrical, to 20 cm, lax; **Bra** 4  $\times$  1.5 mm; **Ped** 10–15 mm; **Fl** red, 25 mm, 4 mm  $\varnothing$  across the ovary; **OTep** free for 12 mm; **St** and **Sty** exerted 0–1 mm.

According to the protologue, Reynolds misidentified this as *A. ibitiensis*. — Only one population is known at present, threatened by habitat destruction and grass fires.

**A. mandotoensis** J.-B. Castillon (J. Bot. Soc. Bot. France 21: 7, ills. (p. 9), 2003). **Type:** Madagascar, Antananarivo (Castillon 3 [P]). — **Distr:** Madagascar (Antananarivo: near Mandoto); on granitoid rocks, 1400 m; known only from the type locality. **I:** Castillon & Castillon (2010: 294–295); Carter & al. (2011: 332).

[5,11] Acaulescent or with a stem to 30 cm, solitary or branching; **L** 15–20, rosulate, deltoid-acute, 40–45  $\times$  5–8 cm, bright green, occasionally with longitudinal pink marks, **marginal teeth** 3 mm, pink, 5–7 mm apart; **Inf** 1 m, erect, with 5–11 **Br**; racemes cylindrical-conical, 20–30 cm, sublux; **Bra** 10 mm; **Ped** 12 mm; **Fl** red, 30 mm, 4–5 mm  $\varnothing$  across the ovary, 7 mm  $\varnothing$  at the mouth; **OTep** free for  $\pm 20$  mm; **St** and **Sty** exerted 3–4 mm.

**A. mandrarenensis** J.-P. Castillon (CactusWorld 30(3): 168–169, ills., 2012). **Type:** Madagascar,

Toliara (Castillon 55 [TAN]). — **Distr:** Madagascar (Toliara); calcareous bush, 150 m.

[5] Acaulescent, suckering to form groups of 5–10 **Ros**; **L** 7–10, rosulate, triangular, 4–6  $\times$  1–2 cm, light green and yellow, finely lineate, **marginal teeth** deltoid, 0.5 mm, white, 4 mm apart, absent towards the leaf tip; **Inf** 40 cm, erect, simple; racemes cylindrical, 8 cm, lax; **Bra** triangular, 5  $\times$  4 mm; **Ped** 10–12 mm; **Fl** pink, white-brown at the mouth, 25 mm; **St** and **Sty** exerted 3–4 mm.

**A. mangeaensis** L. E. Newton & S. Carter (CactusWorld 35(1): 53–54, ills., 2017). **Type:** Kenya, Kilifi County (Robertson 7974 [K, EA]). — **Distr:** SE Kenya; amongst scattered rocks on sandstone hill, 305 m.

[13] Caulescent, occasionally suckering; stem to 50 cm, becoming decumbent, rooting when touching the ground; **L** to 30, semidensely rosulate, lanceolate with acute apex, to 80  $\times$  7 cm, green, surface smooth, exudate yellow, **marginal teeth** deltoid, pungent, 5 mm, green, brown-tipped, 10–15 mm apart; **Inf** 100 cm, erect, with 4–6 **Br**; racemes cylindrical, to 10 cm, subdense; **Bra** ovate, apex acute, 10–12  $\times$  4–5 mm, scarious, with 7 brown nerves; **Ped** 10 mm; **Fl** orange/pink, lobes pale yellow-tipped, 26 mm, base rounded, 4 mm  $\varnothing$  across the ovary, narrowed to 3 mm above, widening to 4 mm at the mouth; **OTep** free for 11 mm; **St** exerted 4–8 mm; **Sty** exerted 6 mm.

**A. maningoryensis** J.-P. Castillon (Adansonia, sér. 3, 39(1): 8–10, ills., 2017). **Type:** Madagascar, Toamasina (Castillon 59 [TAN]). — **Distr:** E Madagascar (Toamasina); forest, 800 m.

[8] Caulescent; stem to 1 m; **L** 20–30, rosulate, narrowly lanceolate, 60–110  $\times$  5–8 cm, bright green, exudate yellow-green, **marginal teeth** 5 mm, green, 6–13 mm apart; **Inf** 50 cm, ascending, with 1–3 **Br**, sometimes producing bulbils; racemes cylindrical-conical, 20 cm, dense; **Bra** triangular-acuminate, 3  $\times$  3 mm, white, scarious, with 1 dark nerve; **Ped** 11 mm; **Fl** rose-red, pale green towards the mouth, 30 mm, 7 mm  $\varnothing$  across the ovary, narrowed above to 5 mm, enlarging to



8 mm towards the mouth, **OTep** free for 7.5 mm; **St** exerted 2–3 mm; **Sty** exerted 4 mm; **Fr** berries.

**A. marlothii** A. Berger (Bot. Jahrb. Syst. 38: 87, 1905). **Type** [syn]: Botswana (*Marloth* 3788 [B]). — **Lit**: Wyk & Smith (1996); Klopper & Smith (2010a). **Distr**: Moçambique, Botswana, RSA, Swaziland.

**Incl.** *Aloe ferox* var. *xanthostachys* A. Berger (1908) (*incorrect name*, Art. 11.4); **incl.** *Aloe ferox* A. Berger (1908) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe marlothii* J. M. Wood (1912) (*nom. illeg.*, ICN Art. 53.1).

The superficially similar *A. spectabilis* was treated as a synonym of *A. marlothii* until recently, but Klopper & Smith (2010a) argue that it should be recognized as separate species, even though the two species seem to intergrade in Zululand.

**A. marlothii** ssp. **orientalis** Glen & D. S. Hardy (Flow. Pl. Afr. 49(3–4): t. 1943 + text, 1987). **Type**: RSA, KwaZulu-Natal (*Plowes* 2260 [PRE, LISC, SRGH]). — **Distr**: S Moçambique, RSA (KwaZulu-Natal), Swaziland; sandy soil, 15–500 m (= lower altitudes than var. *marlothii*).

[8,12] Differs from var. *marlothii*: Often suckering to form clumps; stem erect or procumbent to oblique, to 1.75 m; **L** surface with few or no prickles; **Inf** with oblique racemes.

**A. marlothii** var. **bicolor** Reynolds (J. South Afr. Bot. 2(1): 34, 1936). **Type**: RSA, Mpumalanga (*Reynolds* 1440 [PRE]). — **Distr**: RSA (Mpumalanga); rocky hills.

[9] Differs from var. *marlothii*: **L** with fewer prickles, **marginal teeth** red; **Fl** greenish-white, opening from red buds.

Probably the hybrid *A. marlothii* × *A. rupestris*.

**A. marlothii** var. **marlothii** — **Distr**: SE Botswana, Moçambique, RSA (KwaZulu-Natal, Gauteng, Mpumalanga, Limpopo, North-West Prov.), Swaziland, Zimbabwe; open bushveld to exposed rocky places, 0–1600 m. **I**: Reynolds



**Fig. 44** *Aloe marlothii* var. *marlothii*. (Copyright: G. D. Rowley)

(1950: 480–482, t. 56); Carter & al. (2011: 678–679); Wyk & Smith (2014: 68–69). – Fig. 44.

**Incl.** *Aloe supralaevis* var. *hanburyi* Baker (1896).

[9] Caulescent, simple; stem erect, to 4 (–6) m, covered with dead leaves; **L** 40–50, densely rosulate, lanceolate-attenuate, 1–1.5 m × 20–25 cm, dull grey-green to glaucous, with few to many scattered reddish-brown 3–4 mm long prickles, more numerous on the lower face, **marginal teeth** 3–4 mm, pungent, reddish-brown, 10–15 mm apart; **Inf** ±80 cm, with many **Br**, lower ones rebranched, with a total of 20–30 racemes; racemes horizontal to suboblique with secund flowers, 30–50 × 5–6 cm, dense; **Bra** ovate to lanceolate-acute, ±8–9 × 5 mm, brownish; **Ped** 5 mm; **Fl** orange to yellowish-orange, 30–35 mm, clavate to ventricose, base rounded, ±7 mm Ø across the ovary, enlarging above and narrowing at the mouth; **OTep** free for 20–23 mm; **St** and **Sty**

exserted 15 mm. — **Cytology:**  $2n = 14$  (Resende 1937).

Natural hybrids with other species are not rare, and Reynolds (1950: 483–484) reports crosses with 22 other species alone from RSA, making *A. marlothii* the most promiscuous taxon of the genus in habitat. Hargreaves (2005) adds putative hybrids with *A. lutescens* from Botswana to Reynolds's long list.

As is the case for almost all aloes, *A. marlothii* is pollinated almost exclusively by birds (Hargreaves & al. 2012), and because its winter flowering provides a source of food for nectar-feeding birds it has been the subject of several ecological studies. Symes & al. (2008) found no less than 38 species of birds as flower visitors and identify the species as an important winter-time nectar resource. Most of these birds are opportunistic nectarivores, but none the less, the nectar of *A. marlothii* contributes significantly to their energy budgets (Symes & al. 2011, Blair & Hatch 2011).

The dense stands of *A. marlothii* are interpreted as a climax community that established in the absence of mega-herbivore pressure, as evidenced by a significant density decline within 8 years in a game reserve with introduced elephant and rhinos (Wiseman & al. 2004, Symes 2012). Symes (2012) found a seed production of 26,000–375,000 seeds per plant, with a positive correlation of seed production and plant height. Seed dispersal distance is up to 25 m (and probably up to 50 m in windy conditions). No soil seed bank is formed. In Botswana, Titus & al. (2012) found good regeneration in 2 populations, while a third population consisted purely of old (>4.5 m tall) mature individuals.

**A. martialii** J.-B. Castillon (Cact.-Avent. Int. 85: 3–4, ills., 2010). **Type:** Madagascar, Antsiranana (*Malcomber & al.* 1185 [MO]). — **Distr:** N Madagascar (Antsiranana: Montagne d'Ambre); dense shady humid montane forest.

[2] Acaulescent, or with a stem to 10 cm, solitary; **L** 13–17, laxly rosulate, triangular, acute, 60 × 2.5 cm, green, surface smooth, **marginal teeth** 1–1.5 mm, green, 10–13 mm apart; **Inf** 27–35 cm, erect, simple or with 1 **Br**; racemes

cylindrical, 6–10 cm, lax; **Bra** 10 × 2 mm, green, with several nerves; **Ped** 15 × 1–1.5 mm, brown; **Fl** reddish, lobes whitish-green at the tips, 32 mm, base obtuse, slightly constricted above the ovary, 3 mm wide at the mouth; **OTep** free for 7 mm; **St** and **Sty** not exserted; **Fr** a berry, 1.5 cm Ø.

**A. massawana** Reynolds (J. South Afr. Bot. 25: 207–209, tt. 18–19, 1959). **Type:** Tanzania, Dar es Salaam Distr. (*Reynolds* 8733 [PRE, EA, K]). — **Distr:** Kenya, Tanzania, Moçambique, Madagascar.

**A. massawana** ssp. **massawana** — **Lit:** Carter & al. (1996). **Distr:** Kenya, Tanzania, Moçambique; grass or open thickets on sandy soils near the coast, 0–20 m. **I:** Reynolds (1966: 154); Carter & al. (2011: 464). — Fig. 45.

**Incl.** *Aloe kirkii* Baker (1894).

[7] Acaulescent or shortly caulescent, suckering at the base to form dense clumps to 3 m Ø; **L** ±16, densely rosulate, lanceolate-attenuate, ±50 × 10 cm, dull grey-green, sometimes with a few white spots towards the base, exudate drying yellow, **marginal teeth** 2–3 mm, soft to firm, white with reddish-brown tips, 15–25 mm apart, smaller and closer towards the leaf base; **Inf** 1.2–1.5 m, with 2–3 **Br**; racemes cylindrical-acuminate, 15–20 × 5 cm, subdense; **Bra** ovate-deltoid, 7 × 3 mm; **Ped** 6 mm; **Fl** pale scarlet, 30–32 mm, base rounded, 7 mm Ø across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for 12 mm; **St** and **Sty** exserted 0–1 mm.

Material from Massawa in Eritrea included here by Reynolds (1966) has been described as *A. eumassawana*.

*A. kirkii* is insufficiently known and placed here with a question mark by Carter (1994).

**A. massawana** ssp. **sakoankenke** (J.-B. Castillon) J.-B. Castillon (Cact.-Avent. Int. 84: 32, 2009). **Type:** Madagascar, Antsiranana (*Castillon* 10 [P, MO]). — **Distr:** N Madagascar (Antsiranana: Montagne d'Ambre); rocky slopes; also cultivated. **I:** Castillon & Castillon (2010: 330); Carter & al. (2011: 451, 707).

≡ *Aloe sakoankenke* J.-B. Castillon (2004).

**Fig. 45** *Aloe massawana*  
ssp. *massawana*.  
(Copyright: L. E. Newton)



[7] Differs from ssp. *massawana*: Stem to 40 cm; **L** 15–20; **Inf** to 2 m, with up to 8 **Br**; racemes 20–25 cm, lax; **Bra** 6–10 mm; **Ped** 6–10 mm; **Fl** 30–35 mm, 9 mm  $\varnothing$  across the ovary.

With the transfer of *A. sakoankenke* to *A. massawana*, it was pointed out that the latter is the only *Aloe* species to occur on both the African mainland and Madagascar. However, ssp. *sakoankenke* occurs in a degraded area near human habitation, and is possibly an ancient import from Africa.

**A. mawii** Christian (J. South Afr. Bot. 6(4): 186–188, t. 23, 1940). **Type**: Malawi (*Christian* 942 [SRGH]). — **Distr**: Malawi, C Moçambique, S Tanzania; rocky slopes, bare granite and open grassland, 550–1830 m. **I**: Reynolds (1966: 237–240); Lane (2004: 40, 43–44); Carter & al. (2011: 654); Klopper & al. (2012: 81, 87, incl. distribution map). – Fig. 46.

[4,8] Acaulescent or usually caulescent, simple or with a few branches; stem erect, to 2 m  $\times$  10–12 cm; **L** 20 or more, densely rosulate, lanceolate-ensiform, to 60  $\times$  10 cm, greyish-green or green with bluish tinge, somewhat striate, with narrow reddish margin, surface smooth, exudate pale yellow, **marginal teeth** 3–4 mm, pinkish-tipped, 7–15 mm apart; **Inf** to 1 m, oblique, simple or with 1 **Br**; racemes oblique or horizontal, with secund flowers, 30 cm, dense; **Bra** triangular-acute, shortly cuspidate, 1  $\times$  3



**Fig. 46** *Aloe mawii*. (Copyright: L. E. Newton)

mm; **Ped** 1–2 mm; **Fl** red or orange, 35–40 (–48) mm, ventricose, base rounded, 7 mm  $\varnothing$  across the ovary, enlarging to 10 mm above, then narrowing to the mouth; **OTep** free for 22 mm; **St**



and **Sty** exerted  $\pm 12$  mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

Acaulescent variants are at lower altitudes.

**A. mayottensis** A. Berger (in Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 246, 1908). **Type**: Comoros, Mayotte Island (*Boivin* 3071 [P]). — **Distr**: Comoros; in shade on hill slopes. **I**: Reynolds (1966: 507); Castillon & Castillon (2010: 386–387); Carter & al. (2011: 609).

[15] Caulescent, branching at the base and above; stem  $50 \times 3\text{--}4$  cm; **L**  $\pm 20$ , lanceolate-attenuate,  $40\text{--}50 \times 6\text{--}7$  cm, green, **marginal teeth** 3 mm, pale yellow to pale brown, 10–15 mm apart; **Inf**  $\pm 1$  m, with 3–4 **Br**; racemes cylindrical-acuminate, to  $20 \times 6$  cm, subdense; **Bra** ovate-acute,  $6 \times 4$  mm; **Ped**  $\pm 6$  mm; **Fl** 28 mm, base shortly attenuate, 8 mm  $\varnothing$  across the ovary, very slightly narrowed above; **OTep** free for 14 mm; **St** and **Sty** exerted 2–4 mm.

Originally described only from a poor herbarium specimen. Possibly in the *Lomatophyllum* group, but fruits as yet unknown.

**A. mccoysi** Lavranos & Mies (Cact. Succ. J. (US) 73(3): 150, ills. (pp. 146–150), 2001). **Type**: Yemen, Al-Mahra Prov. (*Lavranos & al.* 31472 [MO, P, UPS]). — **Distr**: Yemen; mountain slopes, often shrouded in clouds, 430 m. **I**: Carter & al. (2011: 504).

[13] Caulescent, solitary; stem to  $200 \times 8$  cm, prostrate; **L** 15–20, rosulate, broadly triangular, acute,  $30\text{--}40 \times 12$  cm, grey- to bluish-green with a waxy bloom, exudate thick, yellow, drying yellow, **marginal teeth** absent; **Inf** 40–50 cm, ascending, with 1–2 **Br**; racemes cylindrical-conical, to 28 cm, lax; **Bra** ovate-acute,  $5 \times 2.5$  mm; **Ped** 7 mm; **Fl** red to rose-pink, mouth yellow, 25–33 mm, 7 mm  $\varnothing$  across the ovary; **OTep** free for 10 mm; **St** and **Sty** exerted 2 mm.

**A. mcloughlinii** Christian (Flow. Pl. Afr. 28: t. 1112 + text, 1951). **Type**: Ethiopia, Harar Prov. (*McLoughlin* 826 [PRE]). — **Distr**: E Ethiopia, Djibouti; open areas on stony ground in scrub, 1060–1250 m. **I**: Reynolds (1966: 64–65); Sebsebe Demissew & Nordal (2010: 70–71); Carter & al. (2011: 344).

**Incl.** *Aloe mclaughlinii* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1).

[5] Acaulescent or shortly caulescent, simple or usually in groups of up to 6 **Ros**; **L** 16–20, densely rosulate, lanceolate-attenuate,  $\pm 40\text{--}50 \times 7$  cm, glossy green with many pale green elongated spots, the spots more numerous and larger on the lower face, surface smooth, **marginal teeth**  $\pm 3\text{--}5$  mm, firm, reddish-brown tipped, 10–15 mm apart; **Inf** 1–1.2 m, with 6–9 **Br**; racemes cylindrical-acuminate, to  $15 \times 6$  cm, lax; **Bra** deltoid-acute,  $5 \times 2$  mm; **Ped** 10 mm; **Fl** strawberry-red with a slight bloom, 20–24 mm, base rounded, 9–10 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for 16 mm; **St** and **Sty** exerted 4–5 mm. — **Cytology**:  $2n = 14$  (Brandham 1971, Fentaw & al. 2013).

**A. medishiana** Reynolds & P. R. O. Bally (J. South Afr. Bot. 24(4): 186–187, t. 29, 1958). **Type**: Somalia (*Reynolds* 8441 [PRE, EA, K]). — **Lit**: Carter (2007). **Distr**: NE Somalia (E end of Al Madu Mts.); exposed limestone rocky slopes, 1400–1800 m. **I**: Reynolds (1966: 307–308); Carter & al. (2011: 650).

[8] Caulescent, simple or branching at the base; stem erect, to  $2 \text{ m} \times 3\text{--}3.5$  cm; **L**  $\pm 24$ , crowded along the apical 20 cm of the stem, ensiform, to  $30 \times 5.5$  cm, grey-green, with narrow white cartilaginous margin, **marginal teeth**  $\pm 1$  mm, firm, white, 5–10 mm apart; **Inf**  $\pm 50$  cm, with 6–8 **Br**; racemes cylindrical,  $8\text{--}10 \times 5$  cm, subdense; **Bra** ovate-acute,  $2\text{--}3 \times 2$  mm, white; **Ped** 9 mm; **Fl** dull scarlet, 19 mm, base shortly attenuate, 5 mm  $\varnothing$  across the ovary, scarcely narrowed above; **OTep** free for 5–6 mm; **St** and **Sty** exerted 1–3 mm.

Very similar to and probably conspecific with *A. gracilicaulis* (Carter 2007).

**A. megalacantha** Baker (in Thiselton-Dyer & al., Fl. Trop. Afr. 7: 469, 1898). **Type**: Ethiopia, Harerge Region (*Riva* 905 [FT]). — **Lit**: Gilbert & Sebsebe Demissew (1997); Carter & al. (2011: 463). **Distr**: Ethiopia, Somalia.

**A. megalacantha** ssp. **alticola** M. G. Gilbert & Sebsebe (Kew Bull. 52(1): 150, 1997). **Type**:

Ethiopia, Harerge Region (*Gilbert* 4080 [K, ETH]). — **Distr:** E Ethiopia (S Harerge Region); edges of evergreen thickets on limestone slopes, 2100–2150 m. **I:** Carter & al. (2011: 630).

[12] Differs from ssp. *megalacantha*: Often forming more compact clumps; stem erect; **L** **marginal teeth**  $\pm 4$  mm; **Bra** 11–12  $\times$  2.5–4 mm; **Ped** 5–8 mm; **Fl** bright red, dark green at the tip, 25 mm, 5 mm  $\varnothing$ , slightly curved; **OTep** free for 10–12 mm. — **Cytology:**  $2n = 14$  (Fentaw & al. 2013).

**A. megalacantha** ssp. *megalacantha* — **Distr:** NE Ethiopia (Bale and Harerge Regions), NW Somalia; dry open bushland on limestone rocky slopes and sandy plains, 1100–1850 m. **I:** Reynolds (1966: 295–297); Sebsebe Demissew & Nordal (2010: 95–96); Carter & al. (2011: 630).

**Incl.** *Aloe magnidentata* I. Verdoorn & Christian (1947).

[12] Caulescent, branching at the base; stem sprawling, to 2 m, covered with dead leaves; **L** 24 or more, rosulate and persisting for 50 cm, lanceolate-attenuate, deeply canaliculate, recurved with tips pointing down, 60–80  $\times$  13–15 cm, dull light green to bluish-green, with pinkish horny margin, surface rough, **marginal teeth** 4–6 mm, blunt, pinkish, reddish-brown-tipped, 14–20 mm apart; **Inf** 0.5–1 m, with 6–13 **Br**, lower ones rebranched; racemes cylindrical-conical, 5–14  $\times$  7 cm, subdense; **Bra** ovate-deltoid, 4–7  $\times$  2–4 mm; **Ped** 8–15 mm; **Fl** yellow, orange or scarlet, 23–28 mm, base rounded, 5–7 mm  $\varnothing$  when pressed, very slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for 12–14 mm; **St** and **Sty** exerted  $\pm 4$  mm. — **Cytology:**  $2n = 14$  (Brandham 1971, Fentaw & al. 2013).

Natural hybrids with other species have been reported (Reynolds 1966).

**A. megalocarpa** Lavranos (Kakt. and. Sukk. 49(7): 162–163, ill., 1998). **Type:** Madagascar, Antsiranana (*Lavranos & al.* 28728 [P]). — **Distr:** N Madagascar (Antsiranana); on crystalline basement rocks in dense dry forest,  $\pm 30$  m. **I:** Castillon & Castillon (2010: 348–349); Carter & al. (2011: 276).

[2] Acaulescent, solitary; **L**  $\pm 25$ , in a spreading **Ros**, up to 55 cm, to 2.5 cm wide at the base, widening to 3.5 cm in the middle, dark green, glossy, **marginal teeth** triangular, 2 mm, whitish, brown-tipped, firm, 5–15 mm apart; **Inf** to 30 cm, simple, somewhat lax, with  $\pm 15$  flowers; **Bra** 2–4 mm; **Ped** 5–8 mm; **Fl** bright red, dark green at the tip, 25 mm, 5 mm  $\varnothing$ , slightly curved; **OTep** free for 4 mm; **St** and **Sty** exerted 0–1 mm; **Fr** berries,  $\geq 2$  cm.

**A. melanacantha** A. Berger (Bot. Jahrb. Syst. 36: 63, 1905). **Type:** RSA, Northern Cape (*Drège* 2697 [W]). — **Distr:** S Namibia, NW RSA (W Northern Cape, NW Western Cape); rocky slopes, 50–700 m. **I:** Reynolds (1950: 182–183); Carter & al. (2011: 236); Wyk & Smith (2014: 174–175). — Fig. 47.

**Incl.** *Aloe muricata* Haworth (1804).

[4] Caulescent, simple or usually in groups; stem erect and short or, with age, decumbent to 50 cm or more, covered with dead leaves; **L** densely rosulate, deltoid-lanceolate, to 20  $\times$  4 cm, tip a black spine, dull deep green to brownish-green, lower face carinate in the upper  $\frac{1}{2}$ , the keel with  $\pm 6$  black prickles to 10 mm, **marginal teeth** 10 mm, pungent, black, 10–15 mm apart; **Inf** to 1 m, simple, sometimes with 1 **Br**; raceme cylindrical-attenuate, 20–25  $\times$  8 cm, dense; **Bra** 25  $\times$  7 mm; **Ped** 15 mm; **Fl** bright scarlet turning yellowish,  $\pm 45$  mm, base rounded, enlarged slightly above the ovary, narrowing slightly at the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Müller 1945).

This name has been proposed for conservation against *A. muricata* Haworth (which most authors list as a synonym of *A. ferox*) by Smith & Figueiredo (2018b), designating a Plukenet (1692) plate as lectotype for *A. muricata*.

**A.  $\times$  menachensis** (Schweinfurth) Blatter (*pro sp.*) (Fl. Arab., 8: 463, 1936). **Type:** Yemen (*Schweinfurth* 1685 [K]). — **Distr:** Yemen; exposed rocky slopes, 2200–2900 m. **I:** Reynolds (1966: 135); Carter & al. (2011: 608).



**Fig. 47** *Aloe melanacantha*. (Copyright: L. E. Newton)



≡ *Aloe percrassa* var. *menachensis* Schweinfurth (1894) ≡ *Aloe trichosantha* var. *menachensis* (Schweinfurth) A. Berger (1908).

[18] Caulescent; stem erect, to 50 cm; **L** densely rosulate, triangular-lanceolate, attenuate, 40 × 16 cm, greenish-purple, with purplish margins, lower face carinate near the tip, keel sometimes with 1–3 prickles, **marginal teeth** 2 mm, blunt, brown-tipped, 15–20 mm apart; **Inf** “tall”, with many **Br**; racemes cylindrical, 15–20 × 5–6 cm, dense; **Bra** 10–15 mm, reflexed; **Ped** 5–7 mm; **Fl** pale or reddish-scarlet, shortly white-tomentose, 30 mm; **OTep** free for 12 mm; **St** and **Sty** not described.

A little-known species, believed by Favell & al. (1999) and McCoy (2019) to be a naturally occurring hybrid between *A. vacillans* and *A. tomentosa*.

**A. mendesii** Reynolds (J. South Afr. Bot. 30 (1): 31–32, t. 10, 1964). **Type**: Angola, Huila (*Santos & Henriques* 1131 [LISC, LISU, LUAI, PRE]). — **Lit**: Smith & Figueiredo (2011b). **Distr**: SW Angola (Huila: Serra da Chela); vertical rock faces, 2220 m. **I**: Reynolds (1966: 170–171); Carter & al. (2011: 512).

[13] Caulescent; stem pendulous, to 1 m × 4 cm Ø; **L** ±10, falcate, hanging downwards, 50 × 7–8 cm, green, obscurely lineate, **marginal teeth** 1–2 mm, blunt, cartilaginous, 10–15 mm apart;

**Inf** to 60 cm, pendulous with racemes arcuate-ascending, with 3–4 **Br**; racemes cylindrical-acuminate, 10 × 6 cm, subdense; **Bra** ovate-acute, 12 × 5 mm, deep pink, imbricate in the bud stage; **Ped** 18–20 mm; **Fl** scarlet, 25 mm, slightly ventricose, base rounded, 4 mm Ø across the ovary, enlarged above towards the mouth, narrowing just below the mouth; **OTep** free for 20 mm; **St** and **Sty** exerted 3 mm.

**A. menyharthii** Baker (in Thiselton-Dyer & al., Fl. Trop. Afr. 7: 459, 1898). **Type**: Moçambique, Tete Prov. (*Menyharth* 1248 [K]). — **Distr**: Malawi, Moçambique.

**A. menyharthii** ssp. *ensifolia* S. Carter (Kew Bull. 51(4): 783–784, 1996). **Type**: Moçambique, Niassa Prov. (*Leach & Rutherford-Smith* 10876 [K, SRGH]). — **Distr**: Moçambique (Niassa Prov.); grassland on sandy soils in open *Brachystegia* woodland, 130–700 m. **I**: Carter & al. (2011: 182).

[5] Differs from var. *menyharthii*: **L** lanceolate-attenuate (ensifoliate), 40–70 × 3–5.5 cm, tip not drying early, **marginal teeth** 2–4 mm; **Inf** with racemes 4–12 cm.

**A. menyharthii** ssp. *menyharthii* — **Lit**: Carter (1996). **Distr**: S & C Malawi, NW Moçambique (Tete Prov.); grassland in open

bush, 300–1500 m. **I:** Reynolds (1966: 85, fig. 85, as *A. swynnertonii*); Carter & al. (2011: 182); Klopper & al. (2012: 81, 87–88, incl. distribution map).

[5] Acaulescent or very shortly caulescent, solitary or in small groups of 3–4 **Ros**; **L** ±20, densely rosulate, lanceolate-attenuate, 25–40 × 6–9 cm, apical 5–10 cm soon drying, upper face dark green with oblong to confluent H-shaped spots in irregular transverse bands, lower face paler green, obscurely lineate, usually without spots, **marginal teeth** 4 mm, pungent, reddish-brown, <1 mm apart; **Inf** 1.5–1.75 m, with 8–12 **Br**, lower ones sometimes rebranched; racemes capitate-corymbose, 6–8 × 7–8 cm, dense; **Bra** lanceolate, ±10–12 mm; **Ped** 20–25 mm; **Fl** coral-red to pinkish-scarlet, 25–30 mm, ±9 mm ∅ across the ovary, abruptly narrowed above, then gradually widening to the mouth; **OTep** free for ±8 mm; **St** and **Sty** exerted 1–2 mm.

This taxon was included in *A. swynnertonii* by Reynolds (1966).

**A. metallica** Engler & Gilg (in Warburg, Kunene-Sambesi Exped., 191, 1903). **Type:** Angola, Bié (*Baum* 891 [B, LISC [photo]]). — **Lit:** Carter & al. (2011: 261). **Distr:** SW Angola (Bié, Cuando-Cubango, Luanda); sandstone rocks; 1300–1430 m. **I:** Reynolds (1966: 152).

[2,3] Acaulescent or shortly caulescent, simple; **L** ±15, densely rosulate, lanceolate-attenuate, 25–40 × 7–9 cm, bluish-grey with metallic sheen (lost in cultivation), with slightly reddish-brown horny margin, **marginal teeth** 2–3 mm, pungent, reddish-brown, 10–20 mm apart; **Inf** to 1.2 m, simple or with few **Br**; racemes cylindrical-acuminate, to 35 × 6 cm, subdense; **Bra** lanceolate-acute, 18–20 × 8 mm, white, imbricate in bud stage; **Ped** 8 mm; **Fl** reddish-pink, 32 mm, base rounded, 7 mm ∅ across the ovary, enlarging slightly towards the mouth; **OTep** free for 13 mm; **St** and **Sty** exerted 0–1 mm.

**A. meyeri** Van Jaarsveld (J. South Afr. Bot. 47 (3): 567–571, ill., 1981). **Type:** RSA, Northern Cape (*Van Jaarsveld* 6137 [NBG]). — **Lit:** Vorster (1983). **Distr:** S Namibia, NW RSA (NW

Northern Cape); S-facing quartzite cliffs, 300–1200 m. **I:** Glen & Hardy (1993); Carter & al. (2011: 484); Wyk & Smith (2014: 132–133).

**Incl.** *Aloe richtersveldensis* Venter & Beukes (1982).

[13] Caulescent, simple or branching at the base, sometimes branching along the stem; stem pendulous, to 1 m, with dead leaves for a short distance below the rosette; **L** rosulate, lanceolate-acuminate, 20 × 3.5 cm, glaucous with a distinct powdery bloom, slightly striate, **marginal teeth** 2 mm, white, 5–8 mm apart; **Inf** 1.5–2.5 m, pendulous-recurved, simple or rarely branched; racemes capitate, ±7 × 8 cm; **Bra** deltoid-acuminate, 5 × 3 mm; **Ped** 20 mm; **Fl** orange-red, green-tipped, to 20 mm, subclavate, base rounded, ±3.5 mm ∅ across the ovary, enlarging above to 4–5 mm at the mouth; **OTep** free to the base; **St** exerted 3 mm; **Sty** exerted 0–1 mm.

**A. micracantha** Haworth (Suppl. Pl. Succ., 105, 1819). **Type** [neo]: RSA, Eastern Cape (*Burchell* 4482 [K]). — **Lit:** Smith & Mössmer (1995). **Distr:** RSA (Eastern Cape, KwaZulu-Natal); well-drained sandy to stony soils, in fynbos; 50–700 m. **I:** Reynolds (1950: 148–150); Craib (2006: 81–84); Carter & al. (2011: 144); Wyk & Smith (2014: 324–325).

**Incl.** *Aloe micracantha* Link & Otto (1825) (*nom. illeg.*, ICN Art. 53.1).

[4] Acaulescent or very shortly caulescent, simple or sometimes with 1–2 **Br**; **R** thick, fusiform; **L** 12–18, multifarious, deltoid-acuminate, to 50 × 2–4 cm, deep green to yellowish-green, with many white subtuberculate and subspinulescent spots, **marginal teeth** to 2 mm, firm, white, 1–3 mm apart; **Inf** 40–50 cm, simple; raceme capitate, 8 × 9 cm, dense, with ±24 flowers; **Bra** ovate-acuminate, 35 mm, somewhat fleshy near the base; **Ped** 35 mm; **Fl** salmon-pink, 38 mm, base shortly attenuate, slightly narrowed above the ovary; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Müller 1941).

**A. microdonta** Chiovenda (Pl. Nov. Min. Not. Ethiop. 1: 7, 1928). **Type:** Somalia (*Puccioni & Stefanini* 49 [FI]). — **Distr:** S Somalia, NE

Kenya; light sandy soils or on limestone in open bushland, 15–400 m. **I:** Reynolds (1966: 301–302); Carter & al. (2011: 616).

[12] Caulescent, branching, sometimes forming large dense groups; stem decumbent with the tip ascending, to 1 m; **L** ±16, densely crowded at the stem tips, triangular, 50–70 × 9–11 cm, dull green to olive-grey, sometimes with reddish tinge, sometimes with a few dull white spots near the base, exudate drying yellow, **marginal teeth** 1 (–2) mm, whitish with pale brown tips, 5–14 mm apart; **Inf** 1.3 m, with 8–12 **Br**, lower ones sometimes rebranched; racemes oblique or ascending, with ± secund flowers, 10–15 cm, lax; **Bra** ovate-acute, 2–4 × 2 mm; **Ped** 5–6 mm; **Fl** scarlet, sometimes paler at the mouth, 23 mm, base rounded or shortly attenuate, 7 mm Ø across the ovary, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted ±3 mm.

According to Lebrun & Stork (2012) the type of *A. defalcata* Chiovenda, currently treated as a name of unresolved application, seems to be a mixture of *A. microdonta* and *A. ruspoliana*. Natural hybrids with *A. rabaiensis* have been reported (Reynolds 1966).

**A. millotii** Reynolds (J. South Afr. Bot. 22(1): 23–26, ills., 1956). **Type:** Madagascar, Toliara (Reynolds 7840 [TAN, K, P, PRE]). — **Distr:** S Madagascar (Toliara: Cap Sainte Marie); xerophytic bush on limestone, 100–150 m; known only from the area of the type locality. **I:** Reynolds (1966: 488–490); Castillon & Castillon (2010: 268–269); Carter & al. (2011: 472).

[11] Caulescent, with up to 20 **Br** at the base; stem decumbent, divergent or ascending, to 25 × 0.7–0.9 cm; **Int** 0.5–1 cm; **L** 8–10, distichous in young shoots, becoming spiral to rosulate, persistent to 7 cm below the stem tip, triangular, tip rounded with ±5 soft white cartilaginous prickles, 8–10 × 7–9 cm, dull grey-green with reddish tinge, upper face sometimes with a few small dull white spots towards the base, lower face with many scattered 2 × 1–1.5 mm white spots, **marginal teeth** 1 mm, white, 5–10 mm apart; **Inf** 12–15 cm, simple; raceme cylindrical,

3–5 × 4–5 cm, lax, with 6–8 flowers; **Bra** ovate-acute, 7 × 4 mm, reflexed; **Ped** 6–8 mm; **Fl** scarlet, paler at the mouth, 22 mm, base truncate, 7 mm Ø across the ovary, narrowed to 6 mm above, then enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. milne-redheadii** Christian (J. South Afr. Bot. 6(4): 177–179, t. 18, 1940). **Type:** Angola, Moxico (*Milne-Redhead* 4253 [SRGH, K]). — **Distr:** E Angola (Moxico), NW Zambia (North-West Prov.); ridge of hills, 1220–1375 m. **I:** Reynolds (1966: 110–111); Carter & al. (2011: 439).

[7] Acaulescent or shortly caulescent, suckering to form small to large groups; **L** ±16–20, densely rosulate, ovate-lanceolate, tip acute, to 30 × 7 cm, brownish-green, obscurely lineate, usually with many pale spots, lower face usually with more spots, in wavy transverse bands, **marginal teeth** 3 mm, brownish, 10–15 mm apart; **Inf** 50–90 cm, with 1–7 **Br**; racemes cylindrical-acuminate, 20–25 × 8 cm, subdense; **Bra** ovate-acute, 6 × 3 mm; **Ped** 18 mm; **Fl** scarlet, 30–35 mm, base truncate, 8 mm Ø across the ovary, narrowed above, then enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 1–2 mm.

**A. minima** Baker (Hooker's Icon. Pl. 25: t. 2423 + text, 1895). **Type:** RSA, KwaZulu-Natal (*Evans* 409 [NH]). — **Distr:** Swaziland, RSA.  
≡ *Leptaloe minima* (Baker) Stapf (1933).

**A. minima** var. **blyderivierensis** (Groenewald) Reynolds (J. South Afr. Bot. 13(2): 101, t. 15: fig. 2, 1947). **Type:** RSA, Mpumalanga (*van der Merwe* 38 [PRE 21361]). — **Distr:** RSA (Mpumalanga: Pilgrim's Rest and Graskop areas); grassland. **I:** Reynolds (1950: 118–119); Craib (2006: 88–90); Carter & al. (2011: 114).

≡ *Leptaloe blyderivierensis* Groenewald (1938).

[2] Differs from var. *minima*: **L** 4–6, distichous, slightly broader; **Inf** to 60 cm; **Fl** 12 mm.

**A. minima** var. **minima** — **Distr:** S Swaziland, RSA (Eastern Cape, KwaZulu-Natal, Mpumalanga); grassland, 0–2000 m. **I:** Reynolds

(1950: 118–119); Craib (2006: 85–88); Carter & al. (2011: 114); Wyk & Smith (2014: 346–347).

[2] Acaulescent, simple; **R** fusiform; **L** 6–10, rosulate, linear, 25–35 × 4–6 cm, green, lower face with many slightly tuberculate spots near the base, **marginal teeth** minute, whitish, in the lower ½ only; **Inf** 30–50 cm, simple; raceme capitate, ±3 × 4 cm, dense, with ±15 flowers; **Bra** ovate-acuminate, ± ½ as long as the pedicels; **Ped** 10–20 mm; **Fl** dull pinkish, 10–11 mm, base attenuate, narrowing above the ovary towards the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. miskatana** S. Carter (Nordic J. Bot. 24(3): 245–247, ills., 2006). **Type:** Somalia, Bari Region (*Thulin & al.* 9460 [UPS, K]). — **Distr:** NE Somalia (Al Miskat Mts.); rocky limestone slopes, 1000–1620 m. **I:** Carter & al. (2011: 651).

[8] Caulescent, simple or branching from the base; stem to 2 m, erect, dead leaves not persistent; **L** rosulate, lanceolate-attenuate, 30–36 × 3–7 cm, mid-green with scattered whitish spots, denser on the lower surface, exudate drying pale purplish-brown, smelling of mice, **marginal teeth** forward-pointing, 1 mm, 5–9 mm apart; **Inf** 70 cm, erect, with 7–18 **Br**, lower ones rebranched; racemes cylindrical, 4–12 cm, lax; **Bra** lanceolate, 5 × 2 mm; **Ped** 7 mm; **Fl** pale yellow, greenish towards the mouth, 25–27 mm, 7–8 mm Ø across the ovary, narrowed slightly above; **OTep** free for ±9 mm; **St** exerted 2 mm; **Sty** exerted 6–8 mm.

**A. mitriformis** Miller (Gard. Dict., Ed. 8, no. 1, 1768). **Type:** [lecto — icono]: Dillenius, Hort. Eltham., 21, t. 17: fig. 19, 1732. — **Lit:** Zonneveld (2002); Carter & al. (2011: 601–603); Mottram (2013). **Distr:** RSA (Western Cape, Eastern Cape).

A very variable species, for which several varietal names have been published. Reynolds (1950) did not accept the varieties as distinct, but some subspecies were later recognised by other authors. Jaarsveld & Condy (2013a) present a key to the subspecies, and related species from ser. *Aloe*. Govaerts (2014+) and The Plant List (2013) treat the name as synonym of *A. perfoliata*, but here, Mottram (2013) is followed.

The name *A. parvispina* Schönland was once used for some populations of this taxon, and also for populations of a different taxon that is now treated as ssp. *comptonii*.

**A. mitriformis** ssp. **comptonii** (Reynolds) Zonneveld (Bradleya 20: 10, 2002). **Type:** RSA, Western Cape (*Reynolds* 5725 [PRE]). — **Lit:** Jaarsveld & Condy (2013a: with ills.). **Distr:** RSA (Western Cape, W Eastern Cape); flat stony country, gentle slopes, Table Mountain sandstone quartzite ridges and rock faces, in karroid vegetation, 400–1000 m. **I:** Carter & al. (2011: 602–603); Wyk & Smith (2014: 126–127, as *A. comptonii*).

≡ *Aloe comptonii* Reynolds (1950); **incl.** *Aloe mitriformis* var. *angustior* Lamarck (1784); **incl.** *Aloe perfoliata* var. *brevifolia* Aiton (1789); **incl.** *Aloe brevifolia* Haworth (1804) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe mitriformis* var. *brevifolia* Aiton (1810).

[13] Differs from ssp. *mitriformis*: Stem short, rarely to 1 m; **L** to 30 × 9 cm, exudate drying deep orange, **marginal teeth** 2–3 mm, pale brown from white base; **Inf** 80–100 cm, with 3–5 (–8) **Br**; racemes subcapitate with rounded tip, sometimes broadly conical, to 15 × 9–10 cm; **Bra** 7 × 3 mm; **Ped** lowest 30–35 mm, slightly shorter above; **Fl** 35–40 mm. — **Cytology:** 2n = 14 (Riley 1959: as *A. comptonii*).

**A. mitriformis** ssp. **distans** (Haworth) Zonneveld (Bradleya 20: 10, 2002). **Type:** not typified. — **Distr:** RSA (W Western Cape); shallow soil on limestone rocks near the coast, 0–100 m. **I:** Reynolds (1950: 377–379); Wyk & Smith (2014: 130–131); both as *A. distans*; Carter & al. (2011: 601–602).

≡ *Aloe distans* Haworth (1812).

[13] Differs from ssp. *mitriformis*: Stem less robust and longer; **L** laxly rosulate, **marginal teeth** 3–4 mm, golden-yellow, 5–8 mm apart; **Bra** ±8 × 5 mm; **Ped** 30–40 mm; **Fl** ±40 mm, base rounded. — **Cytology:** 2n = 14 (Brandham 1971: as *A. distans*).

Wyk & Smith (2014) do not accept Zonneveld's new combination, which was based on genome size analysis, and they still accept this taxon at species rank.



**Fig. 48** *Aloe mitrififormis* ssp. *mitrififormis*.  
(Copyright: L. E. Newton)



**A. mitrififormis** ssp. *mitrififormis* — **Distr:** RSA (W Western Cape); usually flat rocky areas on Table Mountain sandstone, also on vertical cliff faces, 500–1200 m. **I:** Reynolds (1950: 372–376, t. 32); Carter & al. (2011: 601); Wyk & Smith (2014: 134–135). — Fig. 48.

**Incl.** *Aloe perfoliata* var.  $\nu$  Linné (1753); **incl.** *Aloe perfoliata* var. *mitrififormis* Aiton (1789); **incl.** *Aloe perfoliata* var.  $\xi$  Willdenow (1799); **incl.** *Aloe mitrififormis* var. *elatior* Haworth (1804); **incl.** *Aloe mitrififormis* var. *humilior* Haworth (1804); **incl.** *Aloe xanthacantha* Salm-Dyck (1854); **incl.** *Aloe parvispina* Schönland (1905).

[13] Caulescent, branching at the base and above, forming dense sprawling groups; stem decumbent, to 2 m  $\times$  6 cm; **L** densely rosulate, ovate-lanceolate, to 20  $\times$  10–15 cm, tip a single or bifid spine, glaucous-green to green, rarely with spots, lower face usually carinate towards the tip, the keel with  $\pm$ 4–6 prickles, exudate drying yellow, **marginal teeth** 4–6 mm, whitish to yellowish, 10–15 mm apart; **Inf** 40–60 cm, with 2–4 **Br**; racemes capitate, 10  $\times$  12 cm, dense; **Bra** lanceolate-acuminate, 10  $\times$  5–6 mm; **Ped** 40–45 mm; **Fl** dull scarlet, 40–45 mm, base attenuate, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted to 2 mm. — **Cytology:**  $2n = 14$  (Riley 1959).

According to Zonneveld (2003) the hybrid *A. mitrififormis* (ssp. *mitrififormis*)  $\times$  *A. brevifolia* (=

*A.  $\times$ notabilis*) is often confused with *A. mitrififormis*.

**A. mitsioana** J.-B. Castillon (Bradleya 24: 69–71, ill., 2006). **Type:** Madagascar, Antsirana (Castillon 23 [HBG, PJ]). — **Distr:** N Madagascar (Antsirana: Mitsio Island); on basalt rocks and nearly vertical cliffs. **I:** Castillon & Castillon (2010: 334–335); Carter & al. (2011: 278).

[5] Acaulescent or with a sort stem, suckering to form small groups; **L** 12–15, rosulate, lanceolate-acuminate, 40–50  $\times$  6–9 cm, green with reddish tinge, **marginal teeth** 2 mm, white to reddish, 3–10 mm apart; **Inf** 40–50 cm, erect, with 2–3 **Br**; racemes capitate, 3–4 cm, subdense, with 30–40 flowers opening first from the top; **Bra** 4  $\times$  3 mm; **Ped** to 32 mm on the upper flowers, lowest flowers almost sessile; **Fl** yellow (buds red), 32 mm, 6 mm  $\varnothing$  across the ovary, widening to 10 mm at the mouth; **OTep** free almost to the base; **St** and **Sty** exerted to 0–1 mm.

**A. mkushiana** T. A. McCoy (Cact. Succ. J. (US) 89(6): 276–279, ill., 2017). **Type:** Zambia, Central Prov. (McCoy 5712 [FT]). — **Distr:** Zambia (Central Prov.: Mkushi Distr.); vertical rock faces, 600 m.

[13] Caulescent, solitary; stem pendulous, 55–100 cm; **L** 9–15, rosulate, pendent, ensiform, falcate, 80–150  $\times$  9–12 cm, glaucous to dark



green, surface slightly rough to smooth, exudate yellowish-orange drying purplish-brown, **marginal teeth** uncinatae, 1–2 mm, reddish-brown, 10–20 mm apart; **Inf** 90–120 cm, pendulous with 3–5 **Br**, branches and racemes ascending; racemes cylindrical-acuminate, 25–45 cm, subdense; **Bra** ovate-acute, 12–16 × 10–12 mm, reddish with 5–7 nerves; **Ped** 12–15 mm; **Fl** bright red, mouth yellow, 28–32 mm, 5–7 mm  $\varnothing$  across the ovary, not narrowed above, slightly carinate, **OTep** free almost to the base; **St** exerted 1.5–2.5 mm; **Sty** exerted 5 mm.

Known from only 2 localities in the Mkushi River Gorge.

**A. mocamedensis** Van Jaarsveld (Bradleya 30: 173–177, ill., 2012). **Type:** Angola, Namibe (*Van Jaarsveld* 22622 [LUB]). — **Distr:** Angola (Namibe); on limestone outcrops and dolerite soil.

[13] Caulescent, solitary or branching to form groups of up to 6 rosettes; stem to 60 cm, decumbent or erect, with dried leaves persistent; **L** to 24, distichous on young plants for several years, later densely rosulate, triangular-ovate, 25–31 × 5.7–10.5 cm, grey- to pinkish-green, exudate yellowish, drying dark brown to black, **marginal teeth** deltoid, pointing towards the leaf apex, 2–4 mm, brownish-black, 4–10 mm apart; **Inf** 75 cm, erect, with up to 7 **Br**; racemes cylindrical-acuminate, 16–23 cm, lax; **Bra** linear-lanceolate, 7–9 × 2 mm; **Ped** 8–10 mm; **Fl** orange-red, 25 mm, 6 mm  $\varnothing$  across the ovary, cylindrical-trigonal, not widened towards the mouth according to the photographs in the protologue; **OTep** free for  $\pm$ 13 mm; **St** exerted 3–4 mm; **Sty** exerted 1–2 mm.

**A. modesta** Reynolds (J. South Afr. Bot. 22(2): 85–86, ill., 1956). **Type:** RSA, Mpumalanga (*Reynolds* 7626 [PRE]). — **Distr:** RSA (Mpumalanga); high-altitude short grassland on stony ground, 1500–1800 m; known only from 2 localities. **I:** Craib (2006: 91–94); Carter & al. (2011: 108); Wyk & Smith (2014: 366–367); Nel (2017).

[2] Acaulescent, simple, with underground ovoid bulb-like swelling 2.5 × 2 cm; **R** fleshy; **L** 4–6, rosulate, linear-acute, 15–20 × 8–9 cm, dull deep green, lower face with many dull green

lenticular spots near the base, **marginal teeth** absent; **Inf** 25–30 cm, simple; raceme subcapitate, slightly conical, 3.5–4 × 3–3.5 cm, dense; **Bra** ovate-acuminate, 10 × 6 mm; **Ped** 1 mm; **Fl** yellowish-green, 13 mm, base rounded, 4 mm  $\varnothing$  across the ovary, not narrowed above; **OTep** free to the base; **St** and **Sty** exerted 4 mm.

Apparently the only African species with fragrant flowers. Nel (2017) reports some variation in the species in different localities.

**A. molederana** Lavranos & Glen (Flow. Pl. Afr. 50(2): t. 1982 + 6 pp. of text, ill., 1989). Somalia, Northern Region (*Lavranos & Horwood* 10379 [PRE]). — **Distr:** N Somalia; gypsum hills and limestone outcrops in low desert scrub,  $\pm$ 1450 m. **I:** Carter & al. (2011: 318).

[5] Acaulescent or shortly caulescent, simple or in small groups; stem to 50 cm; **L** 12–16, rosulate, falcate, 25–40 × 5.5–9.5 cm, glaucous, surface smooth, exudate golden-yellow, **marginal teeth** absent or minute and sparse; **Inf** 40–70 cm, with up to 4 **Br**; racemes subcylindrical, to 16 cm, lax; **Bra** ovate or deltoid, acute, 7–8 × 3–4 mm; **Ped** 6–9 mm; **Fl** pink, tomentose, 24–28 mm, base rounded, slightly narrowed above the ovary; **OTep** free for 9 mm; **St** and **Sty** exerted 3–5 mm.

**A. momccoyae** T. A. McCoy & Lavranos (*Avonia* 33(4): 186, ill. (pp. 184–191), 2015). **Type:** Saudi Arabia, Asir Prov. (*McCoy* 4120 [FT]). — **Distr:** Saudi Arabia (Asir Prov.); rocky slopes, 2700 m.

[3] Acaulescent, solitary; **L** 20–25, rosulate, lanceolate, 30–40 × 15 cm, grey, pruinose, with red margin, surface smooth, exudate light yellow, drying jade-green, **marginal teeth** deltoid, 1.5–2 mm, reddish-orange, 7–10 mm apart; **Inf** 100–120 cm, erect, with 10–15 **Br**, lowermost often rebranched; racemes cylindrical, 35 cm, dense; **Bra** ovate-cuspidate, 12–15 × 5–7 mm, fleshy, yellow with 7–10 brown nerves; **Ped** 6–8 mm; **Fl** bright yellow, finely hirsute, with white hairs, 20–25 mm, 6–7 mm  $\varnothing$  across the ovary, narrowing above to the mouth; **Tep** with white edges; **OTep** with 3–5 bright green nerves, free for 6–8 mm; **St** exerted 3 mm; **Sty** exerted 4 mm.

**A. monotropa** I. Verdoorn (Flow. Pl. Afr. 34 (3–4): t. 1342 + text, 1961). **Type:** RSA, Limpopo (Smuts 1560 [PRE]). — **Distr:** RSA (Limpopo: Dublin Mine Kloof); in the shade of forest fringes on dolomite slopes, 1000–1400 m. **I:** Carter & al. (2011: 178); Wyk & Smith (2014: 252–253).

[5] Caulescent, simple or sometimes suckering; stem  $\pm$  decumbent, to 30 cm; **L**  $\pm$ 20, laxly rosulate, persisting below the stem tip, ovate-lanceolate, long-attenuate,  $\pm 33 \times 6$  cm, green, lineate and with white oblong or H-shaped spots, lower face with spots sometimes in irregular transverse bands, **marginal teeth**  $\pm 2$  mm, brown-tipped; **Inf**  $\pm 80$  cm, with  $\pm 6$  **Br**, lower ones rebranched; terminal raceme cylindrical,  $\pm 10$ – $20$  cm, lateral racemes with flowers secund, 6–18 cm, lax; **Bra** deltoid-acuminate,  $6 \times 2.5$  mm; **Ped** 7–11 mm; **Fl** old rose with light bloom,  $\pm 30$  mm, base truncate, 5 mm  $\varnothing$  across the ovary, abruptly narrowed above, then enlarging to the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm.

The only member of the *A. maculata* group with secund flowers. Yellow-flowered plants are also reported (Dyer & Hardy 1969).

**A. monticola** Reynolds (J. South Afr. Bot. 23(1): 7–9, tt. 7–8, 1957). **Type:** Ethiopia, Tigray Prov. (Reynolds 8118 [PRE, EA, K]). — **Distr:** N Ethiopia (Tigray Region); steep bare volcanic mountain slopes, 2250–2550 m. **I:** Reynolds (1966: 281–282); Sebsebe Demissew & Nordal (2010: 76–77); Carter & al. (2011: 378).

[5] Acaulescent or very shortly caulescent, usually simple; **L** 24 or more, densely rosulate, lanceolate-attenuate,  $60$ – $70 \times 14$ – $16$  cm, glossy olive-green, with prominent brown horny margin, exudate drying brownish, **marginal teeth** 6 mm, pungent, pale brown, 10–15 mm apart; **Inf** 1 m, with  $\pm 8$  **Br**; racemes subcapitate,  $6$ – $8 \times 8$  cm; **Bra** lanceolate-attenuate,  $15$ – $20 \times 6$ – $7$  mm, imbricate in bud stage; **Ped** 15–20 mm; **Fl** usually yellow, sometimes scarlet, 38 mm, base rounded, 8 mm  $\varnothing$  across the ovary, slightly narrowed above; **OTep** free for 14 mm; **St** exerted 5–6 mm; **Sty** exerted 8 mm. — **Cytology:**  $2n = 14$  (Fentaw & al. 2013).

**A. montis-nabro** Orlando & El Azzouni (CactusWorld 32(3): 201–202, ills. (pp. 201–203), 2014). **Type:** Eritrea (Orlando & El Azzouni 222603 [FT]). — **Distr:** S Eritrea (Southern Red Sea Region: Nabro volcano); on pumice plains, 725 m; known only from the area of the type locality.

[5] Caulescent, branching to form small groups of 2–6 rosettes; stem short, procumbent, with dried leaves persistent; **L** 30–40, densely rosulate, lanceolate-attenuate,  $35$ – $40 \times 5$ – $6$  cm, olive-green, with many whitish elongated spots, sometimes confluent into lines, denser on the lower surface, **marginal teeth** pungent, 3–5 mm, brown-tipped, 10–20 mm apart; **Inf** 1.8 m, erect, with up to 15 **Br**, lowermost rebranching; racemes cylindrical, 12–15 cm, lax; **Bra** acute,  $7 \times 3$  mm; **Ped** 12–14 mm; **Fl** light coral-red, minutely spotted, 20–25 mm, 6–7 mm  $\varnothing$  across the ovary, scarcely narrowed above towards the mouth; **OTep** free for  $\pm 7$ – $8$  mm; **St** and **Sty** exerted 3 mm.

**A. morijensis** S. Carter & Brandham (Cact. Succ. J. Gr. Brit. 41(1): 3–4, ills., 1979). **Type:** Kenya, Rift Valley Prov. (Bally 17021 [K]). — **Distr:** Kenya, Tanzania.

**A. morijensis** var. **morijensis** — **Distr:** SW Kenya, N Tanzania: hills of the W Rift Valley Escarpment; dry bush, and soil pockets on rocky slopes, 2400–2440 m. **I:** Reynolds (1950: 372–376, t. 32); Carter & al. (2011: 543).

[14] Caulescent, branching mostly at the base; stem suberect and spreading, to  $1 \text{ m} \times 1.5 \text{ cm}$ ; **L** scattered along the stem, ovate-attenuate, to  $17 \times 3$  cm, bright green with a few elongated pale spots, lower face darker green with more spots, surface smooth, exudate absent, **marginal teeth** 2–5 mm, green to brownish, 5–15 mm apart, leaf sheath to 2 cm, striate, internally fibrous; **Inf** to 50 cm, simple or sometimes with 1–2 **Br**; racemes conical-acuminate, to  $20 \times 6$  cm; **Bra** ovate-deltoid, aristate, to  $15 \times 8$  mm; **Ped** 20 mm; **Fl** orange-scarlet becoming yellow towards the tip, 28 mm, base attenuate, 6 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to 7 mm at the mouth; **OTep** free for 7 mm; **St** and **Sty**

exserted 0–1 mm. — **Cytology**:  $2n = 14$  (Cutler & al. 1980).

**A. morijensis** var. **ojonokae** Uleh (Cactus-World 33(2): 124, ills. (pp. 123–124), 2015). **Type**: Kenya, Nairobi County (*Uleh* 002 [EA]). — **Distr**: Kenya; rocky outcrop and edge of rocky gorge, 1650–1860 m.

[12] Differs from var. *morijensis*: Erect, shrubby; stem 1–2 cm  $\varnothing$ ; **L** laxly rosulate, 8–12  $\times$  1.5–3 cm, uniformly green; **Inf** 64 cm, with 2–4 **Br**; racemes 25 cm; **Fl** 35 mm. — **Cytology**:  $2n = 14$  (protologue).

**A. mossurilensis** Ellert (Alsterworthia Int. 10(1): 6, 2010). **Type**: Moçambique, Nampula Prov. (*Ellert* 43 [UA]). — **Distr**: NE Moçambique (Nampula Prov.); coastal woodland, near sea level. **I**: Carter & al. (2011: 707).

[11] Caulescent, suckering at the base to form groups of 50–60 rosettes; stem erect, 40–60  $\times$  1–4 cm; **L** 25–50, rosulate and persistent for 30–40 cm below, lanceolate-attenuate, 30–40  $\times$  3–5 cm, green/olive-green to pinkish-brown with pinkish-white to whitish-green elliptic spots in irregular transverse bands, surface smooth, exudate clear, drying dull yellow-green, **marginal teeth** deltoid, 3–5 mm, brownish-red or pinkish-white, 6–15 mm apart, leaf sheath 2–3 cm, pale green to pale pinkish-brown, striated; **Inf** to 1.6 m, erect, with up to 7 **Br**; racemes cylindrical, 9 cm, lax; **Bra** ovate-acute, 17  $\times$  12 mm; **Ped** 16 mm; **Fl** coral-pink to pale pinkish-brown, 30 mm, 8 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, enlarging to 12–13 mm at the mouth; **OTep** free for 10 mm; **St** exserted 5–6 mm; **Sty** exserted 1–2 mm.

The name was first published invalidly (ICN Art. 8.2) by Ellert (2008).

**A. mottramiana** J.-B. Castillon (CactusWorld 29(4): 218–219, ills., 2011). **Type**: Madagascar, Toliara (*Castillon* 51 [TAN]). — **Distr**: S Madagascar (Toliara); rocky areas.

[7] Acaulescent or with stem to 5 cm, suckering freely; **L** rosulate, triangular, 20–35  $\times$  3–5 cm, greenish-blue to brown, surface pustulate, exudate yellow-green, **marginal teeth** 1–2 mm, reddish, 2–3 mm apart; **Inf** 60 cm, erect, with 3–5 **Br**;

racemes cylindrical, 15–28 cm, lax; **Bra** triangular, 2  $\times$  1 mm, fleshy; **Ped** 8–10 mm; **Fl** red, 22 mm, 4 mm  $\varnothing$  across the ovary, slightly narrowed above, widening to the mouth; **OTep** free to the base; **St** not exserted; **Sty** exserted 2–3 mm.

**A. mubendiensis** Christian (J. South Afr. Bot. 8(2): 172–173, t. 5, 1942). **Type**: Uganda, Toro Distr. (*Pole-Evans & Erens* 1685 [SRGH, K, PRE]). — **Distr**: W Uganda (Toro Distr.); granite outcrops, 1220–1370 m. **I**: Reynolds (1966: 260–261); Carter & al. (2011: 442); Cole & Forrest (2017: 100–103).

[7] Acaulescent or shortly caulescent, suckering to form large groups; **L**  $\pm 16$ , densely rosulate, lanceolate, 30–35  $\times$  6.5 cm, dull grey-green, obscurely lineate, sometimes with a few elongated lenticular whitish spots, rarely on the lower face, with slight pinkish cartilaginous margin, exudate drying yellowish, **marginal teeth** 3–4 mm, reddish-brown, paler tipped, 10–15 mm apart; **Inf** 70–90 cm, with 8 **Br**, lower ones sometimes rebranched; racemes cylindrical, laterals with secund flowers,  $\pm 10 \times 6$ –7 cm, subdense; **Bra** ovate-acuminate, 3–4  $\times$  2–3 mm; **Ped** 10 mm; **Fl** dark brick-red, paler at the mouth, 30 mm, base rounded, 7 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for 8–9 mm; **St** and **Sty** exserted 4 mm.

**A. mudenensis** Reynolds (J. South Afr. Bot. 3(1): 39–42, t. 1, 1937). **Type**: RSA, KwaZulu-Natal (*Reynolds* 2029 [PRE, BOL]). — **Distr**: RSA (N KwaZulu-Natal), Swaziland; dry scrub and open savanna or Grassveld vegetation in warm valleys, 500–1700 m. **I**: Reynolds (1950: 245–246, t. 15); Carter & al. (2011: 170); Wyk & Smith (2014: 254–255).

[5] Caulescent, simple or in small groups; stem erect or decumbent, to 80  $\times$  10 cm; **L**  $\pm 20$ , densely rosulate, lanceolate-attenuate, 25–30  $\times$  8–9 cm, bluish-green with many scattered white oblong spots, sometimes lineate, lower face paler, sometimes with oblong dull white spots irregular or  $\pm$  in transverse bands, lineate, exudate drying reddish-purple, **marginal teeth** to 7 mm, pungent, brown, 10–20 mm apart; **Inf** to 1 m, with 4–8 **Br**;

racemes subcapitate,  $\pm 12 \times 8-9$  cm, subdense; **Bra** deltoid-acuminate, usually slightly  $> \frac{1}{2}$  as long as the pedicels; **Ped** 20–25 mm; **Fl** salmon-orange, sometimes reddish, 35 mm, base truncate, 8 mm  $\varnothing$  across the ovary, abruptly narrowed to 5 mm above, then enlarging to the mouth; **OTep** free for 9 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Riley 1959).

Natural hybrids with *A. spectabilis* have been reported (Reynolds 1950: under *A. marlothii*).

**A. multicolor** L. E. Newton (Brit. Cact. Succ. J. 12(2): 51–52, ill., 1994). **Type**: Kenya, Eastern Prov. (Newton & al. 4133 [K, EA]). — **Distr**: N Kenya (Eastern Prov.: Mt. Kulal and Forole Mt.); open dry bush and among rocks, 1530–1800 m. **I**: Carter & al. (2011: 622).

[12] Caulescent, branching at the base; stem erect to 1 m, then becoming decumbent, to 2 m; **L** rosulate and persistent for  $\pm 20$  cm below, triangular,  $36-70 \times 6.5-10$  cm, mid-green, often with red tinge when exposed, lower face with white spots near the base, mostly in longitudinal rows near the midline, surface smooth, exudate yellow, **marginal teeth** to 4 mm, firm, brown-tipped, 8–10 mm apart; **Inf** 60–75 cm, with 5–8 **Br**, lower ones sometimes rebranched; racemes cylindrical, 5–11 cm, subdense; **Bra** ovate-acute,  $10-11 \times 6-7$  mm, whitish; **Ped** 11–12 mm; **Fl** crimson at the base, outer lobes crimson with orange-red margins, inner lobes yellow with white margins, 22–25 mm, clavate, base shortly attenuate, 4–5 mm  $\varnothing$  across the ovary, narrowed to 3.5–4 mm above, then enlarging to 7 mm and narrowing again to 5 mm at the mouth; **OTep** free for  $\pm 14$  mm; **St** and **Sty** exerted 4–6 mm.

**A. munchii** Christian (Flow. Pl. Afr. 28: t. 1091 + text, 1951). **Type**: Zimbabwe, Manicaland Prov. (Munch 2 [SRGH]). — **Distr**: W Moçambique (Manica), E Zimbabwe (Manicaland Prov.): Chimanimani Mts.; woodland on mountain slopes, rock outcrops, 1525–2135 m. **I**: Reynolds (1966: 320–322); Carter & al. (2011: 682).

[9] Caulescent, simple or sparingly branched, usually without persistent dead leaves; stem erect, to 5 m; **L**  $\pm 24-30$ , densely rosulate, ensiform, 50

$\times 6-8$  cm, dull grey-green with reddish tinge, with pinkish cartilaginous margin, **marginal teeth** 1–1.5 mm, pinkish, 10–15 mm apart; **Inf** 60 cm, with 2–3 **Br**; racemes conical-capitate,  $10-12 \times 14$  cm, dense; **Bra** ovate-cuspidate,  $14 \times 10-12$  mm; **Ped** 35–40 mm; **Fl** scarlet or orange, 45 mm, base very shortly attenuate, 7–8 mm  $\varnothing$  across the ovary, enlarging slightly to the mouth; **OTep** free to the base; **St** and **Sty** exerted 2–5 mm.

**A. murina** L. E. Newton (Taxon 41(1): 31–33, ill., 1992). **Type**: Kenya, Rift Valley Prov. (Newton 3497 [K, EA]). — **Distr**: Kenya (Masai Distr.: Nguruman Escarpment); soil pockets on rock slopes in deciduous woodland, 1500 m; known only from the region of the type locality. **I**: Carter & al. (2011: 324).

[3] Acaulescent or shortly caulescent, simple; stem prostrate, to 15 cm; **L** 15–20, rosulate, lanceolate,  $30-40 \times 5-10$  cm, dark green, tinged reddish when exposed, surface rough, exudate very pale yellow, **marginal teeth** 2–3 mm, pungent, brown, 7–12 mm apart; **Inf** to 1 m, with up to 13 **Br**; racemes with secund flowers, 5–20 cm, lax; **Bra** triangular,  $6 \times 2$  mm; **Ped** 11 mm; **Fl** dull brownish-red with heavy white bloom, appearing reddish-grey, 25 mm, base shortly attenuate, 8 mm  $\varnothing$  across the ovary, narrowed to 7 mm above; **OTep** free for 8–11 mm; **St** and **Sty** exerted 2–4 mm.

Originally known from the type locality only and thought to be rare, but since then, several additional populations have been found along the escarpment, not far from the type locality.

**A. musapana** Reynolds (J. South Afr. Bot. 30(3): 125–126, t. 22, 1964). **Type**: Zimbabwe, Manicaland Prov. (Bullock 36/1 [SRGH, K, PRE]). — **Distr**: E Zimbabwe (Manicaland Prov.: Chimanimani Mts.); steep rock faces, 1905–2060 m. **I**: Reynolds (1966: 21–22); Carter & al. (2011: 133).

[10] Caulescent, branching at the base or higher, forming dense groups; stem mostly pendulous, to  $20 \times 1$  cm; **L**  $\pm 10$ , distichous, linear-acute,  $30-40 \times 1.5$  cm, dark green, sometimes with a few white spots near the base, lower face

with many dirty-white lenticular spots near the base, **marginal teeth** minute, cartilaginous, white, near the base only; **Inf** 30–40 cm, simple; raceme cylindrical-acuminate, 15 × 6 cm, sub-dense; **Bra** ovate-acute, 10 × 6 mm; **Ped** 20 mm; **Fl** scarlet, sometimes bright orange, pale green at the mouth, 28–30 mm, base rounded, 6 mm  $\varnothing$  across the ovary, enlarging above to the mouth; **OTep** free to the base; **St** and **Sty** exerted 1–2 mm.

**A. mutabilis** Pillans (South Afr. Gard. 23: 168, 1933). **Type:** RSA, Limpopo (*van Balen* s.n. [BOL 20477]). — **Distr:** RSA (Gauteng, Mpumalanga, Limpopo, North-West Prov.); steep to vertical rock faces, 1200–1900 m. **I:** Reynolds (1950: 418–419); Carter & al. (2011: 523); Wyk & Smith (2014: 98–99).

[13] Caulescent, simple or branching; stem procumbent or pendulous, to 1 m × 10–15 cm; **Ros** upturned; **L** densely rosulate, lanceolate, sometimes falcate, 60–70 × 8–9 cm, glaucous green to dull green, obscurely lineate, with narrow pale brownish-yellow margin, **marginal teeth** ± 2 mm, firm, pale yellow to orange-yellow, 15–25 mm apart; **Inf** 60–90 cm, arcuate-erect, usually simple or with 1–2 **Br**; racemes conical, 25–30 cm, dense; **Bra** oblong-obtuse, ±13 × 5 mm; **Ped** 20–25 mm; **Fl** scarlet in bud, becoming greenish-yellow to yellow at anthesis, 30–35 mm, base shortly attenuate, enlarging above the ovary towards the mouth; **OTep** free to the base; **St** and **Sty** exerted 5–8 mm. — **Cytology:** 2n = 14 (Müller 1941).

Often considered to represent merely a highland form of *A. arborescens* (Wyk & Smith 2014).

**A. myriacantha** (Haworth) Schultes & Schultes *fil.* (Syst. Veg. 7(1): 704, 1829). **Type:** [neo — icono]: K [unpubl. drawing]. — **Distr:** Burundi, Rwanda, Kenya, Tanzania, Uganda, Democratic Republic of the Congo [Zaire], Zimbabwe, Malawi, RSA (S Eastern Cape, E KwaZulu-Natal, Limpopo, Mpumalanga), Swaziland; rocky montane grassland, 0–2630 m. **I:** Reynolds (1950: 116–117); Reynolds (1966: 6–9); Craib (2006: 94–98); Carter & al. (2011: 115); Klopper & al. (2012: 83, 88, incl.

distribution map); Wyk & Smith (2014: 348–349); Cole & Forrest (2017: 104–107).

≡ *Bowiea myriacantha* Haworth (1827) ≡ *Leptaloe myriacantha* (Haworth) Stapf (1933); **incl.** *Aloe johnstonii* Baker (1887); **incl.** *Aloe caricina* A. Berger (1905); **incl.** *Aloe graminifolia* A. Berger (1905).

[1] Acaulescent, simple or suckering to form small groups; **R** fusiform, from a corm-like base; **L** 8–12, rosulate, linear, 25 × 0.8–1 cm, dull green with a few white spots near the base, lower face with more spots near the base, the spots tuberculate, almost spinulescent, **marginal teeth** minute, white, more distant or obsolescent towards the leaf tip; **Inf** 20–25 cm, simple; raceme capitate, ±4.5 × 6 cm, dense, with 20–30 flowers; **Bra** ovate-acuminate, 15 mm; **Ped** 15 mm; **Fl** mostly dull reddish-pink, rarely greenish-white, 20 mm, base attenuate, not or slightly narrowed above the ovary, mouth bilabiate; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

The most widespread species in the genus, from Kenya and Uganda S-wards to RSA.

**A. mzimbana** Christian (Flow. Pl. South Afr. 21: t. 838 + text, 1941). **Type:** Malawi, Northern Prov. (*Pole-Evans & Erens* 643 [PRE]). — **Distr:** SW Tanzania, SE Democratic Republic of the Congo [Zaire], NE Zambia, N Malawi; granite rock outcrops in woodland, 1280–2300 m. **I:** Reynolds (1966: 112–113); Lane (2004: 21–23); Carter & al. (2011: 421); Klopper & al. (2012: 84, 88, incl. distribution map). — Fig. 49.

[7] Acaulescent or shortly caulescent, suckering to form dense groups; **L** ±20, densely rosulate, deltoid-ovate-lanceolate, 20–45 × 7–8 cm, greyish-green, obscurely striate, sometimes with a few scattered spots, with reddish-pink margin, exudate drying yellow, **marginal teeth** 2–4 mm, reddish-pink, 8–10 mm apart; **Inf** 30–80 cm, simple or with 2–8 **Br**; racemes cylindrical, 8–15 cm, dense; **Bra** ovate-lanceolate, 6–10 × 3–4 mm, fleshy; **Ped** 15–20 mm; **Fl** coral-red to scarlet, 35 mm, base attenuate, 8 mm  $\varnothing$  across the ovary, narrowed to 6 mm above, then enlarging to the mouth; **OTep** free for 12 mm; **St** and **Sty**





**Fig. 49** *Aloe mzimbana*. (Copyright: L. E. Newton)

exserted 2 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

**A. namibensis** Giess (Mitt. Bot. Staatssamml. München 8: 123–126, 1970). **Type:** Namibia, Swakopmund (*Giess* 9212 [WIND, M]). — **Distr:** NW Namibia (Swakopmund: Khan River valley); granite outcrops in arid desert with night fogs, 600–1200 m. **I:** Carter & al. (2011: 340).

[3] Acaulescent, simple; **L** densely rosulate, lanceolate, to  $50 \times 7$  cm, glaucous, surface slightly rough, **marginal teeth** to 2 mm, pale, 1 mm apart; **Inf** to 95 cm, with 2–4 **Br**; racemes cylindrical-acuminate, to  $45 \times 6$  cm, dense; **Bra** ovate-lanceolate, to  $35 \times 14$  mm; **Ped** to 3 mm; **Fl** coral-pink with green tips, to 30 mm, sub-cylindrical; **OTep** free to the base; **St** and **Sty** exserted 7–12 mm.

Jaarsveld (2010) recorded the taxon from SW Angola, but his illustrations show plants with lax (rather than dense) inflorescences, and his identification is thus questionable.

**A. namorokaensis** (Rauh) L. E. Newton & G. D. Rowley (*Bradleya* 16: 114, 1998). **Type:** Madagascar, Mahajanga (*Rauh* 72140 [HEID]). — **Distr:** W Madagascar (S Mahajanga: Reserve Naturelle Namoroka); humid cracks in limestone rocks. **I:** Rauh (1998: 99, as *Lomatophyllum*); Castillon & Castillon (2010: 305); Carter & al. (2011: 253).

≡ *Lomatophyllum namorokaense* Rauh (1998).

[2] Acaulescent or shortly caulescent; **L**  $\pm 9$ , laxly rosulate, lanceolate,  $25\text{--}35 \times 3$  cm, dark green with narrow reddish margin, **marginal teeth** deltoid, 2 mm, 6–10 mm apart, leaf sheath 3 cm; **Inf** 30 cm, simple; raceme 10 cm, subdense; **Bra** to 10 mm, reddish; **Ped** 10 mm; **Fl** bright cinnabar-red, 25–30 mm, slightly curved, constricted above the ovary, then enlarging again; **OTep** free to the base; **St** and **Sty** exserted 0–1 mm; **Fr** berries, 15 mm.

**A. neilcrouchii** Klopper & Gideon F. Smith (*Bothalia* 40(1): 94–95, *ills.*, 2010). **Type:** RSA, KwaZulu-Natal (*Crouch & Johnson* 1247 [PRE, NH]). — **Lit:** Smith & al. (2011); Wyk & Smith (2014: 326–327). **Distr:** RSA (C KwaZulu-Natal); SE facing slopes of rocky grassland, 1000–1800 m.

[13] Caulescent, branching at the base and along decumbent stems; stem to  $95 \times 9$  cm, decumbent to erect; **L**  $> 20$ , densely rosulate, deciduous, deltoid to ovate-lanceolate, to  $43 \times 13.5$  cm, green with numerous elongated white somewhat tuberculate spots, exudate clear, **marginal teeth** deltoid, 1–2 mm, whitish, 2–5 mm apart; **Inf** 60–80 cm, erect, simple; racemes capitate,  $12 \times 10$  cm, dense; **Bra** lanceolate-acuminate,  $30 \times 7$  mm, subscariosus to almost fleshy, whitish, with many nerves; **Ped** 30–45 mm, pale yellowish to salmon-pink; **Fl** salmon-pink, green-tipped, 45 mm, 10–13 mm  $\varnothing$  across the ovary, narrowed above to 8–10 mm, then constricted to  $\pm 7$  mm below the mouth; **OTep** free almost to the base; **St** not or slightly exserted; **Sty** exserted  $\pm 5$  mm.

**A. neoqaharensis** T. A. McCoy (*Excelsa* 21: 5, *ills.* (pp. 3–4), 2007). **Type:** Saudi Arabia, Asir

Prov. (McCoy 2144 [MO]). — **Distr:** Saudi Arabia (S Asir Prov.: Jabal Qahar); on limestone, 2100 m; known only from the type locality. **I:** Carter & al. (2011: 582).

[12] Caulescent, branching from the base; stem to 220 × 6 cm; **L** 14–20, crowded at the stem apex, lanceolate-attenuate, 50–60 × 7–8 cm, dull grey-green, spotted on the lower surface near the base, **marginal teeth** 2 mm, white, 10 mm apart; **Inf** 1.4 m, erect, with 1–2 **Br**; racemes cylindrical, to 50 cm, subdense; **Bra** ovate-acute, 2 × 3 mm; **Ped** 1 mm; **Fl** reddish-orange, 30 mm, 8 mm Ø across the ovary; **OTep** free for 10 mm; **St** and **Sty** exerted 3 mm.

**A. neosteudneri** Lavranos & T. A. McCoy (Bradleya 25: 15, ills. (pp. 11, 14), 2007). **Type:** Eritrea (*Penzig* 1424 [K]). — **Distr:** Eritrea (Jebel Saber); rocky slopes, 2400–2500 m; known only from the type locality. **I:** Carter & al. (2011: 285).

[16] Caulescent, usually solitary, sometimes branching with 2–3 **Ros**; stem to 30 cm; **L** to 35, rosulate, 40–60 × 8–12 cm, bluish- or glaucous-green, lineate, exudate drying yellowish-brown, **marginal teeth** soft, 1–2 mm, 7–9 mm apart; **Inf** 70–90 cm, erect, simple or with up to 4 **Br**; racemes cylindrical-conical, 12–35 cm, sublax; **Bra** ovate-deltoid, 10–13 × 5–8 mm; **Ped** 10–18 mm; **Fl** pinkish-red, 36–38 mm, 5–7 mm Ø across the ovary; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. newtonii** J.-B. Castillon (Bradleya 27: 152, ills. (p. 151), 2009). **Type:** Madagascar, Fianarantsoa (*Reynolds* 7885 [TAN, K, PRE]). — **Lit:** Carter & al. (2011: 708). **Distr:** Madagascar (Fianarantsoa); flat rocks on an inselberg, 900–1200 m. **I:** Reynolds (1966: 502, as *A. intermedia*).

[11] Caulescent, suckering freely; stem erect or procumbent, to 100 × 2–4 cm, with dried leaves persistent; **L** 15–25, rosulate, lanceolate-attenuate, 15–35 × 3–5 cm, dull green, bluish- or red-tinged, surface smooth, exudate light yellow-brown, drying brown, **marginal teeth** 3–4 mm, reddish-brown, 5–10 mm apart; **Inf** 50–70 cm, erect, with 2–4 **Br**; racemes cylindrical-acuminate, 10–15 cm, semidense;

**Bra** lanceolate-acute, 15–20 mm; **Ped** 15–20 mm; **Fl** red, 30 mm, base attenuate, 5 mm Ø across the ovary, slightly narrowed above, widening to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 0–2 mm.

Castillon (2009c) believes that the plant on which Reynolds based his description of his *A. intermedia* (an illegitimate name, subsequently renamed *A. subacutissima* by Rowley) was not identical to Perrier's *A. deltoideodonta* var. *intermedia*, the type locality of which was not visited by Reynolds. Carter & al. (2011) suggested that *A. newtonii* matches Perrier's var. *intermedia* apart from the presence of a stem, and it was noted that Perrier did not mention stems in his protologue. However, some other differences were given by Castillon, and as Perrier was describing a new variety of a species that is acaulescent it could be assumed that his new variety has the same growth habit as the type, i.e. also acaulescent, since the diagnosis of an infraspecific taxon usually includes only the differences from the type of the species. Fresh material from the type locality of Perrier's var. *intermedia* is needed to resolve the question finally.

**A. ngongensis** Christian (J. South Afr. Bot. 8(2): 170–172, t. 4, 1942). **Type:** Kenya, Rift Valley Prov. (*Pole-Evans & Erens* 1129 [SRGH, EA, PRE]). — **Distr:** S Kenya, N Tanzania: Rift Valley region; rocky ground in open woodland or at the edge of thickets, 1370–1900 m. **I:** Reynolds (1966: 366–367, as *A. rabaiensis*); Carter & al. (2011: 636). — Fig. 50.

[16] Caulescent, branching at the base; stem erect, to 1.5 m; **L** laxly rosulate and persistent below the stem tip, lanceolate-attenuate, 30–60 × 5–10 cm, bluish-green, sometimes tinged purplish, surface smooth, exudate brown, **marginal teeth** 3–4 mm, brown-tipped, 5–10 mm apart; **Inf** to 60 cm, with 6–8 **Br**, lower ones sometimes rebranched; racemes subcapitate, ±6 × 8 cm, dense; **Bra** lanceolate, 7–10 × 3 mm, pale brown; **Ped** 10–20 mm; **Fl** bright glossy scarlet, yellowish at the mouth, 25–30 mm, base shortly attenuate, 8 mm Ø across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for <math>\frac{1}{3}</math>; **St** and **Sty** exerted 3 mm. —

**Fig. 50** *Aloe ngongensis*.  
(Copyright: L. E. Newton)



**Cytology:**  $2n = 14$  (Cutler & al. 1980: as *A. rabaiensis*).

Reynolds (1966) included this taxon in *A. rabaiensis*. Hybrids with *A. secundiflora* and possibly also with *A. volkensii* ssp. *multicaulis* are reported (Newton 1998a).

**A. nicholsii** Gideon F. Smith & N. Crouch (Bradleya 28: 103–106, ills., 2010). **Type:** RSA, KwaZulu-Natal (Crouch 1270 [PRE, NH]). — **Lit:** Crouch & al. (2011). **Distr:** RSA (KwaZulu-Natal: KwaZulu-Natal Midlands); rocky grassland, 1290 m; known only from the region of the type locality. **I:** Wyk & Smith (2014: 328–329).

[1] Shortly caulescent, solitary or usually suckering with up to 40 **Ros**; stem 6–14 cm; **L** 9–15, distichous, becoming semirosulate, narrowly linear-attenuate, 20–46 × 2–5.3 cm, mid-green to light yellowish-green, sometimes with few scattered white spots near the base, surface smooth, **marginal teeth** absent or <0.5 mm, ivory-coloured to greenish-white, 5–10 mm apart; **Inf** 30–46 cm, erect, simple; raceme capitate, 3–3.5 cm, dense; **Bra** 10–26 mm; **Ped** 25–30 mm; **Fl** salmon-pink, green towards the mouth, 13–16 mm, 5 mm Ø across the ovary; **OTep** free almost to the base; **St** and **Sty** exerted 0–1 mm.

The flower colour is taken from the colour photo in the protologue (repeated by Wyk &

Smith (2014)) and differs from the original description, where the tepal tips are described as purplish-brown.

**A. niebuhriana** Lavranos (J. South Afr. Bot. 31(1): 68–71, t. 13, 1965). **Type:** Yemen (*Rauh & Lavranos* 3159 [PRE, K]). — **Distr:** Yemen (W Aden hinterland, S Tihama); rocky hills and sand banks, 250–500 m. **I:** Reynolds (1966: 121–123); Carter & al. (2011: 426).

[4,6] Acaulescent or shortly caulescent, simple on rocky ground, or suckering freely forming dense groups on sandy soil; stem decumbent; **L** 15–25, rosulate, lanceolate-attenuate, to 45 × 10 cm, grey-green tinged purplish, **marginal teeth** 1.5–2 mm, dark brown, 12–15 mm apart; **Inf** 50–100 cm, usually simple, sometimes with 1–2 **Br**; racemes conical, 12–30 × 5–6 cm, dense; **Bra** deltoid-acute, 8 × 3–4 mm; **Ped** 4–6 mm; **Fl** scarlet tipped greenish-yellow, rarely all greenish-yellow, usually shortly pubescent, 28–31 mm, base shortly attenuate, 6–7 mm Ø across the ovary, not narrowed above; **OTep** free for 19–21 mm; **St** and **Sty** exerted 3–4 mm.

**A. niensiensis** L. E. Newton (CactusWorld 33(1): 51–52, ills. (pp. 50–52), 2015). **Type:** Tanzania, Tabora Region (*Roberts* 55 [EA]). — **Distr:** Tanzania (Tabora Region: Urambo Distr.); no ecological details given by the collector; known only from the type locality.



[13] Caulescent, suckering to form small groups; stem to 30 cm, decumbent, with dried leaves persistent; **L** to 20, rosulate, lanceolate-attenuate, 15 × 5.5 cm, mid-green with numerous pale green spots in irregular transverse rows, surface smooth, exudate yellow, **marginal teeth**, 4 mm, brown-tipped, 6–8 mm apart; **Inf** 85 cm, suberect to oblique, with up to 7 **Br**, lowermost often rebranched; racemes cylindrical with secund flowers, to 22 cm, lax; **Bra** ovate-attenuate, 4 × 2.5 mm; **Ped** 6–7 mm; **Fl** red, becoming paler or whitish towards the mouth, 28 mm, base truncate, 5 mm Ø across the ovary, narrowed slightly to 4 mm above, widening to 6 mm at the mouth; **OTep** free for 10 mm; **St** exerted 4 mm; **Sty** exerted 2 mm.

**A. nigrimontana** T. A. McCoy & Lavranos (CactusWorld 33(3): 183, ill. (pp. 182–184), 2015). **Type:** Somalia, Sanaag Region (McCoy 3112 [FT]). — **Distr:** Somalia; limestone cliff faces, 1825 m.

[13] Caulescent, pendulous, usually branching from the base; stem to 125 × 4.5 cm; **L** rosulate and persistent below the stem apex, deltoid-acuminate, to 35 × 8.5 cm, grey-green, exudate light yellow, drying purplish-brown, **marginal teeth** 4–5 mm, red, white-tipped; **Inf** 60 cm, erect, with up to 15 **Br**; racemes cylindrical, 30 cm, subdense; **Bra** deltoid-acuminate, 5 × 3 mm, scarious, white with 3–5 brown nerves; **Ped** 12–16 mm, dark purplish-pink; **Fl** dull purplish with pruinose waxy bloom, 38–42 mm, lobes minutely pustulate, base shortly stipitate, 10 mm Ø across the ovary, scarcely narrowed above; **OTep** free for 10 mm; **St** exerted 6 mm; **Sty** exerted 10 mm.

**A. ×nobilis** Haworth *pro sp.* (Synops. Pl. Succ., 78, 1812). **Type:** [neo — icono]: Salm-Dyck, Monogr. Aloes Mesembr. 24: fig. 7, 1863. — **Lit:** Smith & Figueiredo (2015: with ill.). **Distr:** Cultivated only.

**Incl.** *Aloe mitriformis* var. *spinosior* Haworth (1804); **incl.** *Aloe brownii* Baker (1889).

Shortly caulescent, branching profusely from the base, forming a dense mound of rosettes on the ground; **L** ±20–40, rosulate, lanceolate-

triangular, 12–15 × 5–5.5 cm, dark green, surface with scattered teeth, esp. on the lower surface, **marginal teeth** 5 mm, white, 8 mm apart; **Inf** 80 cm, erect, simple or with 1 **Br**; racemes cylindrical-conical, to 20 cm, semidense; **Bra** triangular-acute, 14 × 6 mm; **Ped** 25–30 mm; **Fl** red, yellow at the mouth, 40 mm, 6 mm Ø across the ovary, to 8 mm above, narrowing at the mouth; **OTep** free for ±10 mm; **St** and **Sty** exerted 2–4 mm.

Parentage uncertain, possibly *A. mitriformis* × *A. brevifolia* (Smith & Figueiredo 2015). Not known to occur in the wild in South Africa, but widely cultivated in Mediterranean Europe, and locally naturalized, at least in Portugal.

**A. nubigena** Groenewald (Tydskr. Wetensk. Kuns 14: 135–137, 1936). **Type:** RSA, Mpumalanga (*van der Merwe* 133 [PRE]). — **Distr:** RSA (Mpumalanga: Drakensberg Escarpment: Graskop area); shaded rock faces in the mist belt, often in the spray zones of waterfalls, 1500–2100 m. **I:** Reynolds (1950: 132); Craib (2006: 98–101); Carter & al. (2011: 122); Wyk & Smith (2014: 330–331).

[10] Caulescent, suckering and forming dense groups; stem to 25 × 2 cm; **L** usually distichous, sometimes rosulate, linear-acuminate, to 30 × 1.5 cm, green, obscurely lineate, sometimes with a few scattered white spots near the base, lower face with white spots, more numerous towards the base, **marginal teeth** minute, white, 1–2 mm apart, frequently absent; **Inf** to 30 cm, simple; raceme capitate, ±5–6 × 5–6 cm, with 10–15 flowers; **Bra** ovate-acute, to 14 × 8 mm; **Ped** to 25 mm; **Fl** scarlet with green tips, 25 mm, slightly ventricose, base shortly attenuate, ±6.5 mm Ø in the middle; **OTep** free to the base; **St** and **Sty** not exerted. — **Cytology:** 2n = 14 (Müller 1945).

**A. nugalensis** Thulin (Nordic J. Bot. 30: 729–730, ill., 2012). **Type:** Somalia, Nugaal Region (Thulin & Warfa 5420A [UPS, K]). — **Distr:** C-E Somalia (Nugaal Region); open bushland on gypsum hill, 650 m.

[8] Caulescent, simple; stem to 50 cm; **L** ±18, rosulate, drooping, narrowly lanceolate-attenuate, to 55 × 5.5 cm, pale glaucous green, exudate

yellowish, quickly changing to purplish-brown, **marginal teeth** forward-pointing, 1 mm, white or pale brown-tipped, 5–15 mm apart; **Inf** 40 cm, descending, with racemes ascending, with 3–5 **Br**; racemes cylindrical, 5–10 cm, lax; **Bra** narrowly triangular-attenuate, 6–9 × 2.5–3 mm; **Ped** 15–22 mm; **Fl** orange-red, darker at the mouth, 32–35 mm, base rounded, 7–7.5 mm  $\varnothing$  across the ovary, narrowing slightly above, widening to the mouth; **OTep** free for 9–10 mm; **St** and **Sty** exerted 2–3 mm.

**A. nuttii** Baker (Hooker's Icon. Pl. 26: t. 2513 + text, 1897). **Type** [syn]: Zambia, Northern Prov. (Nutt 1896 [K]). — **Distr**: SE Angola (Cuando-Cubango), SW Tanzania, S Democratic Republic of the Congo [Zaire], N Zambia, N Malawi; montane grassland and *Brachystegia* woodland, often on rocky slopes, 1250–2650 m. **I**: Reynolds (1966: 33–35); Lane (2004: 5–6, 9); Carter & al. (2011: 145); Klopper & al. (2012: 86, 89–90, incl. distribution map). — Fig. 51.

**Incl.** *Aloe brunneo-punctata* Engler & Gilg (1903); **incl.** *Aloe corbisieri* De Wildeman (1921); **incl.** *Aloe mketiensis* Christian (1940).

[10] Caulescent, simple or suckering to form groups of up to 12 **Ros**; stem to 20 × 5 cm, often very short; **L** 16–20, rosulate, linear-acute, 40–50 × 1.5–2 cm, green, sometimes obscurely lineate, usually with a few dull pale greenish lenticular spots near the base, esp. on the lower face, with 0.5–1 mm white cartilaginous margin, **marginal teeth** ±1 mm, soft, white, obsolescent towards the tip; **Inf** 60–80 cm, simple; raceme cylindrical-acuminate, 15–25 × 8–9 cm, subdense; **Bra** ovate-acute, 15–20 × 10 mm, imbricate in bud stage; **Ped** 30–35 mm; **Fl** peach-red, strawberry-pink or salmon-pink, 38–42 mm, base shortly attenuate, 9 mm  $\varnothing$  across the ovary, not narrowed above; **OTep** free almost to the base or united in the lower ¼; **St** and **Sty** exerted 0–1 mm.

**A. nyeriensis** Christian ex I. Verdoorn (Flow. Pl. Afr. 29: t. 1126 + text, 1952). **Type**: Kenya, Central Prov. (*Pole-Evans & Erens* 1198 [PRE]). — **Distr**: Kenya (Central Prov.: Nyeri region); fairly open *Acacia* bushland on rocky soils, 1760–2120 m; known only from the region of



**Fig. 51** *Aloe nuttii*. (Copyright: L. E. Newton)

the type locality. **I**: Reynolds (1966: 380–381); Carter & al. (2011: 638).

**Incl.** *Aloe ngobitensis* Reynolds (1953).

[16] Caulescent, branching at or near the base and forming dense groups; stem erect, to 3 m × 7 cm, with dead leaves persistent; **L** ±20, laxly rosulate and persisting to 50 cm below the stem tip, lanceolate-attenuate, 50–60 × 7 cm, greyish-green, with white spots on young growth, exudate yellow, **marginal teeth** 3 mm, pungent, 10 mm apart, leaf sheath 2–4 cm; **Inf** 60 cm, with 5–8 **Br**, lower ones sometimes rebranched; racemes cylindrical-conical, to 15 cm, subdense; **Bra** ovate-acute, 5–7 × 3–4 mm; **Ped** 15–20 mm; **Fl** glossy coral-red to scarlet, 40 mm, base shortly attenuate, 8–9 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 4 mm. — **Cytology**: 2n = 14 (Brandham 1971: as *A. ngobitensis*), 2n = 28 (Cutler & al. 1980).

Natural hybrids with *A. lateritia* var. *graminicola* have been reported (Carter 1994).



**A. nyikaensis** T. A. McCoy (Ingens 56: 9–11, ills., 2017). **Type:** Zimbabwe, Masvingo Prov. (McCoy 4064 [FT]). — **Distr:** Zimbabwe (Masvingo Prov.); grassland, 775 m.

[5] Acaulescent, solitary or dividing into 3–5 **Ros**; **L** 16–20, rosulate, lanceolate-attenuate, 25 × 7–9 cm, dark green, faintly lineate, with scattered H-shaped white spots, lower surface without spots, exudate yellow, drying orangish-brown, **marginal teeth** deltoid, 6–7 mm, reddish-brown, 7–15 mm apart; **Inf** 125 cm, erect, with 8–14 **Br**; racemes cylindrical-acuminate, 25–35 cm, subdense; **Bra** narrowly deltoid-acuminate, 12 × 3 mm, white, scarious, with 3 brown nerves; **Ped** 12–14 mm; **Fl** light pink to reddish-pink, 36 mm, abruptly constricted above the ovary and widening towards the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 4 mm.

The flower description in the protologue of “5–6 mm wide above the ovary, then narrowing towards mouth” does not match the flower shape shown in the photograph.

**A. occidentalis** (H. Perrier) L. E. Newton & G. D. Rowley (Excelsa 17: 61, 1997). **Type** [syn]: Madagascar (Perrier 1137 [P?]). — **Distr:** W Madagascar; on sand, limestone or basalt rocks in dry deciduous forests, mostly in the shade. **I:** Rauh (1995: 330); Castillon & Castillon (2010: 308–309); Carter & al. (2011: 294).

≡ *Lomatophyllum occidentale* H. Perrier (1926).

[2,3,8] Acaulescent or caulescent, simple; stem erect, to 1 m × 6–10 cm; **L** 15–20, densely rosulate, lanceolate-attenuate, 80–100 × 10–12 cm, greenish-yellow, **marginal teeth** 4 mm, greenish-white, 6–25 mm apart; **Inf** shorter than the leaves, simple or with 3–5 **Br**; racemes cylindrical-conical, 12–26 cm, subdense, with 50–80 flowers; **Bra** triangular-acute, ½ as long or longer than the pedicels; **Ped** 5–10 mm; **Fl** purple to scarlet, green-tipped, 26–30 mm, base rounded, very slightly narrowed above the ovary and slightly enlarging to the mouth; **OTep** free for 5–6 mm; **St** and **Sty** exerted 0–1 mm; **Fr** berries.

**A. officinalis** Forsskål (Fl. Aegypt.-Arab., 73, 1775). **Type:** Yemen (*Forsskål* s.n. [C †]). —

**Distr:** Saudi Arabia (Asir Prov.), Yemen (Tihama); stony hillsides and sandy plains, 50–700 m. **I:** Collenette (1999: 23); Carter & al. (2011: 430).

≡ *Aloe vera* var. *officinalis* (Forsskål) Baker (1880); **incl.** *Aloe maculata* Forsskål (1775) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe vera* var. *angustifolia* Schweinfurth (1894) ≡ *Aloe officinalis* var. *angustifolia* (Schweinfurth) Lavranos (1965).

[6] Caulescent, usually suckering to form dense clumps; stem decumbent, short; **L** 10–12, densely rosulate, ensiform-attenuate, ±60–70 × 6–12 cm, yellow-green, often with white spots, lower face sometimes with up to 9 median prickles, surface smooth, **marginal teeth** stout, crowded; **Inf** to 1 m, simple or with 1–3 **Br**; racemes cylindrical, 15–20 cm, lax; **Bra** ovate-acute or lanceolate, 10 mm; **Ped** 6–8 mm; **Fl** red or yellow to orange, 28–30 mm, slightly clavate; **OTep** free for ±15 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Wood 1983).

Wood (1983) treated this as a variety of *A. vera*.

**A. oligophylla** Baker (J. Linn. Soc., Bot. 20: 272, 1883). **Type:** Madagascar (*Baron* 1207 [K]). — **Lit:** Carter & al. (2011: 272). **Distr:** Madagascar; described without precise locality and not currently known neither in nature nor cultivation. **I:** Castillon & Castillon (2010: 59).

≡ *Lomatophyllum oligophyllum* (Baker) H. Perrier (1926).

[1] Caulescent; **L** 2–4, rosulate, linear, 40–50 × 1.2–1.5 cm, green, **marginal teeth** 1–3 mm, green, 12–25 mm apart; **Inf** 20–28 cm, simple; raceme 5–8 cm, subdense; **Bra** deltoid, 1 mm; **Ped** 12–15 mm; **Fl** with base attenuate, otherwise unknown; **Fr** berries.

The type specimen is in poor condition, and the plant has not been found again.

**A. omavandae** Van Jaarsveld (Haseltonia 10: 41, ills. (pp. 42–43), 2004). **Type:** Namibia, Kaokoveld (*Van Jaarsveld* 17480 [WIND]). — **Lit:** Jaarsveld & al. (2005). **Distr:** N Namibia (Kaokoveld: E Baynes Mts.), SW Angola; crevices on sheer sandstone cliffs, 1500–2000 m. **I:**

Jaarsveld & al. (2005: t. 2201); Carter & al. (2011: 508).

[13] Caulescent, solitary; stem pendulous, to 22 cm; **L** to 25, densely rosulate, deltoid-lanceolate, 30–47 × 6.5–8.5 cm, pale green to greyish-green, upper surface with white spots near the base, lower surface more densely spotted, exudate drying pale orange-brown, **marginal teeth** 1–1.5 mm, reddish-brown, 10–15 mm apart; **Inf** 50–70 cm, pendulous with racemes erect, simple or with 2–4 **Br**; racemes cylindrical-acuminate, 14–21 cm, dense; **Bra** linear-lanceolate, 12 × 3 mm; **Ped** 8–10 mm; **Fl** orange-red, 23–25 mm, 5 mm Ø across the ovary; **OTep** free for 8 mm; **St** and **Sty** exerted 3–4 mm.

**A. omoana** T. A. McCoy & Lavranos (CactusWorld 25(3): 139–140, ills., 2007). **Type:** Ethiopia (McCoy 1269 [FT]). — **Distr:** C Ethiopia (headwaters of the Omo River); on basalt outcrops, 1840 m; known only from the type locality. **I:** Carter & al. (2011: 374).

[3] Acaulescent or with a short stem to 10 cm, solitary; **L** 16–20, rosulate, linear-lanceolate, 65 × 8.5 cm, glossy green, lower surface dull green, exudate yellow, **marginal teeth** forward-pointing, 5 mm, bright red, 10–20 mm apart; **Inf** 1.2 m, suberect to oblique, with 7 or more **Br**; racemes cylindrical, 15 cm, subdense; **Bra** ovate-acute, 2 × 1 mm; **Ped** 15 mm; **Fl** yellow or red, 30 mm, 7 mm Ø across the ovary; **OTep** free for 12 mm; **St** and **Sty** exerted 5 mm.

**A. orientalis** (H. Perrier) L. E. Newton & G. D. Rowley (Excelsa 17: 61, 1997). **Type:** Madagascar, Fianarantsoa (Perrier 5367 [P]). — **Distr:** E Madagascar (Fianarantsoa); sand dunes and coastal forests at sea level. **I:** Rauh (1995: 330); Carter & al. (2011: 295).

≡ *Lomatophyllum orientale* H. Perrier (1926).

[7] Acaulescent, suckering to form groups; **L** 20–25, densely rosulate, lanceolate-attenuate, 80–100 × 10–12 cm, **marginal teeth** greenish-white, ±4 mm; **Inf** 40–50 cm, ascending, with 2–3 **Br**; racemes cylindrical-conical, subdense; **Bra** acute, 3 mm; **Ped** 22–24 mm; **Fl** pale red, 22–24 mm, slightly narrowed above the ovary,

then enlarging to the mouth; **OTep** free for 11–12 mm; **St** and **Sty** not exerted; **Fr** berries.

**A. orlandoi** Lavranos (Cact. Succ. J. (US) 78 (2): 65, ills. (pp. 62–64), 2006). **Type:** Somalia, Sanaag Region (Orlando & Azzouni 231802 [FT]). — **Distr:** Somalia (Sanaag Region); arid stony plains, 1760 m; known from the type collection only. **I:** Carter & al. (2011: 212).

[4] Acaulescent, suckering to form small groups, whole plant pruinose; **L** 4–9, rosulate, deltoid-acuminate, 6–9 × 3.5 cm, bluish-green, with irregular whitish spots, **marginal teeth** 1 mm, white, 3–4 mm apart; **Inf** 35 cm, erect, simple; raceme cylindrical, 17 cm, lax; **Bra** 6–7 mm; **Ped** 5–7 mm; **Fl** greenish-yellow to yellowish-white, 15 mm, 5 mm Ø across the ovary; **OTep** free for 4–5 mm; **St** and **Sty** exerted 4–5 mm.

Published with the spelling *A. orlandi*, but the epithet is correctable in accordance with ICN Rec. 60C.1(a).

**A. ortholopha** Christian & Milne-Redhead (Bull. Misc. Inform. Kew 1933: 478, 1933). **Type:** Zimbabwe, Northern Prov. (Eyles 5448 [SRGH]). — **Distr:** Zimbabwe (Northern Prov.: Great Dyke mining area); open grassland on rocky slopes on serpentine hills, 1450–1525 m. **I:** Reynolds (1966: 234–235); Carter & al. (2011: 282).

[3] Acaulescent, simple; **L** 30 or more, densely rosulate, lanceolate, to 50 × 12–14 cm, dull grey-green tinged pink, with pinkish to reddish-brown margin, **marginal teeth** to 4 mm, pungent, 4 (near base) – 20 (towards tip) mm apart; **Inf** 80–90 cm, with 2–3 (–5) **Br**; racemes almost horizontal, with secund flowers, 30 cm, very dense; **Bra** lanceolate-attenuate, 10–15 × 5 mm; **Ped** ±8 mm; **Fl** orange-scarlet to blood-red, 40 mm, ventricose, base rounded, 6–7 mm Ø across the ovary, enlarged to 10–11 mm in the middle, then narrowing to 6–7 mm at the mouth; **OTep** free for 30 mm; **St** and **Sty** exerted 10–16 mm.

The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984), and local use in herbal medicine has caused deaths (Drummond & al. 1975).

**A. otallensis** Baker (in Thiselton-Dyer & al., Fl. Trop. Afr. 7: 458, 1898). **Type:** Ethiopia, Sidamo Region (*Ruspoli & Riva* 1711 [B †?, FI, K [drawings, fragment]]). — **Distr:** S Ethiopia (Gamo Gofa and Sidamo Regions); open *Acacia* bushland, 1200–1600 m. **I:** Gilbert & Sebsebe Demissew (1992); Sebsebe Demissew & Nordal (2010: 87–88); Carter & al. (2011: 343).

**Incl.** *Aloe boranensis* Cufodontis (1939).

[5] Acaulescent, simple or in small groups; **L** ±24, rosulate, triangular-lanceolate, attenuate, 35–50 (–80) × 4–6.5 (–9.5) cm, grey-green, sometimes with round-oblong white spots in longitudinal rows, spots more numerous on the lower face, **marginal teeth** 3–4.5 mm, reddish-brown, 8–10 mm apart; **Inf** with up to 12 **Br**; racemes cylindrical, 5–8 cm, dense; **Bra** ovate-obtuse, shortly cuspidate, 11–17 × 4–6.5 mm, white; **Ped** 7–12 mm; **Fl** pale pink with grey or yellow tip, 19–23 (–27) mm, base attenuate, slightly narrowed above the ovary; **OTep** free for ±10 mm; **St** and **Sty** exerted 0–1 mm.

**A. pachydactylos** T. A. McCoy & Lavranos (Cact. Succ. J. (US) 79(3): 129, ill. (pp. 129–130), 2007). **Type:** Madagascar, Antananarivo (*Razafindratsira* s.n. [TAN, FT]). — **Distr:** Madagascar (Antananarivo: S Ibity Mts.); on quartzitic sandstone, 1400–2200 m. **I:** Castillon & Castillon (2010: 66–67); Carter & al. (2011: 229).

[2] Acaulescent, or with a short stem to 7 cm, solitary; **L** 10–16, rosulate, linear, very thick, apex rounded, 15 × 4.5–5 cm, greyish tinged brownish, exudate pale yellow, **marginal teeth** deltoid, 2–3 mm, red, 1–2 mm apart; **Inf** 30 cm, erect, simple; raceme cylindrical to subcapitate, dense; **Bra** 4–6 mm; **Ped** 5–8 mm; **Fl** orange-yellow, with orange stripes, 25 mm, base rounded, campanulate, 5 mm Ø across the ovary; **OTep** free for 20–22 mm; **St** exerted to 3 mm; **Sty** exerted 10 mm.

**A. pachygaster** Dinter (Repert. Spec. Nov. Regni Veg. 19(11–13): 179, 1923). **Type** [neo]: Namibia, Lüderitz (*Jankowitz* 291 [M, WIND]). — **Distr:** Namibia (Lüderitz, Bethanien); arid dolomitic limestone slopes, 700–1500 m. **I:**

Reynolds (1950: 314–315); Carter & al. (2011: 405).

[6] Acaulescent or almost so, usually in dense groups of up to 20 **Ros**; **L** rosulate, lanceolate, 12–16 × 2.5 cm, bright grey-green, surface rough, **marginal teeth** 2 mm, yellow when young, becoming nearly black, 5.5 mm apart; **Inf** 90 cm, simple; racemes cylindrical, 35–45 cm, dense; **Bra** ovate-acute, 30 × 17–18 mm; **Ped** 5–6 mm; **Fl** coral-red, green-tipped, 32–34 mm, ventricose, base rounded, enlarged above the ovary to 12 mm in the middle, then narrowing to the mouth; **OTep** free for 14–16 mm; **St** exerted 5–6 mm; **Sty** exerted 8 mm.

According to Reynolds (1950) a little-known species needing further investigation. His photographs show erect inflorescences, whereas Jankowitz (1975) and Carter & al. (2011) show plants with inflorescences almost horizontal.

**A. palmiformis** Baker (Trans. Linn. Soc. London, Bot. 1: 263, 1878). **Type:** Angola, Huila (*Welwitsch* 3726 [BM, K, LISU]). — **Lit:** Smith & Figueiredo (2011a). **Distr:** SW Angola (Huambo, Huila, Namibe: Tungavala Plateau); sandstone rocks in woodland, 1250–1500 m. **I:** Reynolds (1966: 354–355); Carter & al. (2011: 632).

[16] Caulescent, branching mostly at the base; stem erect, to 1.5 m × 4 cm Ø; **L** ±14, laxly rosulate and persisting to 30 cm below the stem tip, lanceolate-attenuate, to 30 × 5 cm, dull green tinged reddish, lower face usually with many small pale green spots towards the base, **marginal teeth** 4–5 mm, pungent, pale brown, 10 mm apart, leaf sheath 10 mm, lineate; **Inf** 40–50 cm, with up to 4 **Br**; racemes cylindrical, slightly acuminate, 10–20 × 7 cm, subdense; **Bra** 2–3 × 2 mm; **Ped** 13–15 mm; **Fl** rose-scarlet, 30 mm, base very shortly attenuate, 5.5 mm Ø across the ovary, then slightly enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. parallelifolia** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 31, 1926). **Type:** Madagascar, Antananarivo (*Perrier* 13981 [P, K]). — **Lit:** Lüthy (2006: 45–46, conservation, with ill.).

**Distr:** Madagascar (Fianarantsoa, Antananarivo: Ibity Mts.); quartzite mountains, 1800–2000 m. **I:** Reynolds (1966: 418–419); Castillon & Castillon (2010: 88–89); Carter & al. (2011: 536).

[10] Caulescent, sparingly branched at the base to form compact groups; stem erect, to 4 cm; **L** 4–7, laxly rosulate, linear, 15 × 1 cm, tip rounded with 4–5 pale brown 1 mm teeth, dull olive-green, **marginal teeth** 2 mm, pale brown, 4–8 mm apart; **Inf** 30–40 cm, simple; raceme cylindrical and lax to subcapitate, with 12–18 flowers; **Bra** lanceolate-acute, 10 × 4 mm, fleshy at the base; **Ped** 30 mm; **Fl** rose-pink to rose-red, almost white at the tips, 30 mm, slightly campanulate, base shortly attenuate, 5 mm  $\varnothing$  across the ovary, enlarging above to 8 mm at the mouth; **OTep** free to the base; **St** exerted 0–1 mm; **Sty** exerted 1–2 mm.

**A. parvibracteata** Schönland (Rec. Albany Mus. 2: 139, 1907). **Type:** Moçambique, Maputo (*Burt-Davy* 2853 [GRA]). — **Lit:** Crouch & al. (2015); Klopper & al. (2015). **Distr:** S Moçambique, RSA (KwaZulu-Natal, S Mpumalanga, Limpopo), Swaziland; mostly rock outcrops in flat grassland, but also seasonally swampy areas, 100–1500 m. **I:** Reynolds (1950: 276–277); Carter & al. (2011: 175); Wyk & Smith (2014: 258–259; 242–243, as *A. keithii*).

**Incl.** *Aloe monteiroae* Baker (1889) (*nomen rejiciendum*, Art. 56.1); **incl.** *Aloe pongolensis* Reynolds (1936); **incl.** *Aloe keithii* Reynolds (1937); **incl.** *Aloe pongolensis* var. *zuluensis* Reynolds (1937)  $\equiv$  *Aloe parvibracteata* var. *zuluensis* (Reynolds) Reynolds (1950).

[5,7] Acaulescent or shortly caulescent, solitary or in small groups or, usually, suckering to form large dense groups; stem sometimes to 40 cm; **L** 10–20, densely rosulate, usually spreading-decurved giving the rosettes a flattened appearance, lanceolate-attenuate, 30–40 × 6–10 cm, green to brownish-green, upper face only with many oblong dull white spots usually in  $\pm$  transverse bands, sometimes obscurely lineate, exudate drying deep purple to violet, **marginal teeth** 3–5 mm, pungent, brown, 10–15 mm apart; **Inf** 1–2 m, with 4–8 **Br**, lower ones sometimes rebranched; racemes cylindrical, slightly acuminate, 15–20 (–40) × 6–7 cm, lax, with

40–50 flowers; **Bra** deltoid or lanceolate, acuminate,  $\pm$  as long as the pedicels; **Ped** 6–15 mm; **Fl** coral-red or dull to glossy red, sometimes somewhat pruinose, 30–35 (–40) mm, base truncate, 7–9 mm  $\varnothing$  across the ovary, abruptly narrowed to 5–6 mm above, then enlarging to the mouth; **OTep** free for 8–10 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:** 2n = 14 (Riley 1959).

Formerly included in *A. zebrina* but removed, along with others, by Smith & al. (2012c), who presented a detailed table of differentiating characters. Lebrun & Stork (2012) include *A. burgersfortensis*, *A. decurvidens*, *A. keithii*, *A. komatiensis* and *A. lusitanica* in the synonymy of this species, but without evidence or references. According to Crouch & al. (2015), plants matching *A. monteiroae* Baker have been found and they are identical to *A. parvibracteata*. The name *A. monteiroae* has priority, but as it was regarded as insufficiently known for many years, Klopper & al. (2015) have proposed the name *A. parvibracteata* for conservation under ICN Art. 14, and this was accepted by the General Committee (Wilson 2017), even though the relevant committee voted neither for recommendation nor rejection (Applequist 2017: 504). Natural hybrids with *A. umfoloziensis* have been reported (Reynolds 1950).

**A. parvicapsula** Lavranos & Collenette (Cact. Succ. J. (US) 72(2): 84, 86, ills., 2000). **Type:** Saudi Arabia, Asir Prov. (*Collenette* 7526 [K]). — **Distr:** Saudi Arabia (Asir Prov.: Jabal Fayfah); montane thickets,  $\pm$ 1350 m. **I:** Collenette (1999: 24); Carter & al. (2011: 286).

[3] Acaulescent, solitary; **L** densely rosulate, ascending, rigid, lanceolate-attenuate, 60 × 13 cm, greyish-green, **marginal teeth** 2–3 mm, whitish,  $\pm$ 14 mm apart; **Inf** to 75 cm, erect, usually with 2–3 **Br**; racemes cylindrical; **Bra** lanceolate, 12–15 × 5–6 mm; **Ped** 6–7 mm; **Fl** reddish, densely white-tomentose, to 35 mm, 6–7 mm  $\varnothing$  across the ovary, narrowing above towards the mouth; **OTep** free for 17–20 mm; **St** and **Sty** exerted 0–1 mm.

**A. parvicoma** Lavranos & Collenette (Cact. Succ. J. (US) 72(1): 21–22, ills., 2000). **Type:**

Saudi Arabia, Asir Prov. (*Collette* 8565 [K]). — **Distr:** Saudi Arabia (Asir Prov.: headwaters of Wadi Maraba); cliff top, surrounded by thick vegetation; known only from the type locality. **I:** *Collette* (1999: 24); Carter & al. (2011: 424).

[8] Caulescent, suckering at the base; stem 10 (–30) × 2.5 cm, erect; **L** ±15, crowded at the stem tip, narrowly deltoid, 35–46 × 3.5–5.5 cm, green, **marginal teeth** 1–2 mm, horny, ±15 mm apart; **Inf** to 60 cm, erect, simple or with 1–2 **Br**; racemes cylindrical, subdense; **Bra** 8–10 × 4–7 mm; **Ped** 13–17 mm; **Fl** salmon-pink shading to yellowish at the tip, 25–28 mm, base shortly attenuate, scarcely constricted above the ovary; **OTep** free for 7–10 mm; **St** and **Sty** exerted 3–4 mm.

Close to, and possibly conspecific with, *A. rivierei*.

**A. parvidens** M. G. Gilbert & Sebsebe (Kew Bull. 47(4): 650, 1992). **Type:** Ethiopia, Sidamo Region (*Gilbert & al.* 7714A [ETH, KJ]). — **Distr:** S & E Ethiopia, E Kenya, NE Tanzania, S Somalia; usually in the shade of bushland or woodland on sandy or stony soil, 560–1450 m. **I:** Reynolds (1966: 67–68, as *A. pirottae*); Carter & al. (2011: 325).

[5] Acaulescent or shortly caulescent, simple or in small groups; **L** rosulate, lanceolate-attenuate, 25–42 × 4.5–6.5 (–9) cm, dark green to brownish with many elliptic pale spots, surface smooth, **marginal teeth** 1–2.5 mm, brown-tipped, 8–13 mm apart; **Inf** 1–1.4 m, with 2–10 **Br**; racemes cylindrical, sometimes with some flowers secund, 9–20 cm, lax; **Bra** ovate-acute, 5–6 × 3–4.5 mm; **Ped** 5.5–12 mm; **Fl** pale pink with yellowish lobes, 26–30 mm, base rounded, 6–8 mm Ø across the ovary, slightly narrowed above; **OTep** free for 6–10 mm; **St** and **Sty** exerted 3 mm. — **Cytology:** 2n = 14 (Brandham 1971: as *A. pirottae*).

*A. pirottae sensu* Reynolds (*non* A. Berger) belongs here.

**A. parviflora** Baker (Bull. Herb. Boissier, sér. 2, 8: 782, 1901). **Type:** RSA, KwaZulu-Natal (*Junod* 146 [Z]). — **Distr:** RSA (S-C KwaZulu-Natal); grassland, 1000 m. **I:** Carter & al. (2011: 113); Wyk & Smith (2014: 350–351).

[1] Acaulescent, solitary; **L** 4–6, rosulate, linear, apex rounded, 20–25 × 0.6–0.8 cm, bright green, lower surface with spinulescent white spots, **marginal teeth** minute, white; **Inf** 40 cm, erect, simple; raceme capitate, 3 cm, dense; **Bra** ovate-cuspidate, 8–12 mm; **Ped** 8–12 mm; **Fl** pale pink, 8 mm, ellipsoid; **OTep** free to the base; **St** and **Sty** not exerted.

Included in *A. minima* by Glen & Hardy (2000) and may yet prove to be a variant of that species when more is known of distribution and variation (Wyk & Smith 2004).

**A. parvula** A. Berger (in Engler, A. (ed.), Pflanzenr. IV.38 (Heft 33): 172–173, 1908). **Type:** Madagascar, Fianarantsoa (*Grandidier* s.n. [P]). — **Lit:** Du Puy (2004b); Lüthy (2006: 47–48, conservation, with ill.). **Distr:** Madagascar (Fianarantsoa: Itremo Mts.); amongst grass in quartzite rock cracks, 1500–2000 m. **I:** Reynolds (1966: 399–401); Castillon & Castillon (2010: 112–113); Carter & al. (2011: 210).

≡ *Lemeea parvula* (A. Berger) P. V. Heath (1994); **incl.** *Aloe sempervivoides* H. Perrier (1926).

[4] Acaulescent, simple or sometimes forming small groups; **L** ±24, densely rosulate, triangular-acute, 10 × 1.2 cm, pale bluish-grey with many firm white 0.5–1 mm prickles, **marginal teeth** 1–2 mm, soft to firm, white, 1–2 mm apart; **Inf** ±35 cm, simple; raceme cylindrical, to 10 × 5 cm, lax, with ±12–15 flowers; **Bra** ovate-deltoid, ±½ as long as the pedicels; **Ped** 12–15 mm; **Fl** light coral-red, 26 mm, subventricose, base attenuate, enlarged to the middle, then narrowing to the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm.

**A. patersonii** B. Mathew (Kew Bull. 32(2): 321–322, 1978). **Type:** Democratic Republic of the Congo [Zaire], Shaba (*Paterson* 515 [K]). — **Distr:** S Democratic Republic of the Congo [Zaire] (Shaba: Lualaba River region); rock crevices in full sun, 1300 m. **I:** Carter & al. (2011: 172).

[2] Acaulescent; **L** 17, densely rosulate, lanceolate-attenuate, 30 × 5 cm, pale green with paler oblong blotches forming irregular bands,



**Fig. 52** *Aloe pearsonii*.  
(Copyright: G. F. Smith)



**marginal teeth**  $\pm 1.5$  mm, white or pale brownish, 9–10 mm apart; **Inf** 60 cm, with 1 **Br**; racemes cylindrical, 25 cm; **Bra** lanceolate, 10–20 mm, green, those at the inflorescence base with bulbils in their axils; **Ped** 14 mm; **Fl** salmon with greenish tinge at the base, 30 mm, 6 mm  $\varnothing$  across the ovary, abruptly narrowed to 4 mm above, then enlarging to 8 mm at the mouth; **OTep** free for 13 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (protologue).

Bulbil formation is rare in the genus (cf. *A. bulbifera*).

**A. pavelkae** Van Jaarsveld & al. (*Aloe* 44(3): 75, ill. (pp. 75–79), 2008). **Type**: Namibia, Karas (*Van Jaarsveld & Swanepoel* 19919 [WIND]). — **Lit**: Jaarsveld & Condry (2013b). **Distr**: Namibia (Karas: Kuamsibberg); on sheer SE-facing sandstone cliffs. **I**: Carter & al. (2011: 491).

[13] Usually caulescent, branching from the base; stem pendulous, to 3 m, with dried leaves persistent; **L** rosulate, linear-lanceolate, 18–28  $\times$  2.5–7 cm, dark green, faintly striate, exudate drying orange-yellow, **marginal teeth** 1.5 mm, white, 4–8 mm apart; **Inf** to 32 cm, pendulous, with racemes erect, simple or with 1 **Br**; racemes capitate, 4.5–9 cm, dense; **Bra** 3  $\times$  1.5 mm; **Ped** 20–28 mm; **Fl** orange-red, yellow at the mouth, 20 mm, 4 mm  $\varnothing$  across the ovary, widening above to 6 mm at the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 0–1 mm.

**A. pearsonii** Schönland (*Rec. Albany Mus.* 2: 229, 1911). **Type**: RSA, Northern Cape (*Pearson* 6091 [GRA]). — **Distr**: SW Namibia, NW RSA (NW Northern Cape: Richtersveld); hot arid rocky slopes, 300–1500 m. **I**: Reynolds (1950: 366–368); Carter & al. (2011: 534); Wyk & Smith (2014: 136–137). — Fig. 52.

[16] Caulescent, much branched at the base or higher up, forming dense shrubs to 2 m  $\varnothing$ ; stem erect, to 2 m  $\times$  1.5 cm; **L** scattered along the stem, ovate-acute to ovate-lanceolate, recurved to deflexed, 7–9  $\times$  3–4 cm, green, obscurely lineate, reddish in drought, **marginal teeth** 1–2 mm, pungent, whitish to reddish, to 5 mm apart; **Inf**  $\pm 40$  cm, with 2–3 **Br**; racemes cylindrical, 9–15  $\times$  6–7 cm, lax; **Bra** lanceolate-acuminate, 6–8  $\times$  3 mm; **Ped**  $\pm 20$  mm; **Fl** yellow or brick-red, 25 mm, base attenuate, enlarging above the ovary to the mouth; **OTep** free for 12–13 mm; **St** and **Sty** exerted 4–5 mm. — **Cytology**:  $2n = 14$  (Resende 1937).

**A. peckii** P. R. O. Bally & I. Verdoorn (*Flow. Pl. Afr.* 31: t. 1214 + text, 1956). **Type**: Somalia, Northern Region (*Peck* s.n. in *Bally* 4283 [EA, PRE]). — **Distr**: Somalia (Northern Region: higher parts of Ahl Meadow Range); on gypsum soil, mostly in the shade of bushland, 1500–1750 m. **I**: Reynolds (1966: 62–63); Carter & al. (2011: 305).

[5] Acaulescent, simple or in small dense groups; **L** 14–16, densely rosulate, lanceolate,

16 × 6 cm, olive-green, usually with many elongated whitish-green spots, exudate drying deep brown, **marginal teeth** ±3–4 mm, pungent, brownish, 6–10 mm apart; **Inf** 60–80 cm, with 6–8 **Br**; racemes cylindrical, 15–20 × 5 cm, sub-dense; **Bra** ovate-attenuate, 10–12 × 4 mm, pale brown; **Ped** 10 mm; **Fl** straw-coloured to greenish-yellow, **Tep** with broad pale border, giving the flowers a striped appearance, 25–30 mm, base shortly attenuate, 7 mm ∅ across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for ±14 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology**: 2n = 14 (Brandham 1971).

**A. peglerae** Schönland (Rec. Albany Mus. 1: 120, 1904). **Type**: RSA, North-West (*Pegler* 921 [BOL, GRA, PRE]). — **Lit**: Pfab & Scholes (2004: population biology); Arena & al. (2013: pollination); Phama & al. (2014: population biology); Arena & al. (2015: microsite ecology). **Distr**: RSA (E North-West, Gauteng); N-facing rocky slopes, 1400–1700 m. **I**: Reynolds (1950: 160–161, t. 7); Carter & al. (2011: 246); Wyk & Smith (2014: 176–177).

[4] Acaulescent or very shortly caulescent, simple or sometimes in small groups; stem decumbent; **L** ±30, densely rosulate, lanceolate-acuminate, incurved at the tip, the tip a pungent spine, ±25 × 7 cm, glaucous, becoming reddish at the tip, usually with a few reddish to brown prickles with whitish tuberculate base in mid-line, sometimes 2 rows on the lower face, **marginal teeth** to 6 mm, pungent, whitish, tipped reddish to brown, 15 mm apart; **Inf** 40 cm, simple; raceme cylindrical, slightly acuminate, to 25 × 7–8 cm, very dense; **Bra** ovate-acuminate, 16 × 7 mm; **Ped** 2–4 mm; **Fl** mostly greenish-cream tinged slightly reddish, 26–30 mm, ventricose, base rounded, enlarged above the ovary to the middle, then narrowing to the mouth; **OTep** free almost to the base; **St** exerted 15–20 mm, deep purple with orange anthers; **Sty** exerted 15–20 mm.

Natural hybrids with other species have been reported (Reynolds 1950). An endangered species, mainly because of illegal collecting. In 1971 the present author saw local children offering uprooted plants of this species for sale at a

roadside. Phama & al. (2014) reported a 43% decline of 9 subpopulations between 1999 and 2010. Their data suggest a very low establishment rate diminishing over time for seedlings. Earlier, Pfab & Scholes (2004) had concluded that continued collection of plants from the wild is unsustainable, and they stated that *ex situ* cultivation is vital to avoid extinction of the species.

The pollination ecology was studied by Arena & al. (2013): Plants are partly self-fertile and are visited by birds as well as insects. The opportunistic nectarivore *Monticola rupestris* is responsible for ±60% of seed set, but the species is not dependent on sunbirds as previously thought. Arena & al. (2013) found a low seed viability of only ±19%. Payne & al. (2016) confirmed opportunistic nectarivorous birds as important pollinators but in addition reported nocturnal visits by nectar-feeding mammals, the Namaqua Rock Mouse (*Micaelamys namaquensis*) and the Eastern Rock Sengi (*Elephantulus myurus*), contributing to pollination, though significantly less than that by birds. This last-mentioned study found the species to be self-sterile, and a seed viability of 90% and more.

**A. pambana** L. E. Newton (Cact. Succ. J. (US) 70(1): 27–31, ills., 1998). **Type**: Tanzania (*Brown* 206 [K, EA]). — **Distr**: Tanzania (Pemba and Misali Islands); light shade in coastal forest, on sandy soil, ±3 m. **I**: Carter (1994: t. 3, as *Aloe* unidentified); Castillon & Castillon (2010: 388, 390); Carter & al. (2011: 587).

≡ *Lomatophyllum pambanum* (L. E. Newton) Rauh (1998).

[8] Caulescent, suckering at the base to form dense clumps; stem erect, to 2 m × 8 cm; **L** up to 20, densely rosulate, lanceolate-attenuate, to 110 × 9.6 cm, bright glossy green, sometimes with white hyaline margin, surface smooth, exudate pale yellow, **marginal teeth** 1.5 mm, white, sometimes brown-tipped, 6–10 mm apart; **Inf** to 60 cm, erect, with 2–3 (–5) **Br** usually arising close together; racemes cylindrical, 5–18 × 7–8 cm, dense; **Bra** ovate, attenuate, 3–5 × 2 mm; **Ped** 16–20 mm; **Fl** buds red or yellow with green tips, fading rapidly to cream or white at anthesis; **Fl** creamy-white with green mid-stripe, 20–22

mm, base shortly attenuate, 6 mm  $\varnothing$  across the ovary, slightly narrowed to 5 mm above, then enlarging to 6 mm at the mouth; **OTep** free for 12–16 mm; **St** and **Sty** exerted 5 mm; **Fr** berries.

Similar to *A. peyrierasii* according to Castillon & Castillon (2010: 388), but probably more closely related to *A. aldabrensis*.

**A. pendens** Forsskål (Fl. Aegypt.-Arab., 74, 1775). **Type** [lecto]: Yemen (*Forsskål* 16 [C]). — **Lit**: Wood (1983); Walker (2005). **Distr**: Yemen (Hadiyah: W Yemeni escarpment); steep rock faces, 1500–2300 m. **I**: Reynolds (1966: 164); Carter & al. (2011: 482).

≡ *Aloe variegata* Forsskål (1775) (*nom. illeg.*, ICN Art. 53.1); ≡ *Aloe arabica* Lamarck (1783); **incl.** *Aloe dependens* Steudel (1840).

[13] Caulescent, suckering at the base; stem decumbent or pendulous, to 20 × 1–1.5 cm; **L** scattered along the stem, subdistichous on younger stems, later spiral to rosulate, ensiform-attenuate, deflexed and recurved,  $\pm 20 \times 1.5$  cm, pale green or bronze with narrow horny reddish margin, variegated on young shoots, **marginal teeth** 1 mm, reddish, 5–7 mm apart, leaf sheath 1–2 cm, white-striped and spotted; **Inf**  $\pm 15$  cm, ascending, simple; raceme cylindrical, slightly acuminate, 15–30 cm, subdense; **Bra** ovate-acute, 10 × 5 mm; **Ped** 6 mm; **Fl** usually yellow, rarely orange-red,  $\pm 18$  mm, not narrowed above the ovary; **OTep** free for 14 mm; **St** and **Sty** exerted 3 mm. — **Cytology**:  $2n = 14$  (Wood 1983).

The description is based on Wood (1983), who collected material at the type locality. Schweinfurth, referred to by Reynolds (1966), did not visit the type locality.

**A. penduliflora** Baker (Gard. Chron., ser. 3, 4: 178, 1888). **Type**: Kenya (*Kirk* s.n. [K]). — **Lit**: Carter & Reynolds (1990); Newton (1991). **Distr**: SE Kenya (Kwale and Teita Distr.: Mt. Kasigau, Taita Hills); rock slopes, sometimes in semishade at the edge of bushes, 645–900 m. **I**: Carter & al. (2011: 501).

[16] Caulescent, branching at or near the base forming clumps to 2 m  $\varnothing$ ; stem erect (in deep soil) or sprawling (in shallow soil), to 130 × 3 cm, with

dead leaf bases remaining; **L** laxly rosulate and scattered along the stem for 30–40 cm below the tip, lanceolate to somewhat ensiform, to 41 × 7.5 cm, mid-green or with bluish bloom near the base, with a few scattered whitish spots on young shoots, surface smooth, exudate pale yellow drying brown, **marginal teeth** 2 mm, uncinata, white-tipped, 16–25 mm apart; **Inf** 26–40 (–47) cm, descending at the base and curving upwards again with a U-bend, with 2–5 **Br**, lowest ones sometimes rebranched; racemes subcapitate, 5–18 × 8 cm, dense; **Bra** lanceolate-acuminate, to 10 × 3 mm; **Ped** 15–22 mm; **Fl** yellow, rarely red, 30–33 mm, base shortly attenuate, 9.5–10 mm  $\varnothing$  across the ovary, narrowed to 8 mm above; **OTep** free for 7–10 mm; **St** and **Sty** exerted 3–5 mm.

One of many plants sent to Kew from Zanzibar by the governor, Sir John Kirk, without locality information. Most of these plants had been collected on the mainland, in parts of Kenya and Tanzania. Glen & Hardy (1988b) suggested that *A. penduliflora* was identical to *A. confusa*, but this was refuted by Carter & Reynolds (1990) and Newton (1991).

**A. percrassa** Todaro (Hort. Bot. Panorm. 1: 81, t. 21, 1878). **Type**: [lecto — icono]: l.c. t. 21. — **Lit**: Gilbert & Sebsebe Demissew (1997). **Distr**: Eritrea, N Ethiopia (Tigray and Gonder Regions); rocky slopes with sparse vegetation, 2100–2700 m. **I**: Reynolds (1966: 272–275); Sebsebe Demissew & Nordal (2010: 77–78); Carter & al. (2011: 360).

≡ *Aloe abyssinica* var. *percrassa* (Todaro) Baker (1880); **incl.** *Aloe schimperi* Schweinfurth (1894) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe oligospila* Baker (1902); **incl.** *Aloe schimperi* G. Karsten & Schenk (1905) (*nom. illeg.*, ICN Art. 53.1).

[5] Acaulescent or caulescent, simple or in groups; stem erect or decumbent, to 80 × 15 cm, dried leaves persisting; **L** 24 or more, densely rosulate, deltoid, 40–55 × 10–15 cm, glaucous green or grey-green, with slight bluish to reddish tinge, sometimes with spots in young shoots, with whitish to pinkish margin, exudate drying yellow, **marginal teeth** 3–5 mm, 0.6–16 mm apart; **Inf**

60–80 cm, with 5–12 **Br**; racemes cylindrical-conical, (6.5–) 12–25 × 5–6 cm, dense; **Bra** ovate-acuminate, 8–20 × 3–6 mm; **Ped** 11–20 mm; **Fl** scarlet, paler at the mouth, 17–23 mm, base shortly attenuate, 6 mm  $\varnothing$  across the ovary, not narrowed above; **OTep** free for 5–7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Fernandes 1930, Fentaw & al. 2013).

Natural hybrids with *A. camperi* have been reported (Reynolds 1966).

**A. perdita** Ellert (*Aloe* 46(3): 51, 2010). **Type**: Zimbabwe/Moçambique (*Ellert* 172 [ARIZ]). — **Lit**: Ellert (2009). **Distr**: Zimbabwe, Moçambique: Chimanimani Mts.; habitat not recorded; known only from the type collection.

[1] Acaulescent, suckering to form groups with up to 30 **Ros**; **L** 5–25, rosulate, linear-attenuate, 14.5–36 × 2 cm, pale to dark green to reddish-brown, lineate or with numerous pale green blotches, sometimes in irregular transverse bands, surface smooth to slightly rough, exudate greenish-yellow, **marginal teeth** deltoid, 0.1–1.5 mm, white to green, or reddish-brown-tipped, irregularly spaced, sometimes confluent; **Inf** 55 cm, erect, with 1–4 **Br**, often producing bulbils; racemes cylindrical, 5–15 cm, lax; **Bra** ovate, 7–18 × 2–4 mm; **Ped** 7–16 mm; **Fl** pale reddish to pale orange-scarlet, 20–33 mm, 4.5–7 mm  $\varnothing$  across the ovary, narrowed above to 3.5–4 mm, widening to 6 mm above; **OTep** free for 9–13 mm; **St** exerted 0.5–1.5 mm; **Sty** exerted 1–2 mm.

**A. perfoliata** Linné (*Spec. Pl.* [ed. 1], 1: 319, 1753). **Type**: LINN 442.1. — **Lit**: Mottram (2013). **Distr**: S Namibia (Karas), RSA (S Northern Cape, Western Cape, Eastern Cape); usually flat rocky areas, hot dry flat scrub country, sometimes on steep slopes, 500–1200 m. **I**: Carter & al. (2011: 577); Wyk & Smith (2014: 204–205); both as *A. microstigma*.

**Incl.** *Aloe perfoliata* var.  $\mu$  Linné (1753); **incl.** *Aloe obscura* Miller (1768) (*nomen rejiciendum*, Art. 56.1); **incl.** *Aloe picta* Thunberg (1785) (*nomen rejiciendum*, Art. 56.1); **incl.** *Aloe picta* var. *minor* Willdenow (1799); **incl.** *Aloe microstigma* Salm-Dyck (1854); **incl.** *Aloe juttae* Dinter

(1923); **incl.** *Aloe brunthaleri* A. Berger *ex* Cammerloher (1933).

[4] Caulescent, simple or in small groups; stem usually decumbent, to 50 × 10 cm, covered with dead leaves; **L** densely rosulate, lanceolate-deltoid, 30–50 × 6.5–8 cm, green, sometimes with reddish tinge, usually obscurely lineate, frequently with several scattered white spots, lower face usually with many spots, with reddish-brown cartilaginous margin, **marginal teeth** 2–4 mm, pungent, reddish-brown, 5–10 mm apart; **Inf** 60–80 cm, simple; raceme conical and 20 cm, to cylindrical-acuminate and 40 cm; **Bra** lanceolate-acute,  $\pm \frac{1}{2}$  as long as the pedicels, deep brown; **Ped** 25–30 mm; **Fl** orange, becoming greenish-yellow, rarely red, 25–30 mm, slightly ventricose, base rounded, slightly enlarged above the ovary towards the mouth; **OTep** free to the base; **St** exerted 1–3 mm; **Sty** exerted 3 mm. — **Cytology**:  $2n = 14$  (Resende 1937: as *A. microstigma*).

The identity of this species and its typification, as shown here, are as presented by Mottram (2013), though not accepted by Wyk & Smith (2014). Klopper & al. (2016) dispute Mottram's interpretation and have proposed rejection of the name under ICN Art. 56, but this proposal was declined by the IAPT Nomenclature Committee (Applequist 2017: 509), and the General Committee agreed (Wilson 2017: 743). The names *A. obscura* Miller (1768) and *A. picta* Thunberg (1785) have been proposed for rejection under ICN Art. 56 as well (Klopper & al. 2016) and this was supported by the relevant committees (Applequist 2017, Wilson 2017).

Natural hybrids with other species have been reported (Reynolds 1950: 399–400, as *A. microstigma*). Beer & Wyk (2011) report (under the name *A. microstigma*) that the leaves are eaten by the Agter-Hantam ethnic group of the Northern Cape as energy booster and as tonic and to treat back pain.

Reported as local neophyte in Spain by Aymerich (2015).

**A. perrieri** Reynolds (*J. South Afr. Bot.* 22(3): 131, 1956). **Type**: Madagascar, Fianarantsoa (*Perrier* 10995 [P]). — **Distr**: Madagascar (Fianarantsoa: South Betsileo); gneiss inselbergs



in dense short grass, 800–1100 m; known only from the area of the type locality. **I**: Reynolds (1966: 405); Castillon & Castillon (2010: 188–189); Carter & al. (2011: 409).

≡ *Aloe parvula* H. Perrier (1926) (*nom. illeg.*, ICN Art. 53.1).

[6] Acaulescent, suckering to form dense groups; **R** fusiform; **L** ±10, rosulate, linear-attenuate, to 30 × 1.5–2 cm, green with many pale spots, surface rough, **marginal teeth** ±1 mm, firm, white, 1–2 mm apart; **Inf** 40–50 cm, simple; raceme cylindrical-acuminate, 15–20 cm, lax, with 20–30 flowers; **Bra** ovate-acute, 3–4 × 2 mm; **Ped** 15 mm; **Fl** deep rose, almost white at the mouth, 16 mm, campanulate, base attenuate, slightly enlarged above the ovary to the wide open mouth; **OTep** free for 8 mm; **St** and **Sty** not exerted.

Perrier (1926) misidentified this as *A. parvula* A. Berger.

**A. perryi** Baker (J. Linn. Soc., Bot. 18: 161, 1881). **Type**: Yemen, Socotra (*Perry* s.n. [K]). — **Distr**: Yemen (Socotra); limestone, to 650 m. **I**: Reynolds (1966: 196); Carter & al. (2011: 568).

[18] Caulescent, simple; stem erect or decumbent, ±30 × 5 cm; **L** 12–30, densely rosulate, lanceolate-acute, 35 × 7.5 cm, glaucous-green tinged reddish, **marginal teeth** ±4 mm, pale brown, 6 mm apart; **Inf** 50–60 cm, usually with 2–3 **Br**; racemes oblong-cylindrical, 15–25 × 5–6 cm, dense; **Bra** lanceolate-deltoid, 4–6 mm; **Ped** 8 mm; **Fl** bright red tipped greenish, turning yellow at anthesis, 20–25 mm, base shortly attenuate, slightly narrowed above the ovary, then enlarged again towards the mouth; **OTep** free for 8 mm; **St** and **Sty** exerted 0–1 mm.

Although large numbers of the plant are still to be found on Socotra, the species is regarded as “near threatened” (Oakman & al. 2002). The threats include increasing drought, scale insect infestation, and harvesting of the leaf exudate for medicinal use, both locally and for export.

**A. petricola** Pole-Evans (Trans. Roy. Soc. South Africa 5: 707, 1917). **Type**: RSA, Mpumalanga (*Pole-Evans* 196 [PRE]). — **Lit**: Weisser & Deall (1989: ecology). **Distr**: RSA (Limpopo,

Mpumalanga: around Nelspruit); exposed sandstone slopes and granite outcrops, 500–1000 m. **I**: Reynolds (1950: 451–452, t. 47); Carter & al. (2011: 363); Wyk & Smith (2014: 178–179).

[5] Acaulescent, simple or in small groups; **L** 20–30, densely rosulate, lanceolate-attenuate, ±60 × 10 cm, glaucous, sometimes with a few scattered prickles, lower face usually with a few prickles along an obtuse keel near the tip, **marginal teeth** 5 mm, dark brown, 15 mm apart; **Inf** to 1 m, with 3–6 **Br**; racemes cylindrical, slightly acuminate, 40–50 cm, very dense; **Bra** ovate-acute, ±12 × 5 mm, pale brown, strongly deflexed near the base; **Ped** 2 mm; **Fl** greenish-white to pale orange, 28–30 mm, slightly ventricose, base obconical, enlarging above the ovary; **OTep** free for 19–20 mm; **St** exerted 10–12 mm; **Sty** exerted 12 mm. — **Cytology**: 2n = 14 (Riley 1959).

Natural hybrids with other species have been reported (Reynolds 1950). In an ecological study of one population it was found that most plants have some degree of fire resistance when in an open rocky area (Weisser & Deall 1989).

**A. petrophila** Pillans (South Afr. Gard. 23: 213, 1933). **Type**: RSA, Limpopo (*Frames* s.n. [BOL 20482]). — **Distr**: RSA (Limpopo: Soutpansberg); sheer rock faces, 1000–1600 m. **I**: Reynolds (1950: 217–218); Carter & al. (2011: 163); Wyk & Smith (2014: 260–261).

[5] Acaulescent or rarely shortly caulescent, simple or suckering to form small groups; stem to 8 cm; **L** 10–20, densely rosulate, oblong-lanceolate, acuminate, 20–25 × 5–6 cm, bright green, lineate, with scattered elongated H-shaped dull white spots, **marginal teeth** 3–5 mm, pungent, dark brown, 8–12 mm apart; **Inf** 50–75 cm, with 3–6 **Br**; racemes capitate-corymbose, 4–8 × 5–6 cm, dense, with 20–30 flowers; **Bra** lanceolate-acuminate, ±7 mm, white; **Ped** to 15 mm; **Fl** coral-pink with whitish margins on the tepals, 28 mm, base truncate, 7 mm ∅ across the ovary, abruptly narrowed to 4 mm above, then enlarging to the mouth; **OTep** free for 8 mm; **St** and **Sty** exerted 0–1 mm.

Included in *A. swynnertonii* by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011).



**A. peyrierasii** Cremers (*Adansonia*, n.s. [sér. 2], 15(4): 500–503, ill., 1976). **Type:** Madagascar, Antsiranana (*Cremers* 2495 [P]). — **Distr:** N Madagascar (Antsiranana); dry forest understorey. **I:** Castillon & Castillon (2010: 354–357); Carter & al. (2011: 671).

≡ *Lomatophyllum peyrierasii* (Cremers) Rauh (1998).

[9] Caulescent, simple; stem erect, to 4 m, with dead leaves persistent; **L** ±20, rosulate, lanceolate, 165 × 12 cm, yellowish-green, with 3–4 mm cartilaginous violet-tinged margin, **marginal teeth** 3–5 mm, 12–27 mm apart; **Inf** 60–75 cm, with 2–4 **Br**; racemes cylindrical, 8–10 cm, dense; **Bra** not known; **Ped** 25–30 mm; **Fl** 30 mm, otherwise not known; **Fr** berries.

**A. × philippeii** J.-B. Castillon *pro sp.* (Kakt. and. Sukk. 56(10): 267–269, ill., 2005). **Type:** Madagascar, Toliara (*Castillon* 1615 [HBG]). — **Distr:** SW Madagascar (Toliara: Fiherenana River valley, near Andranovory); on limestone, (100? –) 400 m; known from the type locality only. **I:** Castillon & Castillon (2010: 280–281); Carter & al. (2011: 243).

[11] Caulescent, suckering to form small clumps; stem to 25 cm; **L** 15–20, rosulate, linear-lanceolate, with rounded apex, 20–30 × 2–5 cm, green, **marginal teeth** 2 mm, 5–10 mm apart; **Inf** 40 cm, erect, with 1–2 **Br**; racemes cylindrical-acuminate, 12 cm, lax; **Bra** 3 × 1.5 mm; **Ped** 12 mm; **Fl** scarlet, 25 mm, 6 mm Ø across the ovary, narrowing above to 4 mm at the mouth; **OTep** free for 16 mm; **St** and **Sty** exerted 0–1 mm.

Castillon (2009b) changed the status to hybrid, and Castillon & Castillon (2010) suggested that it is the natural hybrid *A. acutissima* var. *fiherenensis* × *A. viguieri*. In the protologue the altitude of the type locality is stated to be 400 m, but Castillon & Castillon (2010) have it as 100 m.

**A. pictifolia** D. S. Hardy (*Bothalia* 12(1): 62–64, ill., 1976). **Type:** RSA, Eastern Cape (*Marais* s.n. [PRE 32328]). — **Distr:** RSA (W Eastern Cape: Humansdorp: around Kouga Dam); precipitous stony slopes, 250–500 m. **I:** Carter & al. (2011: 544); Wyk & Smith (2014: 206–207).

[15] Caulescent, branching at the base; stem to 12 cm, with dead leaf bases persistent; **L** rosulate, lanceolate-acuminate, 12–15 × 1–2.5 cm, glaucous with many white spots, lower face with prickles on a keel near the tip, **marginal teeth** to 1 mm, pungent, red-brown, 4–5 mm apart; **Inf** 20 cm, simple; raceme cylindrical-acuminate, 14–17 × 3.5–4 cm, subdense; **Bra** ovate-acute, 10 × 3–4 mm; **Ped** 11–12 mm; **Fl** scarlet with greenish mouth, 15–16 mm, base rounded, 3–4 mm Ø across the ovary, slightly narrowing to the mouth; **OTep** free to the base; **St** exerted 1–2 mm; **Sty** exerted 2 mm.

**A. pienaarii** Pole-Evans (*Trans. Roy. Soc. South Africa* 5: 27, tt. 6–7, 1915). **Type:** RSA, Limpopo (*Pienaar* s.n. [PRE]). — **Distr:** RSA (S Limpopo), S Moçambique, Swaziland; bushveld on open flat areas or rocky slopes, 140–1300 m. **I:** Carter & al. (2011: 385).

[5] Acaulescent, solitary or suckering to form small groups; **L** rosulate, erect, lanceolate-attenuate, 90 × 12–15 cm, dark greyish-green, red-tinged when dry, surface slightly rough, **marginal teeth** deltoid, 1–2 mm, brown-tipped, 4–6 mm apart; **Inf** 1.75 m, erect, with 4–8 **Br**; racemes narrowly cylindrical-acuminate, 25–50 cm, dense; **Bra** broadly ovate, 17–22 × 12 mm; **Ped** 20 mm; **Fl** bright scarlet, sometimes yellow at the mouth, 30–45 mm, 9–10 mm Ø across the ovary; **OTep** free to the base; **St** and **Sty** exerted 3 mm.

Formerly included in *A. cryptopoda*.

**A. pillansii** L. Guthrie (*J. Bot.* 66: 15, 1928). **Type:** RSA, Northern Cape (*Pillans* 5012 [BOL, BOL, K]). — **Lit:** Williamson (1998: ecology); Lüthy (2006: 49–50, conservation, with ill.); Jaarsveld & Judd (2015: 52–55, ill., as *Aloidendron*). **Distr:** S Namibia, RSA (NW Northern Cape: Richtersveld); hot arid rocky slopes, 250–1000 m. **I:** Reynolds (1950: 495–497, t. 58); Carter & al. (2011: 693); Wyk & Smith (2014: 43–43). – Fig. 53.

≡ *Aloe dichotoma* ssp. *pillansii* (L. Guthrie) Zonneveld (2002) ≡ *Aloidendron pillansii* (L. Guthrie) Klopper & Gideon F. Smith (2013).

[17] Caulescent, dichotomously branching from ± the middle upwards; stem to 10 m or



**Fig. 53** *Aloe pillansii*. (Copyright: L. E. Newton)

more, 1–2 m  $\varnothing$  at the base, narrowing to  $\pm 20$  cm  $\varnothing$  above; **L** densely rosulate, lanceolate-attenuate, slightly falcate, 50–60  $\times$  10–12 cm, grey-green to brownish-green, with white margin, surface smooth, **marginal teeth** 1–2 mm, white, 5–8 mm apart; **Inf**  $\pm 50$  cm, spreading horizontally with racemes turning upwards, with up to 50 **Br**; racemes cylindrical, to 15 cm, lax, with  $\pm 30$  flowers; **Bra** filiform, slightly  $< 10$  mm; **Ped** 10 mm; **Fl** yellow, to 35 mm, base attenuate,  $\pm 12$  mm  $\varnothing$  across the ovary, slightly narrowing above to the mouth; **OTep** free for 25 mm; **St** and **Sty** exerted 10 mm.

On the basis of genome size, Zonneveld (2002) proposed that this species should be reduced to subspecies rank under *A. dichotoma*. This has not been followed by later authors, and was dismissed by Carter & al. (2011). Populations of up to 1500 individuals have been seen in Namibia, with the tallest plants to 12 m high, though threatened by mining activity and with poor recruitment, due partly to periods of low rainfall and partly to

theft and/or herbivory (Loots & Mannheimer 2003, Powell & al. 2003). Measurements of growth rate in a population in South Africa suggested an estimated age of 382 years for the tallest plants there,  $\pm 8$ m (Duncan & al. 2006). Declining numbers in the Richtersveld have raised fears that the species could face extinction (Powell & al. 2003). As prominent plants in their environment, *A. pillansii* is a keystone species, providing perches for raptors and nesting sites for other birds, nectar for birds, and habitat and moisture to other animals (Midgley & al. 1997).

**A. pirottae** A. Berger (Bot. Jahrb. Syst. 36: 65, 1905). **Type:** Ethiopia, Gamo Gofa/Sidamo Region (*Ruspoli* & *Riva* 1682 [B [† ?], FT]). — **Lit:** Gilbert & Sebsebe Demissew (1992). **Distr:** S & E Ethiopia, NE Kenya; open *Acacia* woodland, on stony soils, 900–1820 m. **I:** Sebsebe Demissew & Nordal (2010: 71–73); Carter & al. (2011: 384).

[7] Acaulescent or very shortly caulescent, suckering to form small groups; **L** rosulate, 45–90  $\times$  6.5–13 cm, dark green with many elongated pale spots, surface smooth, **marginal teeth** (3–) 4–5.5 mm, brown-tipped, 10–14 mm apart; **Inf** with up to 28 **Br**; racemes cylindrical, often with secund flowers, 7–33 cm, lax; **Bra** ovate, acute or acuminate, 3–10  $\times$  2–5 mm; **Ped** 3–9 mm; **Fl** yellow with green markings, orange, or sometimes red, 20–28 mm, cylindrical to sub-clavate; **OTep** free for 6–15 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Fentaw & al. 2013).

Reynolds (1966) misidentified the type locality, and his description is of a different plant, later named *A. parvidens*. Sebsebe Demissew & Nordal (2010) say that the species shows clear regional variations, e.g. in inflorescence architecture (racemes secund or not), etc.

**A. plicatilis** (Linné) Burman *fil.* (Fl. Indica, 10, 1768). **Type:** [lecto — icono]: Commelin, Hort. Med. Amstel., 2: 5, t. 3, 1701. — **Lit:** Cousins & al. (2013: ecology); Cousins & al. (2014: population structure); Jaarsveld & Judd (2015: 60–63, *ills.*, as *Kumara*); Cousins & al. (2016: fire ecology). **Distr:** RSA (SW Western Cape); steep

usually SW-facing rocky slopes, in Fynbos vegetation, 200–1000 m. **I:** Reynolds (1950: 503–505); Carter & al. (2011: 681); Wyk & Smith (2014: 44–45). – Fig. 54.

≡ *Aloe disticha* var. *plicatilis* Linné (1753) ≡ *Rhipidodendrum plicatile* (Linné) Haworth (1821) ≡ *Kumara plicatilis* (Linné) G. D. Rowley (2013); **incl.** *Aloe linguaeformis* Linné fil. (1782) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe tripetala* Medikus (1783) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Aloe lingua* Thunberg (1785); **incl.** *Kumara disticha* Medikus (1786) ≡ *Rhipidodendrum distichum* (Medikus) Willdenow (1811); **incl.** *Aloe flabelliformis* Salisbury (1796); **incl.** *Aloe plicatilis* var. *major* Salm-Dyck (1817).

[16,17] Caulescent, dichotomously branched from low down; stem erect, to 5 m; **L** ±12–16, distichous, linear to lorate, 30 × 4 cm, dull to glaucous green, surface smooth, **marginal teeth** minute in the upper ½, sometimes almost absent; **Inf** to 50 cm, simple; raceme cylindrical, slightly acuminate, 15–25 cm, lax, with 25–30 flowers; **Bra** ovate-deltoid, 8 × 6 mm; **Ped** 10 mm; **Fl** scarlet, to 55 mm, base rounded, not narrowed above the ovary; **OTep** free for ±18 mm; **St** and **Sty** exerted 2–5 mm. — **Cytology:** 2n = 14 (Fernandes 1930).

The taxon is currently known from 31 populations (Cousins & al. 2014). Different authors have given different altitudes, ranging from 200 to 1400 m, but most reports are from within the range 200 to 1000 m. In the wild, plants start flowering when ±80 cm tall. Populations vary from 31 to over 110,000 individuals, with 75–3000 plants/ha. Size class distributions show a bell-shaped curve. Plants raised from seed in cultivation reach flowering size rapidly, and first flowers are produced when the stems were only about 10 cm tall (pers. obs. U. Egli).

Cousins & al. (2013) studied the reproductive ecology and found that pollination is mainly by insects and the Malachite Sunbird. Seed dispersal distance is ±3× the plant height, but occasional long-distance dispersal also occurs. No soil seed bank is formed, although seed viability is at least 24 months. Young (3 months) seed showed distinctly lower germination rates under laboratory conditions than older seeds.



**Fig. 54** *Aloe plicatilis*. (Copyright: G. F. Smith)

As this species grows in an area with frequent bush fires, Cousins & al. (2016) studied how it survives the fires. They found that many plants are killed, but survivors are those with a thick bark and those growing in more rocky areas, where the fire would be less severe.

**A. plowesii** Reynolds (J. South Afr. Bot. 30(2): 71–73, t. 14, 1964). **Type:** Zimbabwe, Eastern Prov. (*Plowes* 2273 [SRGH]). — **Distr:** W Moçambique, E Zimbabwe (Eastern Prov.): Chimanimani Mts.; in montane, in grass among sandstone rocks, 1370–1770 m. **I:** Reynolds (1966: 16); Carter & al. (2011: 124).

[1] Acaulescent; **R** fusiform; **L** ±10, rosulate, linear-acute, 20–30 × 0.6–1 cm, dull green with a few scattered small white spots near the base, lower face with spots near the base, **marginal teeth** 0.5 mm, white, more distant becoming obsolete towards the tip; **Inf** 30–45 cm, simple; raceme cylindrical-conical, to 10 × 6 cm, subdense; **Bra** ovate-acute, 15 × 7 mm, imbricate in



bud stage; **Ped** 30 mm; **Fl** scarlet, paler to greenish at the mouth, 30–35 mm, base shortly attenuate, 8 mm  $\varnothing$  across the ovary, not narrowed above; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. pluridens** Haworth (Philos. Mag. J. 64: 299, 1824). **Type** [neo]: RSA, Eastern Cape (Reynolds 1425 [PRE]). — **Distr**: RSA (Eastern Cape, KwaZulu-Natal); in bush on mountain slopes along a coastal strip, to 500 m. **I**: Reynolds (1950: 415–416); Carter & al. (2011: 684); Wyk & Smith (2014: 70–71).

**Incl.** *Aloe atherstonei* Baker (1880); **incl.** *Aloe pluridens* var. *beckeri* Schönland (1903).

[9,16] Caulescent, branching; stem erect, to 5 m; **L** 30–40, densely rosulate, lanceolate-falcate, 60–70  $\times$  5–6 cm, pale to yellowish-green, obscurely lineate, with narrow white cartilaginous margin, **marginal teeth** 2–3 mm, white or pale pink, 5–10 mm apart; **Inf** 80–100 cm, with up to 4 **Br**; racemes conical, 25–30  $\times$  9–10 cm, dense; **Bra** ovate-acute,  $\pm 20 \times 10$ –12 mm, white; **Ped** 30–35 mm; **Fl** salmon-pink to dull scarlet, 40–45 mm, base rounded, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 2–5 mm. — **Cytology**:  $2n = 14$  (Ferguson 1926).

Natural hybrids with other species have been reported (Reynolds 1950).

**A. polyphylla** Schönland ex Pillans (South Afr. Gard. 24: 267, 1934). **Type**: Lesotho (Reynolds 934 [BOL 21370]). — **Lit**: Lüthy (2006: 51–52, conservation, with ill.). **Distr**: W Lesotho (Maluti Mts.); steep rocky basaltic mountain slopes, 2000–2500 m. **I**: Reynolds (1950: 194–195); Carter & al. (2011: 440); Wyk & Smith (2014: 180–181).

[5] Acaulescent or very shortly caulescent, simple or in dense groups; **L**  $\pm 150$ , densely rosulate with 5 spiral rows, ovate-oblong, acuminate, 20–30  $\times$  6–10 cm, grey-green, becoming dry and deep purplish at the tip, lower face with 1–2 pale green to white keels near the margin in the upper  $\frac{1}{2}$ , surface smooth, **marginal teeth** 5–8 mm, firm, pale green, 2–12 mm apart; **Inf** 50–60 cm, with 3–8 **Br**; racemes cylindrical, 12–15  $\times$  10



**Fig. 55** *Aloe porphyrostachys*. (Copyright: U. Eggli)

cm, dense; **Bra** lanceolate-deltoid, acuminate,  $\pm 4$ –6 mm, fleshy, tinged pink; **Ped** 4–6 mm; **Fl** pale red to salmon-pink, rarely yellow, 45–55 mm, base shortly attenuate, slightly enlarged to  $\pm 10$  mm above the ovary; **OTep** free to the base; **St** and **Sty** exerted 5 mm. — **Cytology**:  $2n = 14$  (Riley 1959).

Senior (2002) and Kirkbright (2010) report that the taxon can be successfully grown outdoors in England in a covered porch. Some water is needed also during the cool winter time.

**A. porphyrostachys** Lavranos & Collenette (Cact. Succ. J. (US) 72(1): 18–19, ills., 2000). **Type**: Saudi Arabia, Hijaz Prov. (Collenette 2900 [K]). — **Distr**: Saudi Arabia (Hijaz Prov.: Jabal Radhwa and edge of N escarpment); on granite,  $\pm 2000$  m. **I**: Collenette (1999: 25); Carter & al. (2011: 455). — Fig. 55.

[7] Acaulescent, usually suckering at the base; **L** to 60, densely rosulate, erect, deltoid-attenuate, 50–55  $\times$  7.5 cm, bluish-grey with white

**Fig. 56** *Aloe powysiorum*. (Copyright: L. E. Newton)



cartilaginous margin, **marginal teeth** firm, 3–5 mm, white, 25–30 mm apart; **Inf** to 1.1 m, erect, with up to 6 **Br**; racemes cylindrical, 45 × 4 cm, very dense; **Bra** ovate-lanceolate, 12–15 mm, papery, 5-nerved; **Ped** 2–5 mm; **Fl** bright red, 30–35 mm, clavate, base rounded, 11 mm Ø in the middle; **OTep** free for ±20–21 mm; **St** exserted 12–15 mm; **Sty** exserted 12 mm.

As the flowers are described as “bright red”, the epithet (meaning purplish-red spikes) is not entirely accurate.

**A. powysiorum** L. E. Newton & Beentje (Cact. Succ. J. (US) 62(5): 252–255, ill., 1990). **Type:** Kenya, Laikipia/Meru Districts (Beentje & al. 4124 [EA, K, MO]). — **Distr:** N Kenya; exposed rock faces and steep rocky slopes, 1600–1970 m. **I:** Carter & al. (2011: 517). — Fig. 56.

[13] Caulescent, branching at the base and higher up, sometimes dichotomously at the tip; stem pendulous, to 1.8 m × 12 cm Ø; **L** densely rosulate, triangular, to 55 × 9 cm, pale green with light bloom, surface smooth, exudate colourless, **marginal teeth** to 1 mm, white, (1–) 3–8 mm apart; **Inf** to 92 cm, slightly ascending, almost horizontal, simple; raceme with secund flowers, to 48 cm, dense; **Bra** triangular, 11 × 3 mm, whitish; **Ped** 5–6 mm; **Fl** salmon-red, paler at the mouth, 32–36 mm, ventricose, base obconical, 10 mm Ø across the ovary, enlarged above to the

middle, then narrowing to 6.5–7 mm at the mouth; **OTep** free for ½; **St** and **Sty** exserted to 10 mm.

**A. praetermissa** T. A. McCoy & Lavranos (Cact. Succ. J. (US) 74(1): 27–28, ill., 2002). **Type:** Oman, Dhofar (McCoy 2298 [MO, K, P]). — **Distr:** Oman (Dhofar); limestone or alluvial soils, occasionally on crystalline rocks, 1000 m. **I:** Carter & al. (2011: 333).

[5] Acaulescent or with short erect or procumbent stem, solitary or suckering to form groups of up to 3 rosettes; **L** 10–18, rosulate, deltoid-acute, 28–45 × 7–12 cm, dull grey-green, **marginal teeth** absent or very few; **Inf** 1.2 m, erect, with 10 or more **Br**, lowermost rebranched; racemes with subsecund flowers, lax; **Bra** 5–8 × 2.5 mm; **Ped** 10 mm; **Fl** reddish, 22–28 mm, 5–7 mm Ø across the ovary, widening above to the mouth; **OTep** free for 7 mm; **St** and **Sty** exserted 1–3 mm.

Earlier gatherings were erroneously assigned to *A. inermis* or *A. luntii*.

**A. pratensis** Baker (J. Linn. Soc., Bot. 18 (108): 156, 1880). **Type** [lecto]: RSA, Eastern Cape (MacOwen 1896 [GRA]). — **Distr:** Lesotho, RSA (C-E Eastern Cape, SW KwaZulu-Natal); grassland on rocky slopes, from near the coast to 2000 m. **I:** Reynolds (1950: 191–192); Carter & al. (2011: 234); Wyk & Smith (2014: 182–183).



[4] Acaulescent, rarely simple, usually in small groups; **L** 30–40, densely rosulate, lanceolate or ovate-lanceolate, to 15 × 4–5 cm, glaucous, lineate, upper face sometimes with a few scattered reddish-brown prickles, lower face usually with a few scattered reddish-brown prickles and sometimes with a median keel towards the tip armed with a few 2–3 mm brown prickles, exudate drying deep orange, **marginal teeth** ±5 mm, pungent, reddish-brown, 10 mm apart; **Inf** to 60 cm, simple; raceme cylindrical, ±20 × 10 cm, dense; **Bra** ovate-acuminate, to 40 × 15–18 mm; **Ped** 25–30 mm; **Fl** rose-red, 35–40 mm, base truncate, enlarged slightly above the ovary; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Riley 1959).

Natural hybrids with *A. maculata* have been reported (Reynolds 1950: as *A. saponaria*).

**A. pretoriensis** Pole-Evans (Gard. Chron., ser. 3, 56: 106, 1914). **Type**: RSA, Gauteng (Pole-Evans 12 [PRE]). — **Distr**: Zimbabwe, RSA (N Gauteng, Mpumalanga, Limpopo), Swaziland; rocky and grassy slopes in deciduous woodland, 600–1825 m. **I**: Reynolds (1950: 307–308); Carter & al. (2011: 646); Wyk & Smith (2014: 72–73). — Fig. 57.

[8] Caulescent, simple; stem suberect or arcuate-erect, to 1 m × 25 cm, with dead leaves persistent; **L** 40–60, densely multifarious, lanceolate-acuminate, to 60 × 15 cm, green with greyish powdery bloom, obscurely lineate, **marginal teeth** ±3–4 mm, pungent, reddish, 10–15 mm apart; **Inf** 2–3.5 m, with 5–8 **Br**; racemes conical to cylindrical-acuminate, 20–30 × 10 cm, dense; **Bra** ovate-deltoid, ±½ as long as the pedicels; **Ped** 25–40 mm; **Fl** rose-pink to rich peach-red with a bloom, sometimes yellowish at the mouth, 40–50 mm, base very shortly attenuate, enlarged slightly above the ovary, narrowing to the mouth; **OTep** free to the base; **St** and **Sty** exerted 1–2 mm. — **Cytology**: 2n = 14 (Müller 1941).

Natural hybrids with *A. greatheadii* var. *davyana* have been reported (Reynolds 1950).

**A. prinslooii** I. Verdoorn & D. S. Hardy (Flow. Pl. Afr. 37: t. 1453 + text, 1965). **Type**: RSA,



**Fig. 57** *Aloe pretoriensis*. (Copyright: G. F. Smith)

KwaZulu-Natal (Hardy 1907 [PRE]). — **Distr**: RSA (C KwaZulu-Natal); grassy slopes in open woodland, 800–1500 m. **I**: Carter & al. (2011: 159); Wyk & Smith (2014: 262–263).

[5] Acaulescent, simple or in small groups; **L** 16–30, rosulate, lanceolate, 14–20 × 4–8 cm, green with few to many irregular oblong white spots, denser on the upper face, sometimes in transverse bands, **marginal teeth** ±4 mm, pungent; **Inf** to 60 cm, with 2–4 **Br**; racemes capitate-corymbose, 6–12 × 6–7 cm, dense; **Bra** attenuate, to 30 × 5 mm; **Ped** to 30 mm; **Fl** pale whitish-green tinged with pale to deep shell-pink, ±17 mm, base rounded, sometimes slightly narrowed above the ovary, enlarging slightly to the mouth; **OTep** free for 5–7 mm; **St** and **Sty** exerted 0–1 mm.

**A. procera** L. C. Leach (J. South Afr. Bot. 40 (2): 117–121, ills., 1974). **Type**: Angola, Cuanza Sul (Leach & Cannell 14617 [LISC, BM, LISC, SRGH]). — **Distr**: W-C Angola (Cuanza Sul); tall

grass in deciduous woodland on steep hillside,  $\pm 1230$  m. **I:** Carter & al. (2011: 359).

[3] Acaulescent or usually shortly caulescent, simple; stem erect, to 25 cm; **L**  $\pm 20$ , densely rosulate, ovate-attenuate, apical portion soon drying, to  $55 \times 8\text{--}9.5$  cm, pale green, obscurely lineate, with narrow cartilaginous pale yellow margin, **marginal teeth** 1.5–3.5 mm, orange-brown tipped, 10–18 mm apart; **Inf** 2.2–2.75 m, with 9–12 **Br**, lower ones rebranched; racemes with secund flowers, 25–40 cm, lax; **Bra** deltate-attenuate,  $5\text{--}6 \times \pm 4$  mm, brownish; **Ped** 1.5–5 mm; **Fl** dull reddish-purple, 28–33 mm, base rounded or truncate, not or slightly narrowed above the ovary; **OTep** free for 9–11 mm; **St** exserted 0–1 mm; **Sty** exserted to 6 mm.

**A. pronkii** Lavranos & al. (Cact. Succ. J. (US) 78(4): 198–200, ills., 2006). **Type:** Madagascar, Antananarivo (*Pronk* s.n. in Lavranos 32024 [TAN, Z]). — **Distr:** Madagascar (Antananarivo: W of Antsirabe); on quartzite, 1500 m; known only from the type locality. **I:** Castillon & Castillon (2010: 96–97); Carter & al. (2011: 220).

[1] Acaulescent, usually solitary; **L**  $\pm 20$ , rosulate, base deltoid, then narrowly linear, apex acute,  $10\text{--}14 \times 2\text{--}2.5$  cm, brownish-green, surface minutely and densely tuberculate, **marginal teeth** deltoid, 0.5 mm, white, 1–3 mm apart; **Inf** 15 cm, erect, simple; raceme elongate-conical, lax; **Bra** 2–3 mm, brownish-red; **Ped** 7 mm; **Fl** red, whitish at the mouth, 14 mm, base stipitate, 4 mm  $\varnothing$  across the ovary; **OTep** free for 5.5 mm; **St** and **Sty** not exserted.

**A. prostrata** (H. Perrier) L. E. Newton & G. D. Rowley (Excelsa 17: 61, 1997). **Type:** Madagascar, Antsiranana (*Perrier* 11014 [P]). — **Lit:** Teissier & Lavranos (2004). **Distr:** NW Madagascar (Antsiranana: Ankarana region); crevices on limestone slopes, usually in the shade. **I:** Rauh (1995: 328); Castillon & Castillon (2010: 307; 56–57, as *A. propagulifera*); Carter & al. (2011: 233). — Fig. 58.

$\equiv$  *Lomatophyllum prostratum* H. Perrier (1926); **incl.** *Lomatophyllum propaguliferum* Rauh & Razafindratsira (1998)  $\equiv$  *Aloe propagulifera* (Rauh & Razafindratsira) L. E. Newton



**Fig. 58** *Aloe prostrata*. (Copyright: M. Grubenmann)

& G. D. Rowley (1998); **incl.** *Aloe ankaranensis* Rauh & Mangelsdorff (2000).

[6] Acaulescent, stoloniferous; **L** 10–20, densely rosulate, lanceolate-attenuate, falcate, tip with 3–4 teeth,  $15\text{--}20 \times 1.5\text{--}2$  cm, dark green to dark brown, with many confluent white spots, **marginal teeth** 3 mm, white, 5–15 mm apart; **Inf** to 12 cm, simple; raceme cylindrical, 4–6 cm, with few flowers; **Bra** longer than the pedicels; **Ped** 4–5 mm; **Fl** bright carmine-red, green tipped, 20–25 mm, base truncate, 6–7 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, then enlarging to 6–7 mm at the mouth; **OTep** free for 7–8 mm; **St** and **Sty** exserted 0–1 mm; **Fr** berries.

It was shown by Teissier & Lavranos (2004) that this species had been misidentified by some authors. Some populations had been given new names, here shown as synonyms. One population assigned to this species by Rauh was found to be distinct and was described as *A. sakarahensis*, and a subspecies transferred to that species. According to Castillon & Castillon (2010) *A. sakarahensis*

ssp. *sakarahensis* is the same as *A. zombitsiensis*, which name has priority.

**A. pruinosa** Reynolds (J. South Afr. Bot. 2(2): 122–124, t. 17, 1936). **Type:** RSA, KwaZulu-Natal (*Reynolds* 377 [PRE, BOL]). — **Lit:** Smith & Crouch (1995: portrait); Wilson & al. (2009: pollination ecology). **Distr:** RSA (S-C KwaZulu-Natal: Pietermaritzburg Distr.); thorn bush, shade, 600–800 m. **I:** Reynolds (1950: 251–252); Carter & al. (2011: 196); Wyk & Smith (2014: 264–265).

[3] Caulescent, simple; stem procumbent and rooting below, to 50 cm; **L** 12–24, densely rosulate, lanceolate-attenuate, to 70 × 8–10 cm, green with many white spots, scattered or in transverse bands, more numerous on the lower face, exudate drying deep violet, **marginal teeth** to 4 mm, pungent, pale pinkish-brown, 15–20 mm apart; **Inf** to 2 m, with ±11 **Br**, lower ones rebranched; racemes cylindrical-acuminate, 10–30 × 7 cm, lax; **Bra** linear-lanceolate, acuminate, 10–20 mm or slightly longer; **Ped** 10–20 mm; **Fl** dull dark brownish-red to pinkish-white, with heavy greyish powdery bloom, 30–40 mm, base truncate, 8 mm Ø across the ovary, abruptly narrowed to 5 mm above, then enlarging to 8 mm at the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Müller 1941).

According to Wilson & al. (2009), *A. pruinosa* is pollinated mostly by the solitary anthophorid bee *Amegilla atrocincta*, with honeybees, membrane bees (*Colletidae*) and Amethyst Sunbirds as further visitors.

**A. pseudoparvula** J.-B. Castillon (Kakt. and Sukk. 55(8): 219–221, ills., 2004). **Type:** Madagascar, Fianarantsoa (*Castillon* 15 [HBG]). — **Distr:** Madagascar (Fianarantsoa: Antoetra hills); on mixed granite and crystalline limestone, 1200 m. **I:** Castillon & Castillon (2010: 114–115); Carter & al. (2011: 211).

[6] Acaulescent, suckering to form groups of up to 10 **Ros**; **L** 10–15, rosulate, deltoid-acuminate, 7 × 1.5 cm, grey-green, often pink-striate, upper surface with scattered, rounded prickles to 2 mm, **marginal teeth** 1 mm, whitish,

2.5 mm apart; **Inf** 55 cm, erect, simple or with 1 **Br**; racemes cylindrical, lax; **Bra** 5–8 × 3 mm, red-tinged; **Ped** 15 mm; **Fl** pinkish-red, 25 mm, widening to 5 mm Ø above the ovary; **OTep** free for 5 mm; **St** and **Sty** not exerted.

The known only site was plundered almost completely soon after its discovery, with only about 5 plants left in 2005 (Castillon 2005).

**A. pseudorubroviolacea** Lavranos & Collenette (Cact. Succ. J. (US) 72(1): 17–18, ills., 2000). **Type:** Saudi Arabia, Hijaz Prov. (*Collenette* 4409 [K]). — **Distr:** Saudi Arabia (Hijaz Prov.); steep hillsides, ±2000 m. **I:** Collenette (1999: 26); Carter & al. (2011: 639).

[13] Caulescent, simple or less frequently sparsely suckering; stem decumbent, to 4 m with persistent dry leaf bases; **L** ±18, densely rosulate, deltoid-attenuate, to 60 × 15 cm, bluish-grey, more vivid green in yellow-flowered plants, **marginal teeth** hard, triangular, 2–3 mm, 25–40 mm apart; **Inf** to 1.2 m, obliquely ascending or recurved, with 4–20 (–52) **Br**; racemes cylindrical, 25–60 cm, dense; **Bra** ovate-deltoid, acute, 7 mm, papery with brown nerves; **Ped** 3 mm; **Fl** bright red, orange, or rarely golden-yellow, 32–40 mm, base rounded, ventricose, 12 mm Ø in the middle; **OTep** free for 20–22 mm; **St** exerted 14 mm; **Sty** exerted 10 mm.

**A. pubescens** Reynolds (J. South Afr. Bot. 23 (1): 10–12, tt. 10–11, 1957). **Type:** Ethiopia, Oromiya (Arsi) (*Reynolds* 8144 [PRE, K]). — **Distr:** E Ethiopia (Shewa, Arsi, Harerge); rocky stream banks and field margins, 1800–2550 m. **I:** Reynolds (1966: 136–137); Sebsebe Demissew & Nordal (2010: 54–55); Carter & al. (2011: 270).

[4] Acaulescent or shortly caulescent, simple or more frequently in groups; **L** ±16, rosulate, lanceolate-attenuate, 45 × 8 cm, grey-green, **marginal teeth** 2–3 mm, pungent, with white base, reddish-brown-tipped, 15–20 mm apart; **Inf** 0.7–1 m, simple or with 1 **Br**; racemes cylindrical-acuminate, ±20 cm, subdense; **Bra** ovate-deltoid, 20 × 6 mm, imbricate in bud stage; **Ped** 15 mm; **Fl** coral-pink, shortly pubescent, 42 mm, base rounded, 8 mm Ø across the ovary, slightly narrowed above, then enlarging slightly and



narrowing to the mouth; **OTep** free for 16 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Brandham 1971, Fentaw & al. 2013).

**A. pulcherrima** M. G. Gilbert & Sebsebe (Kew Bull. 52(1): 147–148, 1997). **Type**: Ethiopia, Shewa (Gilbert 1669 [ETH, K]). — **Lit**: Walker (2017). **Distr**: Ethiopia (Shewa); sparse bush on steep basalt slopes and cliffs, 2480–2750 (–4000) m. **I**: Sebsebe Demissew & Nordal (2010: 82–83); Carter & al. (2011: 514).

[13] Caulescent, branching dichotomously; stem prostrate or pendulous, to 1 m  $\times$  8 cm; **L** 35–50, densely rosulate, lanceolate-attenuate, to 50  $\times$  12 cm, pale blue-green, slightly glaucous, finely striate, with red margin, especially in the dry season, exudate drying purple, **marginal teeth** 0.2–0.3 mm, to 3 cm apart; **Inf** 50–80 cm, descending at the base and curving upwards again with a U-bend, with 3–6 (–11) **Br**; racemes cylindrical, 12–28 cm, lax; **Bra** ovate, acuminate, 8–9 (–15)  $\times$  7–8 mm, rather fleshy; **Ped** 8–12 mm; **Fl** red, 32–33 mm, 6–8.5 mm  $\varnothing$  when pressed; **OTep** free for  $\pm$ 20 mm; **St** and **Sty** exerted 0–1 mm.

**A. purpurea** Lamarck (Encycl. 1: 85, 1783). **Type**: “Réunion” [Mauritius] (Commerson s.n. [P-LA]). — **Lit**: Marais (1975: 601–602). **Distr**: Mauritius; dry mountain slopes. **I**: Castillon & Castillon (2010: 378–381); Carter & al. (2011: 661).

$\equiv$  *Lomatophyllum purpureum* (Lamarck) T. Durand & Schinz (1895); **incl.** *Dracaena marginata* Aiton (1789) (*nom. illeg.*, Art. 52.1)  $\equiv$  *Aloe marginata* (Aiton) Willdenow (1809) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe marginalis* De Candolle (1800) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Dracaena dentata* Persoon (1805) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Lomatophyllum borbonicum* Willdenow (1811) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Phylloma aloiflorum* Ker Gawler (1813) (*nom. illeg.*, ICN Art. 52.1)  $\equiv$  *Lomatophyllum aloiflorum* (Ker Gawler) G. Nicholson (1885) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Aloe rufocincta* Haworth (1819)  $\equiv$  *Phylloma rufocinctum* (Haworth) Sweet (1827)  $\equiv$  *Lomatophyllum rufocinctum* (Haworth) Salm-Dyck

*ex* Schultes & Schultes *fil.* (1829); **incl.** *Lomatophyllum marginatum* Hoffmannsegg (1824) (*nom. inval.*, ICN Art. 32.1c).

[8] Caulescent; stem erect, to 3 m  $\times$  7–10 cm; **L** 12–20, densely rosulate, linear-lanceolate to ensiform, to 100  $\times$  8–12 cm, dark green, with red horny margin, **marginal teeth** small, red; **Inf** 50–60 cm, with up to 10 **Br**; racemes cylindrical, 15–22 cm; **Bra** deltoid, 4–5 mm; **Ped** 20–33 mm; **Fl** yellowish-red, 19 mm, base attenuate, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for 14–15 mm; **St** and **Sty** not exerted; **Fr** berries.

**A. pustuligemma** L. E. Newton (Brit. Cact. Succ. J. 12(2): 53–54, ills., 1994). **Type**: Kenya, Rift Valley Prov. (Newton 3739 [K, EA]). — **Distr**: Kenya; grassland with scattered trees and shrubs, 1370 m. **I**: Carter & al. (2011: 605). — Fig. 59.

[13] Caulescent, branching at the base; stem erect or ascending to  $\pm$ 40 cm, becoming



**Fig. 59** *Aloe pustuligemma*. (Copyright: L. E. Newton)

decumbent to 1.5 m; **L** rosulate and persisting for 30–40 cm below, lanceolate, to 32 × 8.5 cm, dull green, surface slightly rough, exudate yellow, **marginal teeth** 2 mm, firm, brown-tipped, 7–11 mm apart; **Inf** 56–65 cm, with 8–9 **Br**; racemes cylindrical, terminal 13–21 cm, laterals 4–17 cm, subdense; **Bra** triangular, 11–13 × 3 mm, imbricate in bud stage; **Ped** 10 mm; **Fl** pale pink, lobes with white margins, surface minutely pustulate (esp. obvious in bud), 27–28 mm, base obconical, 5 mm  $\varnothing$  across the ovary, narrowed to 4.5 mm above, then enlarging to 5 mm at the mouth; **OTep** free for 15–16 mm; **St** and **Sty** exerted 3–7 mm.

**A. × qaharensis** Lavranos & Collette (Cact. Succ. J. (US) 72(2): 87, ills. (p. 86), 2000). **Type:** Saudi Arabia, Asir Prov. (*Collette* 7749 [K]). — **Distr:** Saudi Arabia (Asir Prov.). **I:** Collette (1999: 27).

Only incompletely described; leaves large, dark green, with numerous small marginal teeth, with slightly rough surface, flowers red, as in *A. fleurentinorum* and *A. woodii*; racemes cylindrical as in *A. woodii*.

= *A. fleurentinorum* × *A. woodii*.

**A. rabaiensis** Rendle (J. Linn. Soc., Bot. 30: 410, 1895). **Type:** Kenya, Coast Prov. (*Taylor* s.n. [BM]). — **Distr:** Somalia, Kenya, Tanzania; mostly coastal regions in sandy soil in open bushland, 18–500 m. **I:** Carter & al. (2011: 633).

[14,16] Caulescent, branching from the base; stem erect or sprawling, often supported by surrounding shrubs, to 2 m, mostly with dead leaves persisting; **L** laxly rosulate, lanceolate-attenuate, 30–45 × 3–8 cm, greyish-green, often tinged reddish, often with a few scattered whitish spots on young shoots, surface smooth, exudate yellow, drying red, **marginal teeth** 2–3 mm, brown-tipped, 8–15 mm apart; **Inf** to 60 cm, with 5–9 **Br**, lower ones sometimes rebranched; racemes subcapitate,  $\pm 8 \times 8$  cm, subdense to dense; **Bra** lanceolate, 10–12 × 3 mm; **Ped** 10–15 (–20) mm; **Fl** shades of orange-red, yellow at the mouth, sometimes entirely yellow, 20–25 mm, base shortly attenuate, 8 mm  $\varnothing$  across the ovary, slightly narrowed above; **OTep** free for  $\pm \frac{1}{2}$  of their length; **St**

and **Sty** exerted 11 mm. — **Cytology:**  $2n = 14$  (Cutler & al. 1980).

Plants from upland Kenya and Tanzania (1370–1900 m) included in this taxon by Reynolds (1966), including his plate 83, are *A. ngongensis*. Possible hybrids with *A. secundiflora* have been reported (Carter 1994).

**A. rapanarivoi** J.-P. Castillon (Cact.-Avent. Int. 81: 16–19, ills., 2009). **Type:** Madagascar, Mahajanga (*Castillon* 39 [TAN]). — **Distr:** Madagascar (Mahajanga: W of Antoshihy); rock slopes, 500–800 m. **I:** Castillon & Castillon (2010: 338–339).

[3] Usually acaulescent, solitary, in woody areas with a stem to 50 cm; **L** 20–28, rosulate, triangular, 50–70 × 3–10 cm, grey-blue, **marginal teeth** visible in protologue photos but not mentioned in the description; **Inf** 80–110 cm, erect, with 6–12 **Br**; racemes capitate, dense, flowers opening from the top; **Bra** 10 × 5 mm; **Ped** 7–25 mm; **Fl** yellow or pale red, 35 mm, base flat or obtusely rounded, 10 mm  $\varnothing$  across the ovary, widened slightly above; **OTep** free to the base; **St** and **Sty** exerted 6 mm.

**A. rauhii** Reynolds (J. South Afr. Bot. 29(4): 151–152, tt. 24–25, 1963). **Type:** Madagascar, Toliara (*Rauh* 7594 [K, HEID]). — **Lit:** Lüthy (2006: 53–54, conservation, with ills.). **Distr:** S Madagascar (Toliara: near Ampanihy); sandstone rocks in dense bush,  $\pm 600$  m; known only from the area of the type locality. **I:** Reynolds (1966: 413); Castillon & Castillon (2010: 208–210); Carter & al. (2011: 402); Solichon (2013). — Fig. 60.

≡ *Guillauminia rauhii* (Reynolds) P. V. Heath (1994).

[11] Acaulescent or very shortly caulescent, branching to form dense groups; **L** to 20, densely rosulate, lanceolate-deltoid, tip acute, 7–10 × 1.5–2 cm, grey-green, sometimes tinged brownish, with many scattered H-shaped spots, with white cartilaginous margin, **marginal teeth**  $\pm 0.5$  mm, white, 1–2 mm apart; **Inf** 30 cm, simple or rarely with 1 **Br**; racemes cylindrical, slightly acuminate,  $\pm 7 \times 4$  cm, lax, with 12–18 flowers; **Bra** ovate-acute, attenuate, 4–5 × 2 mm, white; **Ped** 10 mm; **Fl** rose-scarlet, paler at the mouth, 25



**Fig. 60** *Aloe rauhii*.  
(Copyright: B. Descoings)



mm, base shortly attenuate, 5 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

Close to *A. deltoideodonta* according to Castillon & Castillon (2010: 208).

**A. rebmannii** Lavranos (Cact. Succ. J. (US) 74(3): 118–120, ills., 2002). **Type**: Madagascar, Toliara (*Rebmann* s.n. [P]). — **Distr**: S Madagascar (Toliara); rocky hills, quartzite outcrops, 550 m. **I**: Castillon & Castillon (2010: 246–247); Carter & al. (2011: 214).

[4] Acaulescent or with a very short stem, suckering to form small groups; **L** 9–12, rosulate, triangular, apex acute, 9–12  $\times$  2–2.5 cm, dark green tinged red, with many oblong pale spots, surface smooth, **marginal teeth** 1–1.5 mm, orange-brown, 2–5 mm apart; **Inf** 45–65 cm, erect, with 2 **Br**; racemes cylindrical, 15 cm, lax; **Bra** triangular, acute, 4–7  $\times$  2 mm; **Ped** 12–16 mm; **Fl** carmine-red, paler towards the mouth, 22 mm, 5 mm  $\varnothing$  across the ovary, slightly narrowed above, widening to 5–6 mm at the mouth; **OTep** free for 13 mm; **St** exerted 0–1 mm; **Sty** not exerted.

Similar to *A. deltoideodonta* and *A. rauhii* according to Castillon & Castillon (2010: 246).

**A. reitzii** Reynolds (J. South Afr. Bot. 3(3): 135–137, t. 20, 1937). **Type**: RSA, Mpumalanga

(Reynolds 2308 [PRE, BOL]). — **Distr**: RSA (Mpumalanga, KwaZulu-Natal, Gauteng, Limpopo), Swaziland.

**A. reitzii** var. **reitzii** — **Lit**: Gildenhuis (2005). **Distr**: RSA (NE Mpumalanga, Gauteng, S Limpopo), Swaziland; exposed rocky slopes, in grassland, 1200–1600 m. **I**: Reynolds (1950: 453–454, t. 50); Carter & al. (2011: 376); Wyk & Smith (2014: 184–185).

[5] Acaulescent or caulescent, simple or rarely branched; stem decumbent, to 60 cm; **L** densely rosulate, lanceolate-ensiform, to 65  $\times$  12 cm, the tip a pungent spine, surface smooth, lower face sometimes with 4–8 brownish  $\pm$  2 mm long prickles in a median line near the tip, **marginal teeth** 3 mm, pungent, brownish to reddish-brown, 7–15 mm apart; **Inf** 1–1.3 m, with 2–6 **Br**; racemes cylindrical, slightly acuminate, 35–45  $\times$  5–6 cm, very dense; **Bra** lanceolate-acute, 14  $\times$  7 mm, brownish; **Ped** 3 mm; **Fl** bright red above, lower face lemon-yellow, to 50 mm, base rounded,  $\pm$  7 mm  $\varnothing$  across the ovary, enlarged to  $\pm$  9 mm in the middle, then slightly narrowing to the mouth; **OTep** free for 20 mm; **St** and **Sty** exerted 8–10 mm. — **Cytology**:  $2n = 14$  (Müller 1941).

Symes (2017) found that the flowers are pollinated by one generalist and two specialist nectarivorous birds, and reports anecdotal evidence that the mammal *Elephantulus* sp. (Sengi) has also been seen visiting inflorescences.

**A. reitzii** var. **vernalis** D. S. Hardy (Bothalia 13(3–4): 451–452, ill., 1981). **Type:** RSA, KwaZulu-Natal (Hardy 3589 [PRE]). — **Distr:** RSA (N KwaZulu-Natal: Vryheid Distr.); steep well-drained granitic slopes, 900–1600 m.

[5] Differs from var. *reitzii*: **Bra** deltoid-acuminate, 6 × 4–5 mm; **Fr** smaller; and with different range and flowering season.

**A. rendilliorum** L. E. Newton (Bradleya 24: 107–108, ill., 2006). **Type:** Kenya, Eastern Prov. (Newton & Powys 4511 [K, EA]). — **Distr:** Kenya (Eastern Prov.: Marsabit Distr.); rock slopes, 1375 m; known only from the type locality. **I:** Carter & al. (2011: 595).

[13] Caulescent, branching freely at or near the base; stem to 1 m, erect to 30 cm then decumbent; **L** rosulate and persistent below for 20 cm, triangular, 35 × 4.5–5 cm, dark green with white spots, surface rough, exudate yellow, **marginal teeth** 2 mm, red-tipped, 5–7 mm apart; **Inf** 60 cm, erect, simple or with 1–5 **Br**; racemes cylindrical, 11–22 cm, lax; **Bra** lanceolate-acute, 15 × 4 mm; **Ped** 10 mm; **Fl** dull pink at the base, pale pink with dark midline above, 19–20 mm, 4 mm Ø across the ovary, narrowed above, enlarging to 6 mm at the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 5 mm.

**A. retrospiciens** Reynolds & P. R. O. Bally (J. South Afr. Bot. 24(4): 182–184, tt. 25–26, 1958). **Type:** Somalia (Reynolds 8482 [PRE, EA, K]). — **Lit:** Gilbert & Sebsebe Demissew (1992). **Distr:** N Somalia, SE Ethiopia (Ogaden); amongst boulders on sandy soil in deciduous bushland, 820–1160 m. **I:** Reynolds (1966: 356–357); Sebsebe Demissew & Nordal (2010: 69–70); Carter & al. (2011: 647).

**Incl.** *Aloe ruspoliana* var. *dracaeniformis* A. Berger (1908).

[8] Caulescent, sometimes simple, usually 2- to 6-branched; stem erect, 1–1.25 m × 3 cm; **L** ±12, rosulate and persistent for 10–20 cm below the stem tip, lanceolate-attenuate, tip obtuse with a few small white teeth, 25 × 5–6 cm, bluish-grey tinged reddish, sometimes with a few scattered white spots near the base, with white cartilaginous margin, **marginal teeth** 1 mm, firm, white, 5 mm

apart; **Inf** 45 cm, with ±10 **Br**; terminal raceme cylindrical, laterals mostly with secund flowers pointing backwards, 3 × 5 cm, subdense; **Bra** ovate-deltoid, 5 × 2.5 mm, white; **Ped** 5–6 mm; **Fl** yellow, greenish at the mouth, 20 mm, base rounded, 6 mm Ø across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 3–4 mm. — **Cytology:** 2n = 14 (Fentaw & al. 2013).

**A. reynoldsii** Letty (Flow. Pl. South Afr. 14: t. 558 + text, 1934). **Type:** RSA, Eastern Cape (Reynolds 140 [PRE]). — **Distr:** RSA (E Eastern Cape: valleys of the Bashee River system); rock faces and steep grassy slopes, 150–1000 m. **I:** Reynolds (1950: 300–301); Carter & al. (2011: 444); Wyk & Smith (2014: 186–187).

[7] Acaulescent or shortly caulescent, forming groups of up to 12 **Ros**; stem 5 cm Ø; **L** 16–20, densely rosulate, ovate-lanceolate, acuminate, to 35 × 11 cm, glaucous green, lineate, with many scattered oblong or H-shaped dull white spots, lower face with fewer spots, with 2 mm pink cartilaginous margin, **marginal teeth** minute, soft to firm, 1–4 mm apart; **Inf** 40–60 cm, with ±4 **Br**; racemes subcapitate, 5–6 cm, lax; **Bra** lanceolate-deltoid, 10 mm; **Ped** 20–25 mm; **Fl** yellow, tinged orange towards the mouth, 28 mm, base truncate, 7 mm Ø across the ovary, abruptly narrowed to 5 mm above, then enlarging to the mouth; **OTep** free for 5 mm; **St** and **Sty** exerted 0–2 mm.

**A. rhodesiana** Rendle (J. Linn. Soc., Bot. 40: 215, 1911). **Type:** Zimbabwe, Eastern Prov. (Swynnerton 6047 [BM]). — **Distr:** W Moçambique, E Zimbabwe; montane grassland, mostly on rocky or stony ground, 1200–2100 m. **I:** Reynolds (1966: 27–28); Carter & al. (2011: 139).

**Incl.** *Aloe eylesii* Christian (1936).

[4] Acaulescent or shortly caulescent, simple or with 2–3 **Br** at the base; **R** fusiform; stem to 10 × 3–4 cm; **L** 8–12, densely rosulate, triangular, 25–30 × 4–5 cm, dull green, lower face sometimes with a few elliptic whitish spots near the base, with narrow white cartilaginous margin,

**marginal teeth**  $\pm 0.5$ –1 mm, firm, white, 1–4 mm apart; **Inf** 40–45 cm, simple; raceme cylindrical-acuminate, 12–15  $\times$  8 cm, subdense; **Bra** ovate-acute, cuspidate, 20  $\times$  11 mm, imbricate in bud stage; **Ped** to 30 mm; **Fl** salmon-pink, 35 mm, base obconical-attenuate, 6 mm  $\varnothing$  across the ovary, enlarging slightly to just above the middle; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

The largest of the “grass aloes”.

**A. ribauensis** T. A. McCoy & al. (Cact. Succ. J. (US) 86(2): 51–53, ill. (p. 48–53), 2014). **Type:** Moçambique, Nampula (McCoy 3984 [LMU, FT]). — **Distr:** Moçambique (Nampula); granite outcrops in forest or cliff faces, 1000–1500 m.

[16] Caulescent, irregularly branched at the base or higher; stem to 3 m; **L**  $\pm 25$ , rosulate, lanceolate-long attenuate, 65  $\times$  8.5 cm, shiny dark green, lower face green with white spots near the base, **marginal teeth** uncinatate, 4 mm, white, 18 mm apart; **Inf** to 100 cm, oblique, strongly decurved, with 0–3 **Br**; racemes cylindrical, 16–25 cm, dense, with apical sterile bracts; **Bra** lanceolate-acute, 10–12 mm, greenish-white with 5 brown nerves; **Ped** 4–8 mm; **Fl** usually red, sometimes orange, 45 mm, 8 mm  $\varnothing$  across the ovary, cylindrical-ventricose above; **OTep** free for 30 mm; **St** exerted 15 mm; **Sty** exerted 10 mm.

**A. richardsiae** Reynolds (J. South Afr. Bot. 30 (2): 67–69, tt. 12–13, 1964). **Type:** Tanzania, Iringa Distr. (Richards 15604 [K, PRE]). — **Distr:** SW Tanzania; on clay soils in grassy clearings in woodland, 1075–1275 m. **I:** Reynolds (1966: 37–38); Carter & al. (2011: 117).

[1] Acaulescent, simple; **R** thick, fleshy; **L** 8–10, rosulate, with bases expanded to form an underground bulb 3–4 cm  $\varnothing$ , linear, 20–25  $\times$  1.5 cm, green, obscurely lineate, **marginal teeth** 0.5 mm, firm, white, 1–2 mm apart; **Inf** 35–45 cm, simple; raceme cylindrical-acuminate,  $\pm 25 \times 5$ –6 cm, lax; **Bra** ovate-acute, 25–30  $\times$  7–8 mm, white, imbricate in bud stage; **Ped** 5–7 mm; **Fl** pale orange-scarlet, to 48 mm, base rounded, 7–8 mm  $\varnothing$  across the ovary, slightly narrowed above,

then enlarging to the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 0–1 mm.

The new record of *A. fimbrialis* published by Newton (1998b) belongs here.

**A. richaudii** Rebmann (Cact.-Avent. Int. 79: 8–10, ill., 2008). **Type:** Madagascar, Antsiranana (Rebmann 13 [BR]). — **Distr:** N Madagascar (Antsiranana: N of Maromokotra); granite domes, 320 m; known only from the type locality. **I:** Castillon & Castillon (2010: 336–337); Carter & al. (2011: 251).

[5] Acaulescent, suckering to form clumps of 5–6 **Ros**; **L**  $\pm 18$ , rosulate, lanceolate, 30  $\times$  8 cm, bluish-green, **marginal teeth** 2 mm, yellow, 8 mm apart; **Inf** 32 cm, erect, with 1–2 **Br**; racemes capitate, 4.5–5 cm, dense, flowers opening from the top downwards; **Bra** ovate, 8–9  $\times$  3–5 mm; **Ped** 16–18 mm; **Fl** yellow, 30 mm, 7 mm  $\varnothing$  across the ovary, widening to 10 mm at the mouth; **OTep** free almost to the base; **St** and **Sty** not exerted.

**A. rigens** Reynolds & P. R. O. Bally (J. South Afr. Bot. 24(4): 177–179, tt. 20–21, 1958). **Type:** Somalia (Reynolds 8369 [PRE, EA, K]). — **Distr:** N Somalia (Borama Region); sandy flats or rocky slopes, 700–1200 m. **I:** Reynolds (1966: 124–125); Carter & al. (2011: 291).

[5] Acaulescent or shortly caulescent, usually simple, sometimes in small groups; **L**  $\pm 24$ , densely rosulate, lanceolate-attenuate, 60–80  $\times$  12–15 cm, pale to darker grey-green, sometimes reddish-tinged, exudate drying yellow to orange, **marginal teeth** 4–6 mm, pungent, reddish-brown with pale base, 20–35 mm apart; **Inf** 1.25–1.75 m, with 3–4 **Br**; racemes cylindrical-acuminate, 20–30  $\times$  6 cm, subdense; **Bra** ovate-deltoid, to 15  $\times$  6 mm, white, imbricate in bud stage; **Ped** 5–6 mm; **Fl** rose-pink to dull scarlet, very shortly pubescent, 30–34 mm, base obtuse, 7 mm  $\varnothing$  across the ovary, very slightly narrowed above and enlarging to the mouth; **OTep** free for 10–12 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

A natural hybrid with *A. megalacantha* has been reported (Reynolds 1966).

**A. rivae** Baker (in Thiselton-Dyer & al., Fl. Trop. Afr. 7: 465, 1898). **Type:** Ethiopia, Sidamo Region (*Ruspoli & Riva* 1509 [B]). — **Distr:** S Ethiopia (Sidamo Region), N Kenya; open wooded grassland on rocky slopes, 1000–2000 m. **I:** Reynolds (1966: 115–116); Sebsebe Demissew & Nordal (2010: 84–85); Carter & al. (2011: 354).

[5] Acaulescent or shortly caulescent, simple or in small groups; stem erect, ascending or decumbent, to 60 cm; **L** ±20, densely rosulate, ovate-lanceolate, 50–55 × 17–20 cm, the tip a spine, dull olive-green to brownish-green, with reddish-tinged margin, exudate drying purple, **marginal teeth** ±4 mm, firm, reddish-brown, 10–15 mm apart; **Inf** 60–70 cm, with ±12 **Br**, lower ones rebranched; racemes cylindrical or with flowers slightly secund, 10 × 7 cm, lax; **Bra** ovate-acute, 2–4 × 2–3 mm; **Ped** 12 mm; **Fl** scarlet or yellow with a bloom, 33 mm, base truncate, 10 mm Ø across the ovary, narrowed slightly to the mouth; **OTep** free for 13 mm; **St** and **Sty** exerted 4–5 mm.

**A. rivierei** Lavranos & L. E. Newton (Cact. Succ. J. (US) 49(3): 114–116, ills., 1977). **Type:** Yemen, Ta'izz (*Lavranos & Newton* 13121 [E, K]). — **Lit:** Wood (1983). **Distr:** Yemen (Ta'izz, Ibb); cliffs and rocky slopes, 1300–1900 m. **I:** Carter & al. (2011: 581).

[8] Caulescent, branching mostly at the base; stem erect, to 2 m × 5 cm; **L** ±15, rosulate, triangular-acute, 55 × 8 cm, pale green, with many pale spots on young shoots only, with white hyaline margin, **marginal teeth** 2 mm, pungent, white, tipped reddish-brown, 4–5 mm apart; **Inf** to 1.2 m, with 2 **Br**; racemes cylindrical-acuminate, lax; **Bra** 10 × 7 mm, pale green, imbricate in bud stage; **Ped** to 15 mm; **Fl** coral-red, becoming yellow to orange towards the mouth, sometimes entirely yellow, 30 mm, base rounded, 4 mm Ø across the ovary, very slightly narrowed above, enlarging slightly to the mouth; **OTep** free for 11–13 mm; **St** and **Sty** exerted 5 mm. — **Cytology:** 2n = 14 (Wood 1983).

This is probably conspecific with *A. arborea* Forsskål, which is currently treated as a *nomen ambiguum* but would have priority if its identity were to be confirmed (Wood 1983).

**A. rodolphei** J.-B. Castillon (Cact.-Avent. Int. 77: 3–4, ills., 2008). **Type:** Madagascar, Toamasina (*Castillon* 38 [TAN]). — **Distr:** W Madagascar (Toamasina: near Andapa); quartzitic hills; known only from the area of the type locality. **I:** Castillon & Castillon (2010: 340–341); Carter & al. (2011: 245).

[4] Acaulescent, solitary or suckering to form small groups with up to 3 **Ros**; **L** up to 30, rosulate, lanceolate with rounded toothed apex, 20–30 × 4–6 cm, green, **marginal teeth** 2 mm, yellow, 4–10 mm apart; **Inf** 1 m, erect, simple or with up to 4 **Br**; racemes capitate to shortly cylindrical, subdense, often with bulbils, flowers opening from the top downwards; **Bra** 5 × 5 mm; **Ped** 16–24 mm; **Fl** yellow, 23 mm, 7 mm Ø across the ovary; **OTep** free to the base; **St** and **Sty** exerted to 1 mm.

**A. rooeslii** Lavranos & T. A. McCoy (Kakt. and. Sukk. 56(3): 67–68, ills., 2005). **Type:** Madagascar, Antsiranana (*Röösli & Hoffmann* 53/01 [TAN]). — **Distr:** N Madagascar (Antsiranana: Tsingy de l'Ankarana); tsingy limestone outcrops, ±150 m. **I:** Castillon & Castillon (2010: 322–323); Carter & al. (2011: 336).

[5] Usually acaulescent, solitary; stem when present erect, less often procumbent to 125 cm; **L** up to 30, rosulate, deltoid-acute, 50 × 5.5 cm, silver-grey, tinged pink or reddish, exudate light lemon-yellow, drying light brown, **marginal teeth** 1.5 mm, pink, 5–9 mm apart; **Inf** 90 cm, erect, with many **Br**, lowermost re-branched; racemes conical, 25 cm, lax; **Bra** acute, 6–12 mm; **Ped** 18 mm; **Fl** bright red, yellowish in the upper ½, 35 mm, 5 mm Ø across the ovary, narrowed to 4 mm above; **OTep** free for 20 mm; **St** and **Sty** exerted 1–2 mm.

**A. rosea** (H. Perrier) L. E. Newton & G. D. Rowley (Excelsa 17: 61, 1997). **Type:** Madagascar, Antananarivo (*Perrier* 13979 [K]). — **Distr:** C Madagascar (Antananarivo: Imerina); deep shade in deciduous forest, on limestone, ±400–800 m. **I:** Rauh (1995: 100, 328); Castillon & Castillon (2010: 58); Carter & al. (2011: 267).

≡ *Lomatophyllum roseum* H. Perrier (1926).



[6,7] Acaulescent, suckering; **L** 12–15, laxly rosulate, lanceolate-attenuate, 30–45 × 2.5–4 cm, dull green, **marginal teeth** 5 mm, brown, 6–18 mm apart; **Inf** 25–30 cm, simple or with 1–3 **Br**; racemes cylindrical, 6–12 cm, subdense, with 25–30 flowers; **Bra** acute, to 5–6 mm; **Ped** 5–6 mm; **Fl** white at the base, rose-pink above, 22–25 mm, base rounded, narrowed above the ovary, then enlarging to the mouth; **OTep** free for 4.5–5 mm; **St** and **Sty** exerted 0–1 mm; **Fr** berries.

Plants from the Montagne d’Ambre, in the N of Madagascar, had been labelled “*Aloe cf. rosea*”. Apart from their geographical occurrence far from known localities of *A. rosea*, these show morphological differences and have been described as *A. martialii* (Castillon 2010).

**A. rouxii** Van Jaarsveld (Avonia 34(1): 12, ill., 2016). **Type:** RSA, Mpumalanga (*Roux* s.n. [NBG]). — **Distr:** RSA (Mpumalanga); rocky grassland with scattered small trees and shrubs, ±1000 m.

[10] Caulescent, branching to form tufts of up to 22 stems, rarely solitary; stem to 12 cm, covered with dead leaf remains; **L** 12–18, densely multifarious, linear, 6–12 × 0.15 cm, bright green, **marginal teeth** 0.3 mm, whitish, 1–2 mm apart; **Inf** 11–20 cm, erect, simple; raceme cylindrical, 2–4 cm, dense; **Bra** triangular-attenuate, 10 × 5 mm; **Ped** 12–18 mm; **Fl** yellow, 12–14 mm, 4 mm Ø across the ovary, widening to 5 mm above; **OTep** free for 3–5 mm; **St** and **Sty** exerted 3 mm.

**A. rubrodonta** T. A. McCoy & Lavranos (Haseltonia 13: 31–32, ill., 2008). **Type:** Somalia, Borama (*McCoy* 2903 [FT]). — **Distr:** NW Somalia (Borama); limestone outcrop, 1525 m; known only from the type locality. **I:** Carter & al. (2011: 157).

[5] Acaulescent, solitary or suckering to form groups with up to 3 **Ros**; **L** 12–18, rosulate, ovate-lanceolate, 10–15 × 4 cm, jade-green with H-shaped white spots above, heavily spotted below, exudate clear, drying yellow, **marginal teeth** deltoid, 1.5 mm, red, 4–5 mm apart; **Inf** 30 cm, with up to 3 **Br**; racemes subcapitate, 8–10 cm, dense; **Bra** 13–16 mm, fleshy;

**Ped** 30–32 mm; **Fl** dull orange-yellow with waxy bloom, yellow at the mouth, 30–35 mm, 11–12 mm Ø across the ovary, narrowed above, then widening, and narrowed to 7 mm at the mouth; **OTep** free for 5 mm; **St** exerted 3 mm; **Sty** exerted 6 mm.

**A. rubroviolacea** Schweinfurth (Bull. Herb. Boissier [sér. 1] 2(App. 2): 71, 1894). **Type:** Yemen (*Schweinfurth* 1658 [K [iso]]). — **Lit:** Wood (1983). **Distr:** SW Saudi Arabia, Yemen; rocky slopes, 2500–3300 m. **I:** Lavranos (1970: t. 1610); Collenette (1999: 28); Carter & al. (2011: 584).

[13] Caulescent, suckering; stem decumbent, to 1 m; **L** densely rosulate, lanceolate-ensiform, 60 × 10–11 cm, red-violet with a bloom, **marginal teeth** ±2–3 mm, reddish, hooked, 20–25 mm apart; **Inf** 1 m, arcuate-ascending, simple or with 1 **Br**; racemes cylindrical, 30–40 × 8–10 cm, very dense; **Bra** lanceolate-acute, 20–30 × 11 mm; **Ped** 2–4 mm; **Fl** bright red, 25–35 mm, ventricose, base rounded, enlarged above the ovary to the middle, slightly narrowing to the mouth; **OTep** free for ±15 mm; **St** and **Sty** exerted 10–15 mm. — **Cytology:** 2n = 14 (Wood 1983).

Yellow-flowered plants are also reported, but may belong with *A. pseudorubroviolacea*.

**A. rugosifolia** M. G. Gilbert & Sebsebe (Kew Bull. 47(4): 652–653, 1992). **Type:** Kenya, North East Prov. (*Ruspoli & Riva* 476 [B, FT]). — **Distr:** S Ethiopia (Sidamo), N Kenya (North East Prov.); dry *Acacia-Commiphora* bushland, shelter of bushes, 1060–1700 m. **I:** Reynolds (1966: 159, as *A. otallensis* var. *elongata*); Sebsebe Demissew & Nordal (2010: 74–75); Carter & al. (2011: 604).

≡ *Aloe otallensis* var. *elongata* A. Berger (1908).

[5] Caulescent, sometimes simple, usually in small groups; stem becoming decumbent, to 50 cm; **L** 16–20, densely rosulate, lanceolate-attenuate, 20–40 × 5.5–8 cm, deep green to brownish-green with many scattered dull white lenticular spots, surface finely rugose, exudate drying yellow, **marginal teeth** 3–5 mm, rigid, reddish-brown with paler base, 10–15 mm apart;



**Inf** 1.5–1.8 m, with 8–10 **Br**; racemes cylindrical-acuminate, 10–20 cm, lax; **Bra** ovate-acute, 10–13 × 4–8 mm, white; **Ped** 5.5–7 mm; **Fl** rose-pink, 25–28 mm, base rounded, 5–6 mm Ø across the ovary, slightly enlarged to 8 mm above; **OTep** free for 15 mm; **St** and **Sty** exerted 0–1 mm.

**A. rugosquamosa** (H. Perrier) J.-B. Castillon & J.-P. Castillon (Aloe Madagascar, 28, 2010). **Type:** Madagascar, Antananarivo (Perrier 10993 [P]). — **Distr:** Madagascar (Antananarivo: Ivo-hibe & Iarambo Mts.); quartzite rocks, 1500–1800 m. **I:** Reynolds (1966: 426); Carter & al. (2011: 228); both as *A. compressa* var.; Castillon & Castillon (2010: 74–75).

≡ *Aloe compressa* var. *rugosquamosa* H. Perrier (1926).

[2] Acaulescent, solitary; **L** ±20, distichous, narrowly lanceolate, to 23 × 3–3.5 cm, greyish, upper face rough, with tiny obtuse protuberances, **marginal teeth** < 2 mm, 2–4 mm apart; **Inf** 80 cm, erect, usually with 1 **Br**; racemes cylindrical-capitate, 14 cm, dense; **Bra** 55 × 15 mm; **Ped** ± none; **Fl** white, 55 mm, tubular with flaring tips; **OTep** with green midvein area; **Fil** included; **Sty** exerted up to 5 mm.

**A. rulkensii** T. A. McCoy & O. J. Baptista (Cact. Succ. J. (US) 88(4): 173–176, ill., 2016). **Type:** Moçambique, Nampula (McCoy 4187 [FT]). — **Distr:** Moçambique (Nampula); granite cliffs, 1700 m.

[13] Caulescent, branching at the base; stem to 190 × 0.8–1.4 cm, pendulous; **L** 5–9, distichous, becoming rosulate on older stems, narrowly ensiform, 50 × 10 cm, green, occasionally with few white spots, exudate clear, drying light yellow, **marginal teeth** usually absent, sometimes 1 mm, deltoid, 1–2 mm apart; **Inf** 70 cm, arcuate-ascending, simple; raceme cylindrical-conical, 10–12 cm, lax; **Bra** lanceolate-acute, 4–5 × 3 mm, white, scarious, with 3–5 brown nerves; **Ped** 10–12 mm, orange; **Fl** orange, 20–23 mm, 4.5 mm Ø across the ovary, narrowing towards the mouth; **OTep** free to the base; **St** and **Sty** exerted 1 mm.

**A. rupestris** Baker (in Thiselton-Dyer, Fl. Cap. 6: 327–328, 1896). **Type:** RSA, KwaZulu-

Natal (*MacOwan* 1556 [SAM]). — **Distr:** S Moçambique, Swaziland, RSA (KwaZulu-Natal); tall bush on rocky slopes in hot valleys, 30–1000 m. **I:** Reynolds (1950: 473–474); Carter & al. (2011: 689); Wyk & Smith (2014: 74–75).

**Incl.** *Aloe pycnantha* MacOwan ms. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Aloe nitens* Baker (1880) (*nom. illeg.*, ICN Art. 53.1).

[9] Caulescent, mostly simple; stem erect, to 8 m × 20 cm, dead leaves persisting in the upper 1/3; **L** ±30–40, densely rosulate, lanceolate-attenuate, to 70 × 7–10 cm, dull to slightly glossy deep green, with deep pink to pale red margin, **marginal teeth** 4–6 mm, pungent, reddish-brown, 8–12 mm apart; **Inf** 1–1.25 m, with 6–9 **Br**, lower ones rebranched; racemes cylindrical, slightly acuminate, 20–25 × 7 cm, very dense; **Bra** ±1 × 2 mm; **Ped** 1 mm; **Fl** lemon-yellow, becoming orange-yellow to brownish-yellow towards the mouth, 20 mm, slightly ventricose, base rounded, 4 mm Ø across the ovary, enlarged above to ± the middle, then narrowing to the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 15–20 mm. — **Cytology:** 2n = 14 (Riley 1959).

Natural hybrids with *A. marlothii* have been reported (Reynolds 1950).

**A. rupicola** Reynolds (J. South Afr. Bot. 26 (2): 89–91, tt. 10–11, 1960). **Type:** Angola, Bié (Reynolds 9243 [PRE, K, LUAI]). — **Distr:** C Angola (Bié); rocky hills, 1780 m; known only from the type locality. **I:** Reynolds (1966: 323–324); Carter & al. (2011: 683).

[9] Caulescent, simple or branched at the base; stem erect, to 5 m × 10–12 cm; **L** ±40, densely rosulate, lanceolate, 40–45 × 6 cm, apical 10 cm usually drying early, green, obscurely lineate, exudate drying pale yellow, **marginal teeth** 4–5 mm, pungent, reddish-brown, 10 mm apart; **Inf** 70–90 cm, with 3–8 **Br**; racemes cylindrical, 15–18 × 8–9 cm, subdense; **Bra** ovate-acute, 9 × 5 mm; **Ped** 12 mm; **Fl** orange-scarlet, 42 mm, base very shortly attenuate, 7 mm Ø across the ovary, slightly enlarged above; **OTep** free for 21 mm; **St** and **Sty** exerted 2–3 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. ruspoliana** Baker (in Thiselton-Dyer & al., Fl. Trop. Afr. 7: 460, 1898). **Type:** Ethiopia, Harar Prov. (*Ruspoli & Riva* 918 [B]). — **Distr:** S & SE Ethiopia, Kenya, S & C Somalia; open rocky hillsides in arid *Acacia-Commiphora* bushland, 300–1450 m. **I:** Reynolds (1966: 254); Sebsebe Demissew & Nordal (2010: 67–68); Carter & al. (2011: 460).

**Incl.** *Aloe stephaninii* Chiovenda (1916); **incl.** *Aloe jex-blakeae* Christian (1942).

[7] Acaulescent or shortly caulescent, suckering to form groups, sometimes large; stem ascending or decumbent, to 50 cm; **L** ±16, densely rosulate, lanceolate-attenuate, 50–60 × 12 cm, yellowish-green, sometimes with a few lenticular white spots near the base, surface smooth, exudate very pale yellow, almost colourless, **marginal teeth** to 0.5 mm, white, 5–8 mm apart; **Inf** ≥ 1.5 m, with ≥12 **Br**; racemes capitate, 2–4 × 5 cm, dense; **Bra** deltoid-acute, 3 × 1.5 mm; **Ped** 5 mm; **Fl** yellow, 16–20 mm, base rounded, 5 mm Ø across the ovary, enlarging above to ±6–7 mm at the mouth; **OTep** free for 6–8 mm; **St** and **Sty** exerted 2–4 mm.

According to Lebrun & Stork (2012) the type of *A. defalcata*, currently treated as a name of unresolved application, seems to be a mixture of *A. microdonta* and *A. ruspoliana*. The plant is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984), and has been used locally to kill hyaenas. Some accidental human deaths are also reported, when the plant was mistakenly used medicinally as *A. vera* (Verdcourt & Trump 1969).

**A. ruvuensis** T. A. McCoy & Lavranos (*Aloe* 44(1): 51, ill., 2007). **Type:** Tanzania, Arusha Prov. (*McCoy* 1162 [FT]). — **Distr:** N Tanzania (Arusha Prov.: Lossogoni Plateau); granite inselbergs, 830 m; known only from the type locality. **I:** Carter & al. (2011: 197).

[3] Acaulescent, solitary; **L** 12–15, rosulate, ovate-lanceolate, 60 × 20 cm, dull greyish-green to reddish, usually with oblong whitish spots in transverse bands, lower surface whitish-green without spots, exudate drying brownish, **marginal teeth** deltoid, 6 mm, red, 5–10 mm apart; **Inf** 1 m, erect, with up to 20 **Br**, lowermost

rebranched; racemes capitate to subcapitate, 10–40 cm, subdense; **Bra** linear-lanceolate, 15 × 3 mm; **Ped** to 20 mm, dark violet-red; **Fl** red, with waxy coating, yellowish at the mouth, 38–40 mm, 10 mm Ø across the ovary, narrowed above to 5 mm, widening to the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 0–1 mm.

**A. sabaea** Schweinfurth (Bull. Herb. Boissier [sér. 1] 2(App. 2): 74, 1894). **Type** [lecto]: Yemen (*Schweinfurth* 1010 [G]). — **Distr:** SW Saudi Arabia, Yemen; cliffs and steep rocky slopes, 150–2060 m. **I:** Reynolds (1966: 313, as *A. gillilandii*); Collenette (1999: 28); Carter & al. (2011: 662).

≡ *Aloidendron sabaea* (Schweinfurth) Boatwright & J. C. Manning (2014); **incl.** *Aloe gillilandii* Reynolds (1962).

[9] Caulescent; stem erect, simple, to 3 m × 10 cm; **L** ±16, densely rosulate, lanceolate-acute, lowest leaves decurved, 60–80 × 15 cm, grey-green, with pale pink cartilaginous margin, **marginal teeth** 1–1.5 mm, soft, pale pink, 5–10 mm apart; **Inf** ±90 cm, with ±8 **Br**; racemes cylindrical-acuminate, 15 × 6 cm, subdense; **Bra** ovate-acute, 10–17 × 8–13 mm, imbricate in bud stage; **Ped** 12 mm; **Fl** scarlet to red-brown, paler at the mouth, 22–30 mm, base rounded, 10 mm Ø across the ovary, not narrowed above except at the upturned mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Johnson & Brandham 1997).

The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984).

**A. sanguinalis** Awale & Barkworth (*Phytokeys* 117: 89–90, ill., (pp. 87–88, 90–91), 2019). **Type:** Somaliland (*Barkworth & al.* S17.001 [HARG]). — **Distr:** Somaliland; open plains with sandy soils, 950 m.

[13] Branching to form dense clumps to 10 (–40) m wide; stem decumbent, rooting at the lower nodes; **L** ±10–12, rosulate, lanceolate, 30–40 × 5–8 cm, blue-green, margins diffused reddish with age, exudate yellow changing quickly to bright red, drying to dark red or brownish-red, **marginal teeth** 4–6 mm, red, 10–30 mm apart, closer towards the leaf tip; **Inf**

70–120 cm, erect, with 6 **Br**; racemes cylindrical, 10 cm, lax; **Bra** narrowly triangular, 5–9 mm; **Ped** 10 mm; **Fl** red, 25–30 mm,  $\pm 6$  mm  $\varnothing$  across the ovary, scarcely narrower above; **OTep** free for 10 mm; **St** exerted 1 mm; **Sty** exerted 5–9 mm.

**A. saudiarabica** T. A. McCoy (Excelsa 21: 6, ill. (pp. 3–4), 2007). **Type:** Saudi Arabia, Asir Prov. (McCoy 2744 [MO]). — **Distr:** SW Saudi Arabia (Asir Prov.); sandy alluvial plains, 365 m. **I:** Carter & al. (2011: 293).

[4] Shortly caulescent, suckering to form small groups; **L** 15–18, rosulate, lanceolate-acuminate, 85  $\times$  12 cm, dull greyish-green, exudate orange, drying brown, **marginal teeth** 3 mm, brown-tipped, 10–15 mm apart; **Inf** 1 m, erect, simple or with 1–2 **Br**; racemes cylindrical-acuminate, 20–25 cm, sublax; **Bra** ovate-acute, 10 mm; **Ped** 6–8 mm; **Fl** red or yellow, 27–31 mm, 5–7 mm  $\varnothing$  across the ovary; **OTep** free for 12–15 mm; **St** and **Sty** exerted 0–1 mm.

**A. saundersiae** (Reynolds) Reynolds (J. South Afr. Bot. 13(2): 103, ill., 1947). **Type:** RSA, KwaZulu-Natal (Reynolds 1799 [PRE]). — **Distr:** RSA (C KwaZulu-Natal: near Nkandhla Forest); in clumps of moss in rock crevices or in grass, 1200–1300 m; known only from the area of the type locality. **I:** Reynolds (1950: 111, t. 1); Craib (2006: 104–107); Carter & al. (2011: 109); Wyk & Smith (2014: 352–353).

$\equiv$  *Leptaloe saundersiae* Reynolds (1936); **incl.** *Aloe minima* Medley-Wood (1906) (*nom. illeg.*, ICN Art. 53.1).

[1] Acaulescent, simple or in small groups; **R** fusiform; **L** 10–16, rosulate, linear, 4–8  $\times$  0.3 cm, green, lower face sometimes with a few spots near the base, **marginal teeth**  $\pm 0.5$  mm, soft, white, 1 mm apart; **Inf** 14–18 cm, simple; raceme capitate, 2–2.5  $\times$  3–3.5 cm, subdense, with 12–16 flowers; **Bra** ovate-acuminate, 7  $\times$  3–4 mm, white; **Ped** 9–10 mm; **Fl** pale cream-pink, 10–12 mm, base attenuate, not narrowed above the ovary; **OTep** free to the base; **St** and **Sty** not exerted. — **Cytology:** 2n = 14 (Müller 1945: as *Leptaloe*).

**A. scabrifolia** L. E. Newton & Lavranos (Cact. Succ. J. (US) 62(5): 219–221, ill., 1990). **Type:**

Kenya, Rift Valley Prov. (Newton 3476 [K, EA, MO]). — **Lit:** Reynolds (1996). **Distr:** E Kenya (E of the Rift Valley); open *Acacia* bushland, 1000–1630 m. **I:** Reynolds (1966: 225, as *A. turkanensis*); Carter & al. (2011: 597).

[13] Caulescent, branching sparsely at the base, stem erect for  $\pm 30$  cm, becoming decumbent to 1.2 m  $\times$  3–4 cm  $\varnothing$ ; **L** to 25, laxly rosulate, lanceolate-attenuate, often slightly falcate, to 55  $\times$  10–12.5 cm, dull green to grey-green with few to many scattered elliptic white spots, with narrow white margin, surface rough, exudate drying brown, **marginal teeth** to 2 mm, uncinat, white, 7–15 mm apart; **Inf** to 1.4 m, ascending, with up to 12 **Br**; racemes with secund flowers, 30–45 cm, lax; **Bra** triangular, 3  $\times$  2–3 mm; **Ped** 5 mm; **Fl** dull red, with paler margins on the tepals, 25 mm, base rounded, 6–7 mm  $\varnothing$  across the ovary, narrowed to 5 mm above, then enlarging to 7 mm at the mouth; **OTep** free for 12–13 mm; **St** and **Sty** exerted 2–4 mm.

Reynolds (1966) confused this with *A. turkanensis*, which differs in several characters, notably its tighter growth habit and its very smooth leaves. The two species are also distinct in the chemistry of their leaf exudates (Reynolds 1996).

**A. schelpei** Reynolds (J. South Afr. Bot. 27(1): 1–3, tt. 1–2, 1961). **Type:** Ethiopia, Shoa Prov. [Shewa Region] (Curle & Schelpe 61 [BM]). — **Distr:** C Ethiopia (Shewa Region); grassland on steep basalt slopes and cliffs with evergreen bushland, 1700–2470 m. **I:** Reynolds (1966: 284–286); Sebsebe Demissew & Nordal (2010: 98–99); Carter & al. (2011: 573).

[6] Caulescent, branching at the base and above to form dense groups; stem decumbent, to 50  $\times$  5–6 cm  $\varnothing$ ; **L** 16–20, rosulate, lanceolate-attenuate, 45  $\times$  10–12 cm, glaucous tinged bluish, sometimes with several pale green to creamy lenticular spots near the base, lower face deeper green usually with several spots near the base, with prominent reddish-pink margin, exudate drying dark brown, **marginal teeth** 2–3 mm, firm, reddish-pink, paler tipped,  $\pm 15$  mm apart; **Inf** 50 cm, simple or with 1 **Br**; racemes cylindrical-conical, 6–9  $\times$  6–7 cm, dense; **Bra** ovate-acute,

5 × 3 mm; **Ped** 13–15 mm; **Fl** orange-red, paler at the mouth, 28–30 mm, base rounded, 7 mm Ø across the ovary, slightly narrowed above, then slightly enlarging to the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology**: 2n = 14 (Brandham 1971).

**A. schilliana** L. E. Newton & G. D. Rowley (Excelsa 17: 61, 1997). **Type**: Madagascar, Antsiranana (Perrier 1104 [P]). — **Lit**: Carter & al. (2011: 580). **Distr**: NW Madagascar (Antsiranana: Sambirano, near Migioko); on gneiss, 200 m. **I**: Castillon & Castillon (2010: 353).

≡ *Lomatophyllum viviparum* H. Perrier (1926).

[6] Caulescent, simple; stem prostrate, short; **L** 12–15, laxly rosulate, lanceolate-attenuate, 45–55 × 2.5–3.5 cm, green, tip with 3 spines, **marginal teeth** ±1 mm, green, crowded; **Inf** 50–80 cm, simple, with bulbils developing in the axils of sterile bracts below the raceme; raceme cylindrical, ±13 cm, subdense; **Bra** acute, ½–½ as long as the pedicels; **Ped** 8–10 mm; **Fl** purple-red, green-tipped, 30–33 mm, 6–7 mm Ø across the ovary; **OTep** free for 10–11 mm; **St** and **Sty** disposition not described; **Fr** berries.

**A. ×schimperi** Todaro *pro sp.* (Hort. Bot. Panorm. 1: 70–72, t. 16, 1878). **Type**: [lecto — icono] l.c. t. 16. — **Lit**: Figueiredo & Smith (2016). **Distr**: RSA (E Western Cape, W Eastern Cape); grassland.

**Incl.** *Aloe ×schoenlandii* Baker *pro sp.* (1902).

[7] Acaulescent, suckering to form groups; **L** to 20, rosulate, oblong, 34 × 11 cm, light green, **marginal teeth** red; **Inf** to 75 cm, erect, with 6–7 **Br**; racemes capitate, dense; **Ped** 28 mm; **Fl** bright orange or dull pinkish, 45 mm, 10 mm Ø across the ovary, abruptly narrowed above, then widening to the mouth.

This is the naturally occurring hybrid *A. striata* × *A. maculata*, common wherever the distribution range and flowering time of the parents overlap, and established as neophyte in California (USA), and probably also elsewhere.

**A. schoelleri** Schweinfurth (Bull. Herb. Boissier [sér. 1] 2(App. 2): 107–108, 1894).

**Type**: Eritrea (*Schweinfurth* 158 [B, K]). — **Distr**: Eritrea (Kohaito Plateau); hanging from cliffs, 2300–2600 m; known only from the type locality. **I**: Medhanie & Dioli (2006); Sebsebe Demissew & Nordal (2010: 59–60); Carter & al. (2011: 516).

[13] Caulescent, solitary or forming small groups; stem to 1 m, decumbent or pendulous, with dried leaves persistent; **L** 25–40, rosulate, deltoid, 40–52 × 9–14 cm, grey-green tinged purple, surface smooth, exudate drying reddish-brown, **marginal teeth** deltoid, 1–2 mm, reddish, 50–80 mm apart, more numerous towards the base; **Inf** 50–80 cm, oblique with raceme erect, simple, rarely with 1 **Br**; racemes conical-cylindrical, 30–45 cm, very dense; **Bra** rhomboidal to obovate, acute, 18–24 × 8–10 mm, minutely papillate; **Ped** ±10 mm; **Fl** yellow to pinkish-orange, 26–32 mm, 6–8 mm Ø across the ovary, narrowing towards the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 12–14 mm.

Remained imperfectly known until its rediscovery by D. C. H. Plowes in 1994.

**A. schomeri** Rauh (Kakt. and. Sukk. 17(2): 22–24, ill., 1966). **Type**: Madagascar, Toliara (*Rauh* M1382 [HEID, PRE]). — **Distr**: SE Madagascar (Toliara); gneissic rocky hills. **I**: Reynolds (1966: 429–430); Castillon & Castillon (2010: 222); Carter & al. (2011: 244).

[4] Acaulescent or very shortly caulescent, simple or suckering to form groups; **L** ±30, densely rosulate, lanceolate-attenuate, 20–30 × 3–5 cm, dark green, with pale, almost white, cartilaginous margin, **marginal teeth** 2 mm, pale, almost white, 5–8 mm apart; **Inf** usually simple, sometimes with 1–2 **Br**; racemes subcapitate or shortly cylindrical, 6–10 × 7 cm, dense, with 60–70 flowers; **Bra** ±9 × 5 mm; **Ped** 12 mm; **Fl** yellow, 21 mm, base rounded, enlarging above the ovary to the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 5–8 mm.

Castillon & Castillon (2016: 115) found this species sympatrically with *A. versicolor* and *A. versicolor* ssp. *steffanieana*, and the latter is thought to possibly be the hybrid *A. schomeri* × *A. versicolor*, or alternatively, all these taxa plus

*A. buchlohii* “might be only forms of a still evolving variable species”.

**A. schweinfurthii** Baker (J. Linn. Soc., Bot. 18(108): 175, 1880). **Type:** Democratic Republic of the Congo [Zaire] (*Schweinfurth* ser. 3, 167 [K]). — **Distr:** Burkina Faso, Cameroon, Central African Republic, Ghana, Mali, N & W Nigeria, South Sudan, Sudan, Uganda, NE Democratic Republic of the Congo [Zaire], Benin; granite outcrops, 600–1200 m. **I:** Reynolds (1966: 289–290); Carter & al. (2011: 456); Cole & Forrest (2017: 108–113).

**Incl.** *Aloe barteri* Baker (1880); **incl.** *Aloe barteri* var. *lutea* A. Chevalier (1913); **incl.** *Aloe trivialis* A. Chevalier (1952) (*nom. inval.*, ICN Art. 39.1).

[7] Acaulescent or shortly caulescent, suckering to form dense groups; **L** 16–20, densely rosulate, lanceolate-attenuate, 30–60 × 6–7 cm, grey-green tinged bluish, usually with a few scattered whitish spots near the base, surface smooth, exudate drying purplish, **marginal teeth** 4 mm, pungent, reddish-brown, 10–12 mm apart; **Inf** 90 cm, with 8–10 **Br**; racemes cylindrical-acuminate, 15 × 7 cm, subdense; **Bra** ovate-acute, 5 × 2–3 mm; **Ped** 13 mm; **Fl** scarlet, becoming orange at the mouth, 28 mm, base shortly attenuate, 7 mm Ø across the ovary, slightly narrowed above; **OTep** free for 12 mm; **St** and **Sty** exerted 2–5 mm. — **Cytology:** 2n = 14 (Newton 1970).

Until 1963 only one *Aloe* species was reported from West Africa, *A. barteri*. Keay (1963) showed that the type specimen of this name was a mixture of 2 taxa, *A. buettneri* and *A. schweinfurthii* (see comment under *A. buettneri*).

A natural hybrid with *A. buettneri* is known as *A. ×keayi* (Newton 1976). A natural hybrid with *A. macrocarpa* var. *major* is also known (Newton, unpubl.). The occurrence in Benin was reported by Newton (1970).

**A. scobinifolia** Reynolds & P. R. O. Bally (J. South Afr. Bot. 24(4): 174–175, tt. 17–18, 1958). **Type:** Somalia (Reynolds 8403 [PRE, EA, K]). — **Distr:** N Somalia (Erigavo to Galgallo); exposed gypsum soils on arid limestone slopes,

1250–1800 m. **I:** Reynolds (1966: 197–199); Carter & al. (2011: 313).

[5] Acaulescent or shortly caulescent, simple or usually forming small groups; **L** 16–20, densely rosulate, lanceolate-attenuate, 30 × 7 cm, the tip a spine, dull green, with very narrow pale pink cartilaginous margin, surface rough, exudate drying deep brown, **marginal teeth** absent; **Inf** 60–70 cm, with 5–8 **Br**; racemes capitate-corymbose, 3–4 × 6 cm, dense; **Bra** deltoid, deflexed, 8 × 2 mm, white; **Ped** 15–18 mm; **Fl** yellow, orange or scarlet, 22 mm, slightly clavate, base shortly attenuate, 4–5 mm Ø across the ovary, enlarged above; **OTep** free for 9–10 mm; **St** exerted 3–4 mm; **Sty** exerted 5 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. scorpioides** L. C. Leach (J. South Afr. Bot. 40(2): 106–111, ill., 1974). **Type:** Angola, Namibe (Moçâmedes) (Leach & Cannell 14654 [LISC, BM, BR, K, LUA, LUAI, M, MO, PRE, SRGH, ZSS]). — **Lit:** Jaarsveld (2015). **Distr:** SW Angola (Huila, Namibe: Serra da Chela); rocky slopes, often in the shade of woodland; 1250–1800 m. **I:** Carter & al. (2011: 492).

[11] Caulescent, branching at the base and above; stem usually divergent, 10–50 (–100) cm; **L** 7–11, laxly rosulate, persistent below, ovate-attenuate, 15–30 × 2.5–3.5 cm, yellowish-green, lower face darker, obscurely lineate, rarely with a few spots near the base, surface smooth, **marginal teeth** 2–3 mm, pungent, yellowish- or brownish-tipped, 6–15 mm apart, leaf sheath 1–2 cm, striate; **Inf** 15–43 cm, descending at the base and curving upwards again with U-bend, simple or with 1–2 **Br**; racemes conical or cylindrical-acuminate, 10–25 × 6 cm, subdense; **Bra** ovate, subacute or acuminate, 6.5–9 × 3.5–4 mm, orange-brown; **Ped** 6–13 mm; **Fl** scarlet to dull orange-pink, yellow-striped with green patch at the base, 21–30 mm, base very shortly attenuate, ±7 mm Ø across the ovary, narrowed to ±5.5 mm above, then enlarging to the mouth; **OTep** free for 8.5–10 mm; **St** and **Sty** exerted 1–2 mm.

**A. secundiflora** Engler (Pfl.-welt Ost-Afr., Teil C, 140, 1895). **Type:** Tanzania, Moshi Distr. (Volkens 530 [B]). — **Distr:** Ethiopia, South





**Fig. 61** *Aloe secundiflora* var. *secundiflora*. (Copyright: L. E. Newton)

Sudan, Kenya, Rwanda, Tanzania. **I:** Carter & al. (2011: 379–380).

**A. secundiflora** var. *secundiflora* — **Distr:** S Ethiopia, South Sudan, Kenya, Rwanda, N Tanzania; grassland and open woodland on sandy soil, 750–1980 m. **I:** Reynolds (1966: 231–233); Sebsebe Demissew & Nordal (2010: 85–87); Carter & al. (2011: 379). — Fig. 61.

**Incl.** *Aloe engleri* A. Berger (1905); **incl.** *Aloe floramaculata* Christian (1940); **incl.** *Aloe marsabitensis* I. Verdoorn & Christian (1940).

[5,7] Acaulescent or very shortly caulescent, usually simple, sometimes in small groups; **L** ±20, densely rosulate, ovate-lanceolate, attenuate, 30–75 × 8–30 cm, glossy dull green, often with horny margin, surface smooth, exudate drying yellow, **marginal teeth** 3–6 mm, pungent, dark brown, 10–20 mm apart; **Inf** 1–1.5 m, with 10–12 **Br**, lower ones rebranched; racemes with

second flowers, 15–20 cm, lax; **Bra** ovate-acute, 3–7 × 2–5 mm; **Ped** 5–10 mm; **Fl** rose-pink to dull scarlet, paler at the mouth, 25–35 mm, base truncate, 9 mm Ø across the ovary, slightly narrowed above, then enlarging slightly to the mouth; **OTep** free for ½ their length; **St** and **Sty** exerted 3–6 mm.

In Kenya this species is used locally as a medicinal plant, for humans and farm animals, and is a plantation crop for commercial production of leaf exudate (Newton 2004, Lubia & al. 2008, Newton 2011). The roots are used in brewing beer (Newton 2011). King (2008) and King & Stanton (2008) report that *A. secundiflora* facilitates the establishment of grass seedlings and suggest that the planting of aloes could aid in the restoration of overgrazed grasslands.

**A. secundiflora** var. *sobolifera* S. Carter (Fl. Trop. East Afr., Aloaceae, 32–33, ills., 1994). **Type:** Tanzania, Kilosa Distr. (*Congdon* 282 [K, EA, NHT]). — **Distr:** C Tanzania; woodland on sandy soil, 600–1825 m. **I:** Carter & al. (2011: 380).

≡ *Aloe sobolifera* (S. Carter) Wabuye (2006).

[7] Differs from var. *secundiflora*: Suckering to form groups, often large; **L** lanceolate, to 8–15 (–20) cm wide at the base, dark green, often with bronze hue, **marginal teeth** not pungent, never joined by a horny rim.

**A. seibanica** Orlando & El Azzouni (CactusWorld 28(4): 208–210, ills., 2010). **Type:** Yemen, Hadhramaut (*Orlando & El Azzouni* 241504 [FT]). — **Distr:** Yemen (Hadhramaut); vertical cliffs, 2000 m. **I:** Carter & al. (2011: 708).

[10] Caulescent, suckering to form groups; stem erect or ascending; **L** 4–7, rosulate, linear, apex acute, 12–26 × 2 cm, bluish-green, exudate light yellow, drying light brown, **marginal teeth** deltoid, 1 mm, brown, 2–5 mm apart; **Inf** 25–40 cm, erect, simple; raceme cylindrical, 16 cm, dense; **Bra** lanceolate-acute, 12 × 7 mm, red, green-tipped; **Ped** 6–7 mm; **Fl** coral-red to pinkish-red, 24 mm, 6 mm Ø across the ovary; **OTep** free for 10 mm; **St** and **Sty** exerted 4 mm.

**A. seretii** De Wildeman (Pl. Bequaert. 1: 28, 1921). **Type:** Democratic Republic of the Congo [Zaire], Oriental Prov. (*Seret* 299 [BR]). — **Distr:** E Democratic Republic of the Congo [Zaire]; granite rock outcrops in grass savanna, 945–1770 m. **I:** Reynolds (1966: 257–258); Carter & al. (2011: 423).

[7] Acaulescent or shortly caulescent, suckering to form dense groups; **L** ±16, densely rosulate, lanceolate-attenuate, 40 × 6–7 cm, grey bluish-green tinged reddish, sometimes with obscure dull white spots, with pinkish margin, **marginal teeth** 3–4 mm, pungent, white with reddish-brown tips, 8–10 mm apart; **Inf** 60–70 cm, with 3 **Br**; racemes cylindrical-conical, 15–20 × 5–6 cm, dense; **Bra** ovate-acute, 9–15 × 5–10 mm, pink, fleshy; **Ped** 14–18 mm; **Fl** dull to bright scarlet, 28–33 mm, base shortly attenuate, 7 mm Ø across the ovary, very slightly narrowed above; **OTep** free for 9–10 mm; **St** and **Sty** exerted 3–4 mm.

**A. sergoitensis** L. E. Newton (Haseltonia 25: 125–127, ill., 2018). **Type:** Kenya, Rift Valley Prov. (*Kruger* s.n. [EA]). — **Distr:** W Kenya (Rift Valley Prov.); rock slopes and steep cliffs, 2250 m.

[13] Caulescent, branching at the base; stem decumbent, to 140 cm; **L** 25–30, rosulate and persistent to 30 cm below, lanceolate-acuminate, to 46 × 8 cm, mid-green, with light bluish bloom, margin lighter green, surface smooth, exudate yellow, **marginal teeth** deltoid or mostly forked, 3 mm, green with reddish-brown tips, 10 mm apart, ending 7–8 cm below the leaf apex; **Inf** 45 cm, oblique, with racemes erect, with 6 **Br**; racemes cylindrical, to 10 cm, semidense; **Bra** ovate-aristate, 5 × 3 mm, scarious with prominent brown nerve continuing to the apex; **Ped** 16 mm; **Fl** coral-red, lobes paler with yellow margins towards the mouth, 22 mm, base slightly rounded, 6 mm Ø across the ovary and above; **OTep** free for 8 mm; **St** exerted 1–3 mm; **Sty** exerted 1–2 mm.

**A. serriyensis** Lavranos (J. South Afr. Bot. 31 (1): 76–77, t. 15, 1965). **Type:** Yemen (*Lavranos* 2101 [PRE]). — **Distr:** Yemen (Audhali, S slopes of Jebel Arays); wooded valleys, 300 m. **I:** Reynolds (1966: 140); Carter & al. (2011: 256).

[5] Acaulescent, usually forming small groups; **L** rosulate, attenuate, 30–35 × 6–7 cm, green, sometimes tinged brownish, obscurely lineate, **marginal teeth** small, horny, blunt, dark brown, 20–40 mm apart; **Inf** 40 cm, with 2–3 **Br**; racemes conical, 20–25 × 5 cm, lax; **Bra** deltoid, 8–10 × 3 mm; **Ped** 10 mm; **Fl** scarlet-pink with powdery bloom, 27 mm, base attenuate, 6 mm Ø across the ovary, slightly narrowed above; **OTep** free for 7–9 mm; **St** and **Sty** exerted 0–1 mm.

**A. shadensis** Lavranos & Collette (Cact. Succ. J. (US) 72(2): 82, ill., 2000). **Type:** Saudi Arabia, Hijaz Prov. (*Collette* 6718 [K]). — **Distr:** Saudi Arabia (Hijaz Prov.: Jabal Shada region); in woody vegetation, on granite slopes, 750–1800 m. **I:** Collette (1999: 29); Carter & al. (2011: 371).

[3] Acaulescent, solitary; **L** densely rosulate, spreading to ascending, lanceolate-attenuate, ±60 × 15 cm, pinkish-grey, **marginal teeth** small, pale brown, widely spaced; **Inf** to 1.5 m, erect, with 2–5 **Br**; racemes cylindrical, subdense; **Bra** 7–9 × 3–4 mm; **Ped** 7–11 mm; **Fl** pale pink, 30–35 mm, curved, base shortly attenuate, 6–7 mm Ø across the ovary, not constricted above; **OTep** free for 17 mm; **St** not exerted; **Sty** exerted 5 mm.

**A. sharoniae** N. Crouch & Gideon F. Smith (Bradleya 29: 116, figs. 1–5 (pp. 117–118), 2011). **Type:** RSA, KwaZulu-Natal (*Harrison* 980 [PRE]). — **Distr:** RSA (N to C KwaZulu-Natal), Swaziland; open grassland on rocky hillsides, 45–1700 m **I:** Wyk & Smith (2014: 332–333).

≡ *Aloe cooperi* ssp. *pulchra* Glen & D. S. Hardy (1987).

[4] Acaulescent, solitary or rarely with up to 8 **Ros**; stem to 6 cm, subterranean; **L** 6–11, distichous, attenuate, 30–44 (–82) × 1.6–2.6 (–3.9) cm, mid-green, profusely white-spotted towards the base, exudate drying translucent, **marginal teeth** hair-like, rubbery, 3–5 mm, ivory to greenish-white; **Inf** 33–59 cm, erect, simple; raceme capitate to slightly cylindrical, 3–9.5 cm, lax; **Bra** attenuate, 23–30 mm, greenish-brown becoming orange; **Ped** 33–43 mm; **Fl** bright orange-red, 25–35 mm, 6–8 mm Ø across the

ovary; **OTep** free almost to the base; **St** and **Sty** not exerted.

**A. sheilae** Lavranos (Cact. Succ. J. (US) 57(2): 71–72, ills., 1985). **Type:** Saudi Arabia, Hijaz Prov. (*Collette* 3397 [K, E, MO]). — **Distr:** Saudi Arabia (Hijaz Prov.: W of Bishah); amongst tonolite rocks,  $\pm 1600$  m. **I:** *Collette* (1999: 29); Carter & al. (2011: 357).

[5] Acaulescent or sometimes shortly caulescent, simple or sometimes with 2–3 basal suckers; **L** laxly rosulate, deltoid-acuminate, to  $55 \times 6.5$  cm, green, often with a few pale green rounded spots, with narrow white cartilaginous margin, surface rough, **marginal teeth** absent or few, to 1.5 mm, white, brown-tipped, 30–80 mm apart; **Inf** 50–70 cm, with 2–4 (–7) **Br**; racemes subcapitate or conical, subdense; **Bra** ovate-deltoid,  $5\text{--}7 \times 3\text{--}4$  mm; **Ped** 15–18 mm; **Fl** coral-red becoming yellowish, 30–35 mm, base attenuate, 5 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 20 mm; **St** and **Sty** exerted 5–7 mm.

**A. silicicola** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 42, 1926). **Type:** Madagascar, Antananarivo (*Perrier* 13160 [P]). — **Distr:** Madagascar (Antananarivo: Ibity Mts.); on quartzite, 1900–2000 m. **I:** Reynolds (1966: 454); Castillon & Castillon (2010: 98); Carter & al. (2011: 345).

[8] Caulescent, simple; stem to 2 m  $\times$  5 cm; **L** densely rosulate, lanceolate-attenuate,  $45\text{--}50 \times 7\text{--}8$  cm, green, **marginal teeth** 1–1.5 mm, green, to 7 mm apart; **Inf** 50–60 cm, with 3–4 **Br**; racemes cylindrical, 6–8 cm, subdense, with 20–25 flowers; **Bra** lanceolate-acute,  $5\text{--}6 \times 1\text{--}2$  mm; **Ped** 20–22 mm; **Fl** reddish-orange, 28–30 mm, narrowed above the ovary, from the middle enlarging to the mouth; **OTep** free to the base; **St** and **Sty** not exerted.

Castillon & Castillon (2010) incorrectly state that this species was not recollected after its discovery, see Carter & al. (2011).

**A. simii** Pole-Evans (Trans. Roy. Soc. South Africa 5: 704, 1917). **Type:** RSA, Mpumalanga (*Sim* 137 [PRE]). — **Distr:** RSA (Mpumalanga); in tall open grassveld on steep rocky slopes,

1000–1500 m. **I:** Reynolds (1950: 280–281); Carter & al. (2011: 195); Wyk & Smith (2014: 266–267).

[5] Acaulescent, simple or rarely suckering to form small groups; **L** 15–20, densely rosulate, lanceolate-attenuate,  $40\text{--}60 \times 9\text{--}12$  cm, bright to milky green, obscurely lineate, sometimes with a few obscure paler spots, **marginal teeth** 3–4 mm, horny, light brown, 10–15 mm apart; **Inf** 1–2 m, with 5–9 **Br**, lower ones sometimes rebranched; racemes cylindrical-acuminate, 30–65 cm, lax; **Bra** lanceolate-acuminate,  $\pm 12\text{--}15$  mm; **Ped** 12–15 mm; **Fl** strawberry-pink, 35–40 mm, base truncate, 12 mm  $\varnothing$  across the ovary, abruptly narrowed to 5 mm above, then enlarging to the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:**  $2n = 14$  (Müller 1945).

**A. sinana** Reynolds (J. South Afr. Bot. 23(1): 3–5, tt. 3–4, 1957). **Type:** Ethiopia, Shoa Prov. (*Reynolds* 8126 [PRE, EA, K]). — **Lit:** Carter & al. (2011: 623). **Distr:** N and C Ethiopia; basaltic slopes, often in evergreen bushland, 1250–1950 m. **I:** Reynolds (1966: 210); Sebsebe Demissew & Nordal (2010: 92–93).

[15] Caulescent, branching; stem erect or divergent, to 1 m  $\times$  8–10 cm  $\varnothing$ ; **L** 12–16, rosulate, persistent for 20 cm below, lanceolate-attenuate,  $60\text{--}70 \times 10\text{--}13$  cm, grey-green, usually with a few scattered pale green lenticular spots towards the base, spots usually more numerous on the lower face, with horny reddish margin, exudate drying deep brown, **marginal teeth** 3–4 mm, pungent, reddish-brown, 10–20 mm apart; **Inf**  $\pm 1$  m, with 4–7 **Br**; racemes conical to subcapitate,  $6\text{--}10 \times 8$  cm, subdense; **Bra** ovate-attenuate,  $5 \times 3$  mm; **Ped** 18–20 mm; **Fl** orange-scarlet, paler at the mouth, 28 mm, slightly clavate, base obconical, shortly attenuate, 6 mm  $\varnothing$  across the ovary, enlarging above; **OTep** free for 14 mm; **St** and **Sty** exerted 2–4 mm. — **Cytology:**  $2n = 14$  (Fentaw & al. 2013).

**A. sinkatana** Reynolds (J. South Afr. Bot. 23(2): 39–42, tt. 14–16, 1957). **Type:** Sudan, Kassala Prov. (*Reynolds* 8020 [PRE, K, KHU]). — **Lit:** McCoy & Lavranos (2015). **Distr:** E Sudan (Kassala Prov.: Red Sea Hills); flat sandy

ephemeral water courses, 850–1200 m. **I:** Reynolds (1966: 201–202); Carter & al. (2011: 361).

[5] Acaulescent, simple or usually suckering to form groups; **L** 16–20, densely rosulate, lanceolate-attenuate, tip rounded with 3–5 small reddish teeth, 50–60 × 6–8 cm, dull grey-green, sometimes with scattered dull white lenticular spots, usually with reddish margin, **marginal teeth** 2–3 mm, firm, pale red, 15–25 mm apart; **Inf** 75–90 cm, with 5–6 **Br**; racemes capitate or subcapitate, 4–6 × 7 cm, dense; **Bra** ±3–4 × 2 mm; **Ped** 16–20 mm; **Fl** scarlet, orange or yellow, 22 mm, base obconical and shortly attenuate, 5 mm Ø across the ovary, enlarged above; **OTep** free for 9–10 mm; **St** and **Sty** exerted 3–5 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Gilbert & Sebsebe Demissew (1997) regard this as possibly conspecific with *A. elegans*.

McCoy & Lavranos (2015) investigated material at the type locality and found that material commonly seen in cultivation as *A. sinkatana* is not conspecific with Reynolds's species, but represents a new species, which they named *A. zubb*.

**A. sladeniana** Pole-Evans (Ann. Bolus Herb. 3(1): 13, 1920). **Type:** Namibia, Windhoek (*Pearson* PSNE9000 [PRE]). — **Distr:** Namibia (Windhoek: Khomas Hochland; quartz hills, 900–1500 m. **I:** Reynolds (1950: 213); Carter & al. (2011: 400).

≡ *Gonialoe sladeniana* (Pole-Evans) Boatwright & J. C. Manning (2014) ≡ *Tulista sladeniana* (Pole-Evans) G. D. Rowley (2014); **incl.** *Aloe carowii* Reynolds (1938).

[6] Acaulescent, suckering to form groups; **L** 6–8, trifarious, lanceolate-acute, 4–8 × 3–4 cm, green with many white elongate-confluent spots scattered or in irregular transverse bands, lower face obscurely carinate towards the tip, the keel with a few small white hard prickles, with narrow whitish cartilaginous margin, **marginal teeth** ±1 mm, hard, white, 2–5 mm apart; **Inf** ±50 cm, simple or with 1–2 **Br**; racemes cylindrical-acuminate, ±18 × 7 cm, lax, with 30–40 flowers; **Bra** deltoid-acuminate, ±6 × 4 mm; **Ped** 17 mm; **Fl** dull pink, slightly greenish at the mouth, 30 mm, base truncate, 7 mm Ø across the ovary, abruptly narrowed to 5 mm above, then enlarging

to 8 mm near the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 0–1 mm.

**A. socialis** (H. Perrier) L. E. Newton & G. D. Rowley (Excelsa 17: 61, 1997). **Type** [syn]: Madagascar, Toliara (*Perrier* 1807 [P?]). — **Lit:** Carter & al. (2011: 570). **Distr:** Madagascar (Toliara, Toamasina); in forests on basalt or limestone, 600–900 m; not recently recollected in nature. **I:** Perrier (1938: 73); Castillon & Castillon (2010: 306).

≡ *Lomatophyllum sociale* H. Perrier (1926).

[15] Caulescent, branching to form dense bushes; stem prostrate or ascending, to 30 cm; **L** 14–16, laxly rosulate, narrowly lanceolate-attenuate, 30–40 × 1–1.5 cm, green, **marginal teeth** 3 mm, greenish, 12 mm apart, leaf sheath to 2 cm; **Inf** 15–25 cm, usually simple, rarely with 1 **Br**; racemes ovate to subcapitate, 4–9 × 4–5 cm, dense; **Bra** acute, 2–4 mm; **Ped** 8–12 mm; **Fl** carmine-red, lobes green bordered white, 16–22 mm, 7 mm Ø across the ovary, narrowed to 4 mm above, then enlarging to 5 mm at the mouth; **OTep** free for ±5–7 mm; **St** and **Sty** disposition not described; **Fr** berries.

**A. somaliensis** W. Watson (Gard. Chron., ser. 3, 26: 430, 1899). **Type:** Somalia (*Cole* 261/1895 [K]). — **Distr:** Somalia (Northern Region); arid bushland and rocky slopes on limestone, 700–1700 m. **I:** Reynolds (1966: 56–59, incl. var. *marmorata*); Carter & al. (2011: 306); Starha (2013).

**Incl.** *Aloe somaliensis* var. *marmorata* Reynolds & P. R. O. Bally (1964).

[5] Acaulescent or shortly caulescent, simple or suckering to form small groups; **L** 12–16, densely rosulate, lanceolate-attenuate, 20 × 7 cm, glossy brownish-green with many pale green lenticular spots, lower face paler with more spots, surface smooth, exudate drying brown, **marginal teeth** 4 mm, pungent, reddish-brown, 8–10 mm apart; **Inf** 60–80 cm, suberect to oblique, with 5–8 **Br**, lower ones sometimes rebranched; racemes cylindrical or with flowers subsecund on oblique branches, 15–20 × 5–6 cm, subdense; **Bra** ovate-attenuate, ±8 × 4 mm; **Ped** 8 mm; **Fl** pinkish-scarlet, minutely speckled, 28–30 mm, base



**Fig. 62** *Aloe soutpansbergensis*.  
(Copyright: U. Eggli)



rounded, 9 mm  $\varnothing$  across the ovary, very slightly narrowed above and towards the mouth; **OTep** free for 10 mm; **St** exserted 1–2 mm; **Sty** exserted 3 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

**A. soutpansbergensis** I. Verdoorn (Flow. Pl. Afr. 35: t. 1381 + text, 1962). **Type:** RSA, Limpopo (*Crundall* s.n. [PRE 27035 (= 29005)]). — **Lit:** Glen & Hardy (1991: typification). **Distr:** RSA (N-C Limpopo: W-most Soutpansberg range); S-facing shady rocky slopes with dense fog in the wet season,  $\pm 1500$  m. **I:** Craib (2006: 107–110); Carter & al. (2011: 121); Wyk & Smith (2014: 334–335). – Fig. 62.

[10] Caulescent, simple or suckering to form small groups; **R** fleshy; stem to  $5 \times 0.8$  cm; **L**  $\pm 7$ , distichous at first, soon becoming rosulate, linear,  $\pm 25 \times 1$  cm, green with a few obscure white spots, lower face with more spots, esp. near the base, with narrow translucent cartilaginous margin, **marginal teeth** 0.5 mm, translucent,  $\pm 3$ –4 mm apart; **Inf**  $\pm 20$  cm, simple; raceme subcapitate, lax, with 8 or more flowers; **Bra** lanceolate-acuminate,  $\pm 17 \times 10$  mm; **Ped**  $\pm 25$  mm; **Fl** apricot-orange,  $\pm 27$  mm, base truncate, 7 mm  $\varnothing$  across the ovary, narrowing slightly above; **OTep** free to the base; **St** and **Sty** exserted 0–1 mm.

**A. speciosa** Baker (J. Linn. Soc., Bot. 18(108): 178, 1880). **Type:** RSA, Eastern Cape (*MacOwan*

1922 [K, PRE [photo]]). — **Distr:** RSA (Western Cape, Eastern Cape); rocky slopes, 0–1000 m. **I:** Reynolds (1950: 423–425); Carter & al. (2011: 677); Wyk & Smith (2014: 76–77).

[9,16] Caulescent, simple or branched; stem to 4 (–6) m, dead leaves persistent; **L** densely rosulate, lanceolate-attenuate,  $60$ – $80 \times 7$ – $9$  cm, dull glaucous-green, tinged bluish to reddish, with very narrow deep pink to pale reddish margin, **marginal teeth** 1 mm, pale red,  $\pm 10$  mm apart; **Inf**  $\pm 50$  cm, arcuate-erect, simple; raceme cylindrical, slightly acuminate,  $\pm 30 \times 12$  cm, very dense; **Bra** lanceolate-obtuse, to  $20 \times 10$  mm, brownish; **Ped** 5–8 mm; **Fl** white, tinged greenish, 30–35 mm, ventricose, base rounded, enlarged above the ovary, narrowing slightly at the mouth; **OTep** free almost to the base; **St** and **Sty** exserted to 16 mm. — **Cytology:**  $2n = 14$  (Resende 1937).

Natural hybrids with other species have been reported (Reynolds 1950).

**A. spectabilis** Reynolds (J. South Afr. Bot. 3: 129, 1927). **Type:** RSA, KwaZulu-Natal (*Reynolds* 2033 [PRE, BOL]). — **Lit:** Klopper & Smith (2010a). **Distr:** RSA (C KwaZulu-Natal); open rocky places. **I:** Reynolds (1950: 477–479); Wyk & Smith (2014: 78–79).

[8] Caulescent, solitary; stem to 4 m, dried leaves persistent; **L**  $\pm 50$ , densely rosulate, lanceolate-ensiform,  $100 \times 12$ – $15$  cm, dull



green, upper surface prickly, **marginal teeth** deltoid, 5–7 mm, reddish or brownish, 10–20 mm apart; **Inf** erect, with up to 14 **Br**; racemes cylindrical, 25 cm, dense; **Bra** ovate-acute, 4–5 × 5 mm; **Ped** 3 mm; **Fl** yellow to golden yellow, 32 mm, 5 mm  $\varnothing$  across the ovary, enlarging to 8 mm above; **OTep** free for 16 mm; **St** and **Sty** exerted 20 mm.

Formerly regarded as synonymous with *A. marlothii* (e.g. by Carter & al. (2011)), but reinstated by Klopper & Smith (2010a).

This species is locally naturalized in the Free State, originating from a deliberate planting of a few specimens at a farm in 1900, and this developed into a still localized population of >30,000 plants (Oliver 1986, Klopper & al. 2010).

**A. spicata** Linné *fil.* (Suppl. Pl., 205, 1782). **Type:** S Africa, sine loco (*Thunberg* 8599 [UPS]). — **Lit:** Glen & Hardy (1995). **Distr:** S Moçambique, SE Zimbabwe, RSA (N KwaZulu-Natal, Mpumalanga, Limpopo), Swaziland; steep rocky slopes in bushveld, 0–1760 m. **I:** Reynolds (1950: 432–433, as *A. sessiliflora*); Carter & al. (2011: 653); Wyk & Smith (2014: 100–101).

**Incl.** *Aloe sessiliflora* Pole-Evans (1917).

[8] Caulescent, simple or branching; stem to 2 m, erect; **L**  $\pm$ 30, densely rosulate, lanceolate-attenuate,  $\pm$ 50–60 × 7–9 cm, green to reddish, with reddish margin, **marginal teeth** 1–1.5 mm, deep pink to reddish, 8–12 mm apart; **Inf** 1 m or more, simple; raceme cylindrical,  $\pm$ 30–40 × 4–5 cm, very dense; **Bra** ovate-cuspidate; **Ped** absent; **Fl** greenish-yellow, 14–15 mm, campanulate; **OTep** free to the base; **St** and **Sty** exerted  $\pm$ 10 mm.

Natural hybrids with other species have been reported (Reynolds 1950).

**A. spinitriaggregata** J.-B. Castillon (Cact.-Avent. Int. 90: 2–5, ills., 2011). **Type:** Madagascar, Fianarantsoa (*Castillon* 47 [TAN, P]). — **Distr:** Madagascar (Fianarantsoa); herb-covered rocky hills.

[5] Acaulescent or with very short stem to 10 cm, branching from the base to form groups of up to 5 rosettes; **L** 7–10, rosulate, triangular, apex

rounded, 12–18 × 3–6 cm, green to reddish, exudate colourless, **marginal teeth** forked, 2 mm, reddish; **Inf** 40 cm, erect, with 1–2 **Br**; racemes subcapitate, 1–2 cm, dense; **Bra** 3 × 2 mm; **Ped** 2.5 mm; **Fl** reddish, 20 mm, base obconical, 4 mm  $\varnothing$  across the ovary, enlarging above to 8 mm at the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. springatei-neumannii** L. E. Newton (Bradleya 29: 58, figs. 1–2 (p. 59), 2011). **Type:** Kenya, Nyanza Prov. (*Springate* 99.008A [EA]). — **Distr:** SW Kenya (Nyanza Prov.); gaps in low forest of almost pure *Catha edulis* on hillside.

[3] Acaulescent or with a short stem to 30 cm with age, solitary; **L**  $\pm$ 20, rosulate, lanceolate-attenuate, apex acute, 35 × 8.5 cm, mid-green with numerous pale elongated spots in irregular transverse bands, surface smooth, exudate pale yellow, **marginal teeth** deltoid, 4 mm, white, red-tipped, 7–12 mm apart; **Inf** 1.2 m, erect, with 3 **Br**; racemes cylindrical, 22 cm, subdense; **Bra** triangular, long-attenuate, 10 × 1.5 mm; **Ped** 20 mm; **Fl** yellow, lobes paler with reddish mid-stripe towards the mouth, 35 mm, base flat, 10 mm  $\varnothing$  across the ovary, abruptly constricted to 5.5 mm above, widening to 9 mm at the mouth; **OTep** free for 10–12 mm; **St** exerted 2 mm; **Sty** exerted 4 mm.

**A. squarrosa** Baker (Proc. Roy. Soc. Edinburgh 12: 97, 1883). **Type:** Yemen, Socotra (*Balfour* 282 [K]). — **Lit:** Lavranos (1969). **Distr:** Yemen (Socotra: Jabal Ma'ali); limestone cliffs,  $\pm$ 300 m. **I:** Lavranos (1970: t. 1611); Carter & al. (2011: 474).

**Incl.** *Aloe concinna* Baker (1898) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe zanzibarica* Milne-Redhead (1947).

[13] Caulescent, branching at the base; stem pendulous, to 40 cm; **L** rosulate, lanceolate-attenuate, 5–7 × 2–3 cm, light green with many whitish rounded spots, surface rough, **marginal teeth** 3–4 mm, firm, whitish,  $\pm$ 5 mm apart; **Inf** 10–20 cm, usually pendulous and arcuate-ascending, simple; raceme cylindrical, 6 × 4.5 cm, lax; **Bra** deltoid, 5 mm; **Ped** 7–8 mm; **Fl**

scarlet, 23–25 mm, base shortly attenuate, 5 mm  $\emptyset$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 5–6 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology**:  $2n = 14$  (Resende 1937: as *A. concinna*).

**A. steudneri** Schweinfurth (Bull. Herb. Boissier [sér. 1] 2(App. 2): 73, 1894). **Type** [lecto]: Ethiopia, Tigre Prov. (*Penzig* 448 [B, K [photo]]). — **Lit**: Lavranos & McCoy (2007). **Distr**: N Ethiopia (Semien Highlands); steep slopes and cliff faces, mountain peaks, 2600–3500 m. **I**: Reynolds (1966: 277); Sebsebe Demissew & Nordal (2010: 80–81); Carter & al. (2011: 578).

[5,13] Caulescent, solitary or branching to form small groups; stem short or decumbent to 1.25 m; **L** to 45, rosulate, narrowly deltoid, 40–50  $\times$  10 cm, bright green, often red-tinged, obscurely striate, exudate light yellow, drying purple-brown, **marginal teeth** 2–3 mm, reddish, 7–22 mm apart; **Inf** 50–60 cm, simple or with up to 4 **Br**; racemes conical-cylindrical, 20–35 cm, lax; **Bra** deltoid, 8–12 mm; **Ped** 11–14 mm; **Fl** bright red, 50 mm, 10 mm  $\emptyset$  across the ovary, not narrowed above; **OTep** free to the base; **St** and **Sty** exerted to 2 mm. — **Cytology**:  $2n = 14$  (Resende 1937).

A population in Eritrea formerly included in this species (Medhanie & Dioli 2006) was later shown to be distinct and described as *A. neosteudneri*.

**A. stolonifera** T. A. McCoy & Plowes (Ingens 56: 6–11, ill., 2017). **Type**: Zimbabwe, Manicaland Prov. (*McCoy* 3998 [FT]). — **Distr**: Zimbabwe (Manicaland Prov.); in the open or beneath trees in open bushland, 520 m.

[7] Acaulescent or with stems to 10 cm, stoloniferous, forming large dense groups; **L** 16–24, rosulate, narrowly lanceolate-attenuate, 50  $\times$  5 cm, green with many white spots mostly in irregular transverse bands, lower surface with fewer spots, lineate, exudate orange, drying brownish, **marginal teeth** deltoid, 7 mm, reddish-brown, 10–12 mm apart; **Inf** 110 cm, erect, with 10–15 **Br**, lowermost often rebranched; racemes cylindrical-conical, 35 cm,

sublax; **Bra** lanceolate-acute, 4–5  $\times$  2.5 mm, white, scarious, with 3–5 red nerves; **Ped** 10–12 mm; **Fl** reddish-pink, 36 mm, abruptly constricted above the ovary and widening towards the mouth; **OTep** free for 12 mm; **St** and **Sty** exerted 5 mm.

**A. striata** Haworth (Trans. Linn. Soc. London 7: 18, 1804). **Type** [neo]: RSA, Eastern Cape (*Bottomley* s.n. [PRE 27]). — **Lit**: Lavranos (2004); Klopper & al. (2008). **Distr**: RSA (Western Cape, Eastern Cape); in grass or bush on rocky slopes, 250–2200 m; neophyte in Spain (Valencia). **I**: Reynolds (1950: 295–296, t. 20); Carter & al. (2011: 356); Wyk & Smith (2014: 188–189).

**Incl.** *Aloe paniculata* Jacquin (1809); **incl.** *Aloe albocincta* Haworth (1819); **incl.** *Aloe hanburiana* Naudin (1875); **incl.** *Aloe rhodocincta* hort. ex Baker (1880); **incl.** *Aloe striata* var. *oligospila* Baker (1894).

[13] Caulescent, usually simple, sometimes with up to 5 branches; stem decumbent, to 1 m, with dead leaves persistent; **L** 12–20, densely rosulate, lanceolate-attenuate, to 50  $\times$  20 cm, glaucous-green to reddish-tinged, usually striate, sometimes with obscure spots on the upper face, with broad pale pink to almost red margin, **marginal teeth** absent; **Inf** to 1 m, with 6–12 **Br**, lower ones rebranched; racemes capitate to slightly conical,  $\pm 6 \times 6$  cm, dense; **Bra** deltoid-acuminate,  $\pm 5$  mm; **Ped** 15–25 mm; **Fl** peach-red to coral-red, 30 mm, base truncate, 6 mm  $\emptyset$  across the ovary, abruptly narrowed above, then enlarging to the mouth; **OTep** free for 6–8 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology**:  $2n = 14$  (Vosa 1982).

Lavranos (2004) argues for accepting *A. striata* as distinct from those treated by some other authors as subspecies within it.

Guillot (2013) reports the species as locally naturalized in Spain. Natural hybrids with other species have been reported (Reynolds 1950).

**A. striatula** Haworth (Philos. Mag. J. 1825: 281, 1825). **Type**: RSA, Eastern Cape (*Bowie* s.n. [K [lecto — icono: plate by F. Bauer, reproduced in Reynolds, Aloes South Afr., 362, 1950]]). — **Distr**: Lesotho, RSA.

≡ *Aloiampelos striatula* (Haworth) Klopper & Gideon F. Smith (2013).

**A. striatula** var. **caesia** Reynolds (Flow. Pl. South Afr. 16: t. 633 + text, 1936). **Type:** RSA, Eastern Cape (*Reynolds* 1607 [PRE, BOL]). — **Distr:** RSA (Eastern Cape); rocky slopes. **I:** Reynolds (1950: 365, t. 41); Carter & al. (2011: 552).

≡ *Aloiampelos striatula* var. *caesia* (Reynolds) Klopper & Gideon F. Smith (2013); **incl.** *Aloe striatula* fa. *conimbricensis* Resende (1943); **incl.** *Aloe striatula* fa. *haworthii* Resende (1943); **incl.** *Aloe striatula* fa. *typica* Resende (1943) (*nom. inval.*, ICN Art. 24.3).

[16] Differs from var. *striatula*: Stem to 2 m × 1.5–2 cm; **L** 10–15 × 1.5–2.5 cm, milky-green, leaf sheath 5–15 mm, obscurely green-lineate; **Fl** yellow, tipped greenish, 30–33 mm, slightly narrowed above the ovary, then enlarging to the mouth.

**A. striatula** var. **striatula** — **Distr:** Lesotho, RSA (Eastern Cape); amongst rocks on mountain tops, 500–2000 m. **I:** Reynolds (1950: 362–364, t. 41); Carter & al. (2011: 552); Wyk & Smith (2014: 118–119).

**Incl.** *Aloe macowanii* Baker (1880); **incl.** *Aloe aurantiaca* Baker (1892); **incl.** *Aloe cascadenis* Kuntze (1898).

[16] Caulescent, branching; stem to 1.75 m × 2.5 cm; **L** scattered along the stem for 40–60 cm, linear-lanceolate, acuminate, to 25 × 2.5 cm, semiglossy green, with very narrow white cartilaginous margin, **marginal teeth** ±1 mm, firm, white, 3–8 mm apart, leaf sheath 15–20 mm, prominently green-lineate; **Inf** to 40 cm, simple; raceme cylindrical-conical, 10–15 cm, dense; **Br** deltoid-subulate, ± ½ as long as the pedicels; **Ped** 3–5 mm; **Fl** reddish-orange to orange, 40–45 mm, base truncate, very slightly narrowed above the ovary; **OTep** free almost to the base; **St** and **Sty** exerted 5–7 mm. — **Cytology:** 2n = 14 (Fernandes 1930).

**A. suarezensis** H. Perrier (Mém. Soc. Linn. Normandie, Bot. 1(1): 21, 1926). **Type:** Madagascar, Mahajanga (*Perrier* 16221 [P]). — **Distr:** Madagascar (Mahajanga, Antsiranana); limestone outcrops, 10–490 m. **I:** Reynolds (1966: 459–461); Castillon & Castillon (2010: 318–321); Carter & al. (2011: 362). — Fig. 63.

[3] Acaulescent or caulescent, simple; stem erect, to 30 cm, with dead leaves persistent; **L** 20–24, densely rosulate, lanceolate-attenuate, tip rounded with 2–3 short teeth, to 50–60 × 9–10 cm, dull green tinged reddish, exudate drying pale yellow, **marginal teeth** ±2 mm, dirty-white to pale pinkish, 10 mm apart; **Inf** 60–80 cm, with 4–12 **Br**, lower ones sometimes rebranched;

**Fig. 63** *Aloe suarezensis*.  
(Copyright: D. J. Supthut)



racemes cylindrical, 10–15 × 6 cm, dense; **Bra** ovate-attenuate, 10–12 × 4–6 mm, dirty white; **Ped** 10–12 mm; **Fl** dull to pale scarlet, paler at the mouth, minutely puberulent, 28 mm, base rounded and very shortly attenuate, 7 mm Ø across the ovary, narrowed to 5.5 mm above, then enlarging to the mouth; **OTep** free to the base; **St** and **Sty** exerted 2–3 mm.

Phylogenetic studies by Dee & al. (2018) indicate a close relationship with two species on Mauritius, *A. purpurea* and *A. tormentorii*.

**A. subspicata** (Baker) Boatwright & J. C. Manning (Taxon 62(1): 75, 2013). **Type:** RSA, Gauteng (*Conrath* 645 [Z, K]). — **Distr:** Botswana, Lesotho, Namibia, RSA (Eastern Cape, Free State, Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga, Northern Cape, North-West), Zimbabwe; grasslands. **I:** Craib (2006: 129, as *Chortolirion angolense*); Zonneveld & Fritz (2010: 28, as *C. angolense*); Wyk & Smith (2014: 368–369).

≡ *Haworthia subspicata* Baker (1904) ≡ *Chortolirion subspicatum* (Baker) A. Berger (1908).

[2] Acaulescent, with short subterranean bulb, usually solitary; **L** rosulate, slightly succulent, flaccid to erect, twisted, 3–5 × 0.3 cm, light green to glaucous-green, margins denticulate; **Inf** 25–35 cm, simple; raceme with the flowers slightly subsecund; **Ped** short; **Fl** whitish to light greenish-brown with greenish keels, base obtuse, zygomorphic, tube straight, 10–14 × ±3 mm, limb bilabiate; **Tep** free almost to the base.

**A. succotrina** Weston (Bot. Univ. 1: 5, 1770). **Type:** [lecto — icono]: Commelin, Hort. Med. Amstel. 1: fig. 48, 1697. — **Lit:** Walker & al. (2015). **Distr:** RSA (SW Western Cape: Cape Peninsula to Hangklip and Hermanus); between sandstone boulders, 0–900 m. **I:** Reynolds (1950: 390–394); Carter & al. (2011: 579); Wyk & Smith (2014: 102–103).

**Incl.** *Aloe perfoliata* var.  $\xi$  Linné (1753); **incl.** *Aloe succotrina* Garsault (1767) (*nom. inval.*, ICN Art. 34.1); **incl.** *Aloe vera* Miller (1768) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe succotrina* Allioni (1773) (*nom. illeg.*, ICN Art. 53.1); **incl.**

*Aloe succotrina* Lamarck (1783) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe perfoliata* var. *purpurascens* Aiton (1789) ≡ *Aloe purpurascens* (Aiton) Haworth (1804); **incl.** *Aloe perfoliata* var. *succotrina* Aiton (1789); **incl.** *Aloe sinuata* Thunberg (1794); **incl.** *Aloe succotrina* var. *purpurascens* Ker Gawler (1812); **incl.** *Aloe succotorina* Schultes & Schultes fil. (1829) (*nom. inval.*, ICN Art. 61.1); **incl.** *Aloe succotrina* var. *saxigena* A. Berger (1908).

[4,12] Caulescent, sometimes almost acaulescent, simple or branching at the base or above; stem erect or decumbent, short or to 2 m × 15 cm Ø, with dead leaves persistent; **L** densely rosulate, lanceolate-attenuate, to 50 × 10 cm, dull green to grey-green, obscurely lineate, sometimes with a few small scattered white spots, usually with dull white narrow cartilaginous margin, **marginal teeth** 2–4 mm, firm, white, to 10 mm apart; **Inf** ±1 m, usually simple; raceme cylindrical-acuminate, 25–35 cm, subdense; **Bra** lanceolate, 20 × 10 mm; **Ped** 30 mm; **Fl** glossy red to reddish-salmon, green-tipped, 40 mm, base truncate, not narrowed above the ovary; **OTep** free to the base; **St** and **Sty** exerted 3–5 mm. — **Cytology:** 2n = 14 (Resende 1937).

The name *A. succotrina* Garsault, published 1767, is commonly cited as a synonym here; it would have priority but it is invalid since Garsault did not consistently follow Linnean nomenclature in his book, which has therefore been designated as a suppressed work under the Code.

**A. suffulta** Reynolds (J. South Afr. Bot. 3: 151, 1937). **Type:** Moçambique, Maputo (*Reynolds* 2457 [PRE, BOL]). — **Lit:** Smith & Crouch (2001: with ill.). **Distr:** W & S Moçambique, S Malawi, SE Zimbabwe, RSA (NE KwaZulu-Natal); in the shade of shrubs on sandy soil or black cotton clays or termite mounds, 90–550 m. **I:** Reynolds (1950: 343–344); Lane (2004: 44–45); Carter & al. (2011: 509); Klopper & al. (2012: 89, 90–91, incl. distribution map); Wyk & Smith (2014: 268–269).

**Incl.** *Aloe subfulva* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1).



[3] Caulescent, simple; stem to  $20 \times 2$  cm; **L**  $\pm 16$ , scattered along the stem, attenuate,  $40\text{--}50 \times 4$  cm, green with dull white spots, the spots sometimes scattered, usually  $\pm$  in transverse bands, **marginal teeth** 1–2 mm, usually uncinuate, whitish, 5–10 mm apart, leaf sheath 5–10 mm, striatulate; **Inf**  $\pm 1.75$  m, supported by shrubs, with up to 9 **Br**; racemes cylindrical, slightly acuminate,  $\pm 8\text{--}15 \times 5$  cm, lax, with up to 20 flowers; **Bra** 9 mm; **Ped** 9 mm; **Fl** light jasper-red, whitish at the mouth, 30–35 mm, base shortly attenuate, 6 mm  $\varnothing$  across the ovary, narrowed to 5.5 mm above, then enlarging to the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 6–8 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

**A. suprafoliata** Pole-Evans (Trans. Roy. Soc. South Africa 5: 603, 1916). **Type**: Swaziland (Pole-Evans 215 [PRE]). — **Distr**: Swaziland, RSA (N KwaZulu-Natal, Mpumalanga); rocky slopes on mountains, mostly with mist or low clouds, 300–1600 m. **I**: Reynolds (1950: 303–304, t. 18); Carter & al. (2011: 260); Wyk & Smith (2014: 190–191).

**Incl.** *Aloe suprafoliolata* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1).

[4] Acaulescent or shortly caulescent, usually simple; stem erect or procumbent, rarely to 50 cm; **L**  $\pm 30$ , distichous in young plants, densely rosulate later, lanceolate-acuminate,  $30\text{--}40 \times 7$  cm, bluish-green to bluish-grey, becoming reddish-brown towards tip, obscurely lineate, **marginal teeth** 2–5 mm, reddish-brown, sometimes bifid, 5–10 mm apart; **Inf** to 1 m, simple; raceme conical to cylindrical-acuminate, to  $25 \times 10$  cm, subdense; **Bra** lanceolate-acute,  $\pm 20$  mm; **Ped** to 20 mm; **Fl** rose-pink to scarlet, with a bloom, greenish at the mouth, 40–50 mm, base rounded or very slightly attenuate, not narrowed above the ovary; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Müller 1941).

Natural hybrids with *A. arborescens* have been reported (Reynolds 1950).

**A. suzannae** Decary (Bull. Écon. Trimestriel [Madagascar] 18: 26, 1921). **Type** [neo]: Madagascar, Ambovombe (Decary 2913 [P]). — **Lit**:

Lüthy (2006: 55–56, conservation, with ills.); Smith & Molteno (2019). **Distr**: S and SW Madagascar (Toliara); in dense bush, 30–100 m. **I**: Reynolds (1966: 515–517); Castillon & Castillon (2010: 274–275); Carter & al. (2011: 676). — Fig. 64.

$\equiv$  *Aloestrela suzannae* (Decary) Molteno & Gideon F. Smith (2019).

[9] Caulescent, usually simple, sometimes with 1 or 2 branches; stem erect, to  $4 \text{ m} \times 30 \text{ cm } \varnothing$ ; **L** 60–100, densely rosulate and persistent for up to 1 m below, lanceolate-attenuate, tip rounded with 5–7 short teeth,  $1 \text{ m} \times 8\text{--}9 \text{ cm}$ , dull green, surface very rough, exudate drying deep brown-orange, **marginal teeth** 2 mm, pungent, pale brown, 8–10 mm apart; **Inf**  $\pm 3$  m, simple; raceme cylindrical,  $\pm 2 \text{ m} \times 17 \text{ cm}$ , dense; **Bra** linear-deltoid,  $\pm 15 \times 2$  mm, green with pale margin; **Ped** 28–30 mm; **Fl** ivory tinged with pale rose, 33 mm, base rounded, 10 mm  $\varnothing$  across the ovary, slightly narrowed above, lobes spreading;



**Fig. 64** *Aloe suzannae*. (Copyright: B. Descouings)



**OTep** free for 16–17 mm, reflexed; **St** and **Sty** exerted 10 mm. — **Cytology**:  $2n = 14$  (Brandham 1971).

Phylogenetic studies by Dee & al. (2018) suggest that this species is more closely related to the African species *Aloe haemanthifolia*.

The flowers are described as nocturnal and fragrant in the literature, but have been found to stay open at midday, and were visited by sunbirds (Spath & Griffin 2013). At least one good population survives, with peak flowering time mid-July to mid-August, and sets copious amounts of seeds, but is threatened by agriculture (Spath & Griffin 2013).

**A. swynnertonii** Rendle (J. Linn. Soc., Bot. 40: 215, 1911). **Type**: Zimbabwe (*Swynnerton* 722 [BM, K]). — **Distr**: Zimbabwe/Moçambique boundary; montane grassland and dry forest, 610–1830 m. **I**: Reynolds (1966: 85, figs. 84–85); Carter & al. (2011: 194).

**Incl.** *Aloe chimanimaniensis* Christian (1936); **incl.** *Aloe melsetterensis* Christian (1938).

[5] Acaulescent or very shortly caulescent, simple or in small groups of 3–4 rosettes; **L**  $\pm 20$ , densely rosulate, lanceolate-attenuate, to  $75 \times 8$ – $10$  cm, apical 10 cm soon drying, upper face dark green with oblong to confluent H-shaped spots in irregular transverse bands, lower face paler green, lineate, usually without spots, exudate drying yellow, **marginal teeth** 4 mm, pungent, reddish-brown, 10–25 mm apart; **Inf** 1.5–1.75 m, with 8–12 **Br**, lower ones sometimes rebranched; racemes capitate-corymbose,  $6$ – $8 \times 7$ – $8$  cm, dense; **Bra** deltoid,  $8 \times 3$  mm; **Ped** 25–30 mm; **Fl** flesh-pink to dull coral-red, with a slight bloom, 30 mm, base truncate, 8 mm  $\varnothing$  across the ovary, abruptly narrowed to 5 mm above the ovary, then enlarging above and slightly narrowing to the mouth; **OTep** free for 9 mm; **St** and **Sty** exerted 0–1 mm.

Populations in Malawi and Moçambique documented by Reynolds (1966) have been distinguished as *A. menyharthii* by Carter (1996). A disjunct population in Limpopo Province, RSA, was described as *A. hahnii* (Klopper & Smith 2009). The plants in Malawi tentatively identified as *A. swynnertonii* by Lane (2004) are probably *A. menyharthii*.

**A. tartarensis** T. A. McCoy & Lavranos (CactusWorld 25(4): 212–213, ills., 2007). **Type**: Kenya, Rift Valley Prov. (*McCoy* 2219 [EA]). — **Distr**: W Kenya; hanging from cliff faces. **I**: Carter & al. (2011: 521).

[13] Caulescent, solitary or with 1–2 branches from the base; stem to 2 m, pendulous; **L** 12–15, loosely rosulate, lanceolate-attenuate, falcate,  $70 \times 7$  cm, glaucous, exudate yellow, **marginal teeth** forward-facing, 5 mm, reddish, 10 mm apart; **Inf** 75 cm, oblique, pendulous with racemes ascending, with 7–10 **Br**, lowermost rebranched; racemes cylindrical, to 23 cm, lax; **Bra**  $4.5 \times 2$  mm, brownish; **Ped** 20 mm; **Fl** red, yellow at the mouth, 25 mm, 5 mm  $\varnothing$  across the ovary; **OTep** free for 8 mm; **St** and **Sty** exerted 0–1 mm.

**A. tauri** L. C. Leach (J. South Afr. Bot. 34: 363–370, ills., 1968). **Type**: Zimbabwe, Southern Prov. (*Leach & Bullock* 13321 [SRGH, BM, G, K, LISC, PRE]). — **Distr**: S Zimbabwe (along the S escarpment); with grasses on steep rock slabs, 1065–1220 m. **I**: Carter & al. (2011: 429).

[2, 6] Acaulescent, solitary, or shortly caulescent and suckering to form large groups; stem to 30 cm, decumbent, with dried leaves persistent; **L** densely rosulate, lanceolate-attenuate,  $30$ – $60 \times 6$ – $8$  cm, dark green or coppery-red-tinted, **marginal teeth** 1–2 mm, reddish, brown-tipped, 6–12 mm apart; **Inf** to 1 m, erect, simple or rarely with 1 **Br**; racemes cylindrical, 15–30 cm, very dense; **Bra** ovate-acuminate,  $12 \times 7$  mm; **Ped** 1 mm; **Fl** bright yellow, 18 mm, campanulate, 10 mm  $\varnothing$  at the mouth; **OTep** free to the base; **St** and **Sty** exerted 10 mm.

**A. tegetiformis** L. E. Newton (Bradleya 29: 60, figs. 3–5 (p. 59), 2011). **Type**: Kenya, Rift Valley Prov. (*Powys* 1259 [EA]). — **Distr**: N Kenya (Rift Valley Prov.: Samburu Distr.); deep shade on rocky mountain slope; known only from the type locality.

[13] Caulescent, branching profusely from the base, forming a dense mass of rosettes on the ground; stem to 1 m, decumbent; **L** 30–40, rosulate and persisting below the stem tip, ovate-attenuate, to  $12 \times 3$  cm, bright green, with numerous elongated whitish spots, surface smooth, interior tissue fibrous, exudate absent, **marginal teeth**

3 mm, brown-tipped, 3–7 mm apart; **Inf** 30 cm, erect, simple; raceme cylindrical, 8.5 cm, subdense; **Bra** ovate-attenuate, 10–14 × 5–7 mm; **Ped** 10–14 mm; **Fl** orange-red, lobes with paler or yellowing margins, 26–30 mm, base rounded, 6 mm Ø across the ovary, slightly narrowed to 5 mm above; **OTep** free for 5–7 mm; **St** exerted 2–3 mm; **Sty** exerted 2 mm. — **Cytology**: 2n = 14 (Newton, unpublished).

**A. teissieri** Lavranos (Cact. Succ. J. (US) 74(2): 65–66, ills., 2002). **Type**: Madagascar, Toliara (*Teissier* 232 [P]). — **Distr**: Madagascar (Toliara: mostly Andohahela Reserve); granite hills, ±400–500 m. **I**: Castillon & Castillon (2010: 228–229); Carter & al. (2011: 247).

**Incl.** *Aloe andohahelensis* J.-B. Castillon (2002).

[2] Acaulescent or with very short stem, solitary; **L** 15–20, rosulate, lanceolate-acuminate, 20–40 × 4–6 cm, grey-green, sometimes tinged pinkish, obscurely lineate, exudate greenish-yellow, drying light brown, **marginal teeth** 2 mm, pinkish-red, 7–10 mm apart; **Inf** 25–40 cm, erect, simple; raceme cylindrical, 10–12 cm, dense; **Bra** broadly ovate, 4–5 × 3 mm, fleshy; **Ped** 2–5 mm; **Fl** orange-yellow, 15–17 mm, clavate, 3–4 mm Ø across the ovary, widening to 6–7 mm near the mouth; **OTep** free for 10–12 mm; **St** and **Sty** exerted 2–7 mm.

**A. tenuior** Haworth (Philos. Mag. J. 1825: 281, 1825). **Type**: RSA, Eastern Cape (*Bowie* s.n. [K [lecto — icono]: plate by F. Bauer, reproduced in Reynolds, Aloes South Afr., 347, 1950]). — **Lit**: Jaarsveld (2008: with key to varieties). **Distr**: RSA (Eastern Cape).

≡ *Aloiampelos tenuior* (Haworth) Klopper & Gideon F. Smith (2013); **incl.** *Aloe tenuior* var. *glaucescens* Zahlbruckner (1900); **incl.** *Aloe tenuior* var. *decidua* Reynolds (1936); **incl.** *Aloe tenuior* var. *rubriflora* Reynolds (1936); **incl.** *Aloe tenuior* var. *densiflora* Reynolds (1950).

**A. tenuior** var. **tenuior** — **Lit**: Duffy & al. (2014: pollination ecology). **Distr**: RSA (Eastern Cape, KwaZulu-Natal); thorn-bush or more open ground, sometimes on steep slopes, 0–2300 m. **I**:

Reynolds (1950: 347–352); Carter & al. (2011: 546); Wyk & Smith (2014: 120–121).

[14,15] Caulescent, branching, with large, almost tuberous, rootstock; stem erect, to 60 cm, or spreading to decumbent, scandent, or supported by bushes, to 3 m × 1.5 cm; **L** laxly rosulate, sometimes persistent for up to 20 cm below the stem tip, linear-lanceolate, 10–18 × 1–2.2 cm, glaucous-green, with very narrow white cartilaginous margin, **marginal teeth** to 0.5 mm, white, 1–2 mm apart, leaf sheath 5–25 mm, obscurely green-lineate; **Inf** 35–40 (–50) cm, simple or with 1–2 **Br**; racemes cylindrical, slightly acuminate, 10–20 × 4 cm, subdense to dense; **Bra** linear-deltoid, acuminate, ±5 mm; **Ped** 3–5 mm; **Fl** yellow or red with yellow tips, 11–15 mm, base shortly attenuate, very slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for ±3–6 mm; **St** and **Sty** exerted 4–6 mm. — **Cytology**: 2n = 14 (Müller 1941).

Wyk & Smith (2014): state: “Isolated populations are known from the border between KwaZulu-Natal, Swaziland and Mpumalanga”, but without stating in which country/countries they should be recorded. Whilst highly unlikely, a possible intergeneric natural hybrid with *Bulbine aloides* has been reported (Reynolds 1950: 352).

Hargreaves & al. (2012) found that Allogdopine bees are important pollinators (50% of all visits with stigma contact) of this species. Duffy & al. (2014) confirm Allogdopine bees as important visitors and add the introduced honey bee and an unidentified Halictid bee as further important visitors.

**A. tenuior** var. **viridifolia** Van Jaarsveld (Aloe 44(3): 60–61, ills., 2008). **Type**: RSA, Eastern Cape (*Van Jaarsveld & al.* 17832 [NBSG]). — **Distr**: RSA (Eastern Cape: Kabouga); dry quartzite Fynbos vegetation, 300–500 m; known only from the area of the type locality.

[14,15] Differs from var. *tenuior*: **L** 5–9 × 0.6–1 cm, bright glossy green, **marginal teeth** absent.

**A. termetophila** De Wildeman (Pl. Bequaert. 30, 1921). **Type**: Democratic Republic of the Congo [Zaire], Haut-Katanga (*Homblé* 655

[BR]). — **Lit:** McCoy (2018). **Distr:** Democratic Republic of the Congo [Zaire], Zambia; termite mounds and shaded forest floor.

[3] Acaulescent or shortly caulescent, suckering at the base to form small or large groups; stem to 6 cm; **L** 18–25, densely rosulate, lanceolate-acute, 30–75 × 7–12 cm, glossy dark green with elliptical white spots, lower surface lighter green with more white spots in wavy transverse bands, surface smooth, **marginal teeth** uncinuate, rarely deltoid, 4–7 mm, reddish-brown, 6–20 mm apart, exudate yellow drying greenish-yellow; **Inf** 70–110 cm, erect, with 3–5 **Br**; racemes cylindrical-acuminate, 25–45 cm, sublux; **Bra** narrowly lanceolate-acuminate, 6–11 × 2–3 mm, scarious, white, with 3–5 brownish-red nerves; **Ped** 8–12 mm; **Fl** pink to dark reddish-pink, becoming white towards the mouth, 28–32 mm, 4.5–6 mm Ø across the ovary, abruptly narrowed above, widening towards the mouth; **OTep** free to mid-length; **St** exerted 1.5–2.5 mm; **Sty** exerted 2 mm.

Formerly included in the synonymy of *A. greatheadii*. Natural hybrids with *A. zimbana* have been reported (McCoy 2018).

**A. tewoldei** M. G. Gilbert & Sebsebe (Kew Bull. 52(1): 143, 1997). **Type:** Ethiopia, Harerge Region (*Tewolde-Berhan Gebre-Egziabher* s.n. [K]). — **Distr:** E Ethiopia (Harerge Region); hanging from limestone cliff faces; known only from the type collection. **I:** Sebsebe Demissew & Nordal (2010: 105–106); Carter & al. (2011: 475).

[13] Caulescent; stem sprawling or pendulous, to 50 × 0.6 cm; **L** scattered along the stem, oblong-lanceolate, semiterete, up to 13.5 (–32) × 1.5–2 (–2.2) cm, grey-green, obscurely spotted, **marginal teeth** ±0.5 mm, white, 2–3 mm apart; **Inf** simple; raceme cylindrical, ±27 cm, lax; **Bra** ±4 × 2 mm; **Ped** ±12 mm; **Fl** glaucous-orange, tipped greenish, 20 mm, base truncate, 7 mm Ø when pressed; **St** and **Sty** exerted 0–1 mm.

**A. thompsoniae** Groenewald (Tydskr. Wetensk. Kuns 14: 64, 1936). **Type** [lecto]: RSA, Northern Prov. (*Thompson* s.n. [PRE 274]). — **Distr:** RSA (Limpopo: Wolkberg); rocky cliffs in the mist belt, in short grass or

moss in fissures in quartzite, 1600–2100 m. **I:** Reynolds (1950: 131); Craib (2006: 111–113); Carter & al. (2011: 110); Wyk & Smith (2014: 336–337).

[1] Acaulescent or very shortly caulescent, suckering and branching at the base, forming dense groups; **R** fusiform; **L** 12–18, rosulate-multifarious, lanceolate-attenuate, 15–20 × ±1.5 cm, green, obscurely lineate, with a few scattered white elongated spots near the base, surface with spots more numerous and more rounded, **marginal teeth** ±1 mm, firm, white, 1–2 mm apart; **Inf** to 20 cm, simple; raceme pyramidal-capitate, 3–4 × 4–5 cm, dense, with 10–15 flowers; **Bra** ovate-acuminate, ±10 × 5–6 mm; **Ped** 15–20 mm; **Fl** coral-red, 25–28 mm, base shortly attenuate, not narrowed above the ovary; **OTep** free to the base; **St** and **Sty** not exerted.

**A. thorncroftii** Pole-Evans (Trans. Roy. Soc. South Africa 5: 709, 1917). **Type:** RSA, Mpumalanga (*Thorncroft* s.n. [PRE 247]). — **Distr:** RSA (Mpumalanga: near Barberton); mountain slopes, amongst rocks, 1400–1500 m. **I:** Reynolds (1950: 305–306); Carter & al. (2011: 266); Wyk & Smith (2014: 192–193).

[2] Acaulescent or sometimes shortly caulescent, simple; **L** ±25–30, densely rosulate, lanceolate, to 40 × 10–14 cm, dull grey-green, reddish-green towards the tip, indistinctly lineate, surface rough, **marginal teeth** 3–4 mm, pungent, reddish-brown, 8–12 mm apart; **Inf** to 1 m, simple, rarely branched; raceme cylindrical-acuminate, 40–50 cm, lax; **Bra** lanceolate-ovate, 20 × 15 mm, thick and fleshy, closely imbricate in bud stage; **Ped** 20 mm; **Fl** dull rose-red to scarlet, with pale bluish-grey bloom, to 55 mm, base shortly attenuate, slightly enlarged above the ovary, then narrowing slightly to the mouth; **OTep** free for 20 mm; **St** and **Sty** exerted 0–1 mm.

**A. thraskii** Baker (J. Linn. Soc., Bot. 18(108): 180–181, 1880). **Type:** RSA, Eastern Cape? (*Cooper* s.n. [K]). — **Distr:** RSA (E Eastern Cape, S KwaZulu-Natal); almost pure sand in low coastal vegetation or taller bush, 0–100 m.

**I:** Reynolds (1950: 475, t. 54); Carter & al. (2011: 652); Wyk & Smith (2014: 80–81).

**Incl.** *Aloe candelabrum* Engler & Drude (1910) (*nom. illeg.*, ICN Art. 53.1).

[9] Caulescent, simple, dead leaves persistent; stem usually to 2 m, to 4 m in dense bush; **L** densely rosulate, lanceolate-attenuate, to 1.6 m × 22 cm, dull green to glaucous, lower face sometimes with a few median prickles in the upper ½, with narrow reddish or brownish-red margin, **marginal teeth** ±2 mm, reddish, 10–20 mm apart; **Inf** with 4–8 **Br**; racemes cylindrical, slightly acuminate, to 25 × 10–12 cm, very dense; **Bra** ovate-acute, 9 × 6 mm; **Ped** 1–2 mm, green; **Fl** lemon-yellow to pale orange, greenish-tipped, ±25 mm, base truncate, 6 mm Ø across the ovary, enlarged above, narrowed at the mouth; **OTep** free for ±17 mm; **St** and **Sty** exerted 15–20 mm. — **Cytology:** 2n = 14 (Müller 1941).

Natural hybrids with *A. maculata* (as *A. saponaria*) have been reported (Reynolds 1950).

**A. tomentosa** Defflers (Voy. Yemen, 211, 1889). **Type:** Yemen (*Defflers* 616 [P ?]). — **Lit:** Walker (2016: with ills.). **Distr:** Yemen; rocky slopes, 2400–3100 m. **I:** Reynolds (1966: 128–129); Carter & al. (2011: 341). – Fig. 65.

**Incl.** *Aloe tomentosa* fa. *viridiflora* Lodé (1997) (*nom. inval.*, ICN Art. 36.1b, 39.1).

[7] Caulescent, suckering to form dense groups; stem decumbent, short; **L** 16–20, densely rosulate, lanceolate-deltoid, ±35 × 9 cm, grey-green tinged reddish, with narrow pinkish-brown cartilaginous margin, exudate drying pale yellow, **marginal teeth** 0.5–1 mm, blunt, 20–40 mm apart, sometimes absent; **Inf** 60–70 cm, with 3–4 **Br**; racemes cylindrical-conical, to 15 × 5–6 cm, subdense; **Bra** ovate-deltoid, 7 × 4 mm; **Ped** 6–9 mm; **Fl** rose-pink, conspicuously tomentose, 24–28 mm, base rounded, 7–8 mm Ø across the ovary, slightly narrowed above; **OTep** free for 9 mm; **St** and **Sty** exerted 0–1 mm.

**A. tongaensis** Van Jaarsveld (*Aloe* 47(3): 71, ills. (pp. 64–65, 71), 2011). **Type:** RSA, KwaZulu-Natal (*Van Jaarsveld & Powrie* 12202 [PRE]). — **Lit:** Jaarsveld & Judd (2015: 40–43,



**Fig. 65** *Aloe tomentosa*. (Copyright: L. E. Newton)

ills., as *Aloidendron*). **Distr:** RSA (NE KwaZulu-Natal: Tongaland), S Moçambique; coastal forest on sandy soil, 5–30 m. **I:** Wyk & Smith (2014: 48–49).

≡ *Aloidendron tongaense* (Van Jaarsveld) Klopper & Gideon F. Smith (2013).

[9] Caulescent, dichotomously branched above; stem to 8 m, 60–80 cm Ø at the base; **L** ±20, rosulate, ensiform, 40–59 × 4.5 cm, dull green, **marginal teeth** 2 mm, 5–10 mm apart; **Inf** 35 cm, erect, with up to 5 **Br**; racemes capitate, 4–6 cm, lax; **Bra** deltoid, acuminate, 12–14 × 3–4 mm; **Ped** 10–14 mm; **Fl** yellowish-orange, 47–50 mm, 8–9 mm Ø across the ovary; **OTep** free for 10 mm; **St** exerted 3–5 mm; **Sty** exerted 7 mm.

**A. tormentorii** (Marais) L. E. Newton & G. D. Rowley (*Excelsa* 17: 61, 1997). **Type:** Mauritius (*Guého* s.n. [MAU 13060]). — **Distr:** Mauritius (Round Island, Gunner's Quoin); exposed rocky hillsides, 240–310 m. **I:** Marais (1978: 12);



Castillon & Castillon (2010: 384–385); Carter & al. (2011: 461).

≡ *Lomatophyllum tormentorii* Marais (1975).

[7] Acaulescent or shortly caulescent, sometimes forming large groups; stem decumbent; **L** densely rosulate, ovate-acuminate,  $\pm 60 \times 15$  cm, pale green or bluish, **marginal teeth** cartilaginous; **Inf** 60–120 cm, with 3–4 **Br**; racemes to 30 cm, dense; **Bra** deltoid, 1–2 mm; **Ped** 13–20 mm; **Fl** orange-red, green-tipped, 14–17 mm, base shortly attenuate, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for 9–12 mm; **St** and **Sty** exerted to 1 mm; **Fr** berries.

**A. tororoana** Reynolds (Flow. Pl. Afr. 29: t. 1144 + text, 1953). **Type:** Uganda, Mbale Distr. (*Bally & Reynolds* 6594 [PRE]). — **Distr:** SE Uganda (Mbale Distr.: Tororo Rock); steep rock faces, 1340–1465 m; known only from the type locality. **I:** Reynolds (1966: 335); Carter & al. (2011: 486); Cole & Forrest (2017: 114–119).

[11] Caulescent, branching; stem  $\pm 20 \times 1.5$  cm  $\varnothing$ ; **L**  $\pm 12$ , densely rosulate, lanceolate-attenuate,  $15 \times 3$ – $5$  cm, dull milky-green with few to many small oblong dull white spots, more numerous and crowded on the lower face, **marginal teeth** 2–3 mm, pungent, whitish, brown-tipped, 5–10 mm apart; **Inf** to 40 cm, simple or with 1–2 **Br**; racemes cylindrical-acuminate, 8–10 cm, subdense; **Bra** ovate-deltoid,  $3 \times 2$  mm; **Ped** 8–10 mm; **Fl** coral-red to scarlet, green-tipped, 20–22 mm, base rounded, 5 mm  $\varnothing$  across the ovary, narrowed to 4 mm above, slightly enlarging to the mouth; **OTep** free for 7 mm; **St** and **Sty** exerted 2–3 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

**A. torrei** I. Verdoorn & Christian (Flow. Pl. Afr. 25: t. 987 + text, 1946). **Type:** Moçambique, Zambézia (*da Torre* s.n. [PRE 27239]). — **Distr:** Moçambique (Zambézia: Namuli Mts.); in grass on exposed granite slabs, 1525–1600 m. **I:** Reynolds (1966: 14–15); Carter & al. (2011: 126).

[10] Caulescent, branching at the base forming dense clumps; stem erect, to  $15 \times 1.5$  cm  $\varnothing$ ; **L**  $\pm 10$ , rosulate, linear,  $40$ – $45 \times 0.5$  cm, limp and deflexed, green with a few white spots near the

base, lower face with many, sometimes tuberculate, spots, **marginal teeth** minute,  $\pm 1$ – $2$  mm apart; **Inf**  $\pm 50$  cm, simple; raceme cylindrical, slightly acuminate,  $9 \times 4$ – $5$  cm, lax, with  $\pm 10$  flowers; **Bra** ovate-acute,  $15 \times 7$  mm; **Ped** 15 mm; **Fl** scarlet, grey-green at the mouth, 30 mm, slightly ventricose, base shortly attenuate, enlarged to 6–7 mm above the ovary, then narrowing to the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. trachyticola** (H. Perrier) Reynolds (J. South Afr. Bot. 23(2): 72–73, t. 26–27, 1957). **Type** [lecto]: Madagascar, Antananarivo (*Perrier* 11000 [P]). — **Distr:** Madagascar. **I:** Castillon & Castillon (2010: 68–71); Carter & al. (2011: 223).

≡ *Aloe capitata* var. *trachyticola* H. Perrier (1926).

**A. trachyticola** var. **multifolia** J.-B. Castillon (*Haseltonia* 10: 46–47, ills., 2004). **Type:** Madagascar, Antananarivo (*Castillon* 7 [P]). — **Distr:** Madagascar (Antananarivo: SE of Antsirabe); grassland on granite outcrops, 1800–2000 m; known only from the type locality. **I:** Castillon & Castillon (2010: 70–71); Carter & al. (2011: 223).

[2] Differs from var. *trachyticola*: **L** to 30, 15–30 cm, dark green, margin tinged reddish.

**A. trachyticola** var. **trachyticola** — **Distr:** Madagascar (Antananarivo, Fianarantsoa); mountain slopes, on trachyte and quartzite, 1600–2200 m. **I:** Reynolds (1966: 462–463); Castillon & Castillon (2010: 68–69); Carter & al. (2011: 223).

[2] Acaulescent, sometimes shortly caulescent, simple; stem procumbent, short; **L** 6–10 and distichous when young, to 14 and spiral to subrosulate later, lanceolate, tip rounded with short teeth,  $10$ – $15 \times 3$ – $4$  cm, bluish-grey tinged reddish, **marginal teeth** 1–1.5 mm, pungent, reddish-brown, 3–5 mm apart; **Inf** 65–90 cm, simple; raceme capitate,  $2$ – $3 \times 7$ – $8$  cm, dense; **Bra** ovate-acute,  $10 \times 6$  mm; **Ped** lowest 3–5 mm, uppermost 15–20 mm; **Fl** red, to 35 mm, base rounded, 8 mm  $\varnothing$  across the ovary, slightly enlarged above; **OTep** free almost to the base; **St** and **Sty** exerted 1–2 mm.



**A. transvaalensis** Kuntze (Rev. Gen. Pl. 3(2): 314, 1898). **Type:** RSA, Gauteng (*Kuntze* s.n. [NY, K]). — **Lit:** Smith & al. (2012c). **Distr:** RSA (Northern Prov., Gauteng, W Mpumalanga), E Botswana; rocky slopes, often at the foot of small hills, frequently between shrubs and bushes. **I:** Reynolds (1950: 262); Wyk & Smith (2014: 270–271).

[5] Acaulescent, solitary or suckering to form groups; **L** 12–16, densely rosulate, lanceolate-attenuate, 20–25 × 6–7 cm, dull milky green, with numerous dull white oval spots in irregular transverse bands, lower surface paler, **marginal teeth** deltoid, light brown, 3–4 mm apart; **Inf** 1–1.5 m, erect, with 5–8 **Br**, lowermost rebranched; racemes cylindrical-acuminate, to 30 cm, lax; **Bra** lanceolate-acuminate, 5–7 mm; **Ped** 10–15 mm; **Fl** flesh-pink to light coral-red, 36 mm, 9–10 mm Ø across the ovary, narrowed above to 5 mm, enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exserted 2–4 mm. — **Cytology:** 2n = 14 (Brandham 1971).

Included in *A. zebrina* by some authors, e.g. Carter & al. (2011).

**A. trichosantha** A. Berger (Bot. Jahrb. Syst. 36: 62, 1905). **Type** [lecto]: Eritrea (*Schweinfurth & Riva* 2291 [K, FT, G]). — **Lit:** Gilbert & Sebsebe Demissew (1997). **Distr:** Eritrea, Ethiopia.

The choice of a new lectotype by Gilbert & Sebsebe Demissew (1997), superseding the earlier choice by Reynolds, appears contrary to the rules and is not followed here.

**A. trichosantha** ssp. *longiflora* M. G. Gilbert & Sebsebe (Kew Bull. 52(1): 142–143, 1997). **Type:** Ethiopia, Harerge Region (*Burger* 3394 [K, ETH, FT]). — **Distr:** C & E Ethiopia (Harerge, Shewa); open deciduous bushland on volcanic rocks and alluvial soils, 1000–1950 (–2200) m. **I:** Reynolds (1966: 133, fig. 134, lower, as *A. trichosantha*); Carter & al. (2011: 279).

[5] Differs from ssp. *trichosantha*: **L** marginal teeth 2–4 mm; **Fl** 25–30 mm.

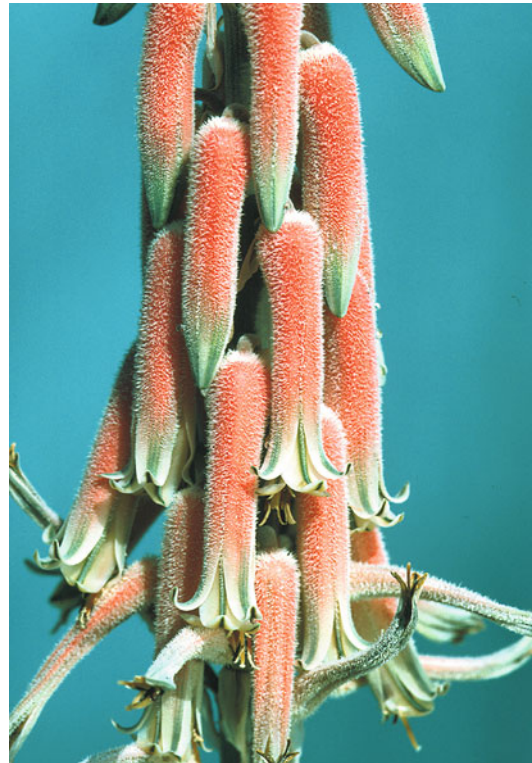
This occurs further S than ssp. *trichosantha*.

**A. trichosantha** ssp. *trichosantha* — **Distr:** Eritrea, N Ethiopia: Tigray floristic region; rocky

slopes or arid flat areas, 520–1700 m. **I:** Reynolds (1966: 132–133); Sebsebe Demissew & Nordal (2010: 53–54); Carter & al. (2011: 279). — Fig. 66.

**Incl.** *Aloe percrassa* Schweinfurth (1894) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Aloe percrassa* var. *albopicta* Schweinfurth (1894) (*incorrect name*, Art. 11.4).

[5] Acaulescent or very shortly caulescent, simple or suckering to form groups; **L** 12–16, densely rosulate, lanceolate-attenuate, 40–50 × 10 cm, dull green, sometimes with a few scattered spots, rarely with many spots, exudate drying yellow, **marginal teeth** ±4.5–5.5 mm, pungent, reddish-brown, 12–15 mm apart; **Inf** 1–1.5 m, with 2–3 **Br**; racemes cylindrical-acuminate, ±30 (–50) cm, subdense; **Bra** ovate-lanceolate, acute, 14 × 6 mm; **Ped** 5–6 mm; **Fl** strawberry-pink or coral-pink, white-tomentose, 20–23 mm, base rounded, 7–8 mm Ø across the ovary, not or



**Fig. 66** *Aloe trichosantha* ssp. *trichosantha*. (Copyright: U. Eggli)

very slightly narrowed above; **OTep** free for 10–12 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**:  $2n = 14$  (Brandham 1971, Fentaw & al. 2013).

Plants in S Ethiopia, Kenya (near Garissa), and Somalia, mentioned by Reynolds (1966: 143) as an undescribed species, are now *A. citrina*.

**A. trigonantha** L. C. Leach (J. South Afr. Bot. 37(1): 46–51, ills., 1971). **Type**: Ethiopia, Begemdir Prov. [Gonder] (*McLeay* s.n. in *Reynolds* 11618 [PRE, SRGH]). — **Distr**: NW Ethiopia (Gonder and Gojam Regions); dry stony grassland, 1900–2500 m. **I**: Sebsebe Demissew & Nordal (2010: 83–84); Carter & al. (2011: 449).

[7] Acaulescent, suckering at the base to form dense groups; **L**  $\pm 24$ , densely rosulate, lanceolate-attenuate,  $30\text{--}45 \times 5\text{--}10$  cm, pale green, pinkish-brown towards the tip, with a few elongated whitish spots, lower face bluish-green with many spots, **marginal teeth**  $\pm 3$  mm, pinkish-brown, 10–20 mm apart; **Inf** 60–90 cm, with  $\pm 3$  **Br**, each rebranched; racemes cylindrical-acuminate,  $\pm 20 \times 7$  cm, lax; **Bra** deltoid-attenuate to ovate-acuminate,  $5\text{--}10 \times 3\text{--}5$  mm; **Ped** to 15 mm; **Fl** bright scarlet to orange-scarlet, very thick and fleshy, 35 mm, base shortly attenuate, 10–12 mm  $\varnothing$  across the ovary, narrowed to 7–8 mm above, and to 3–4 mm at the mouth; **OTep** free for  $\pm 10$  mm; **St** and **Sty** exerted 1–2 mm.

**A. tsitongambarikana** J.-P. Castillon & J.-B. Castillon (CactusWorld 34(2): 112–113, ills. (pp. 111–113), 2016). **Type**: Madagascar, Toliara (Castillon 61 [TAN, TAN]). — **Distr**: S Madagascar (Toliara); rocky cliffs in the shade of trees in humid forest, 500–800 m.

[14] Caulescent, usually solitary, sometimes with 2–3 branches at the base; stem to 1 m, supported by surrounding vegetation, creeping, or pendulous; **L** 10–15, lax, nearly rosulate at the stem tip, triangular,  $40\text{--}60 \times 2$  cm, green, exudate colourless, drying light yellow, **marginal teeth** 1 mm, 4–7 mm apart; **Inf** 40–80 cm, erect, simple; raceme conical, 10–20 cm, dense; **Bra** rectangular, acute,  $10 \times 3$  mm; **Ped** 10–15 mm, green; **Fl** yellow at the base, white with green

nerves towards the mouth, slightly clavate, 25–30 mm, base obconical, 4–5 mm  $\varnothing$ ; **OTep** free for 15–18 mm; **St** not exerted; **Sty** exerted 5 mm.

**A. tugenensis** L. E. Newton & Lavranos (Cact. Succ. J. (US) 62(5): 215–217, ills., 1990). **Type**: Kenya, Rift Valley Prov. (Newton 3514 [K, EA, MO]). — **Distr**: Kenya (Rift Valley Prov.: Tugen Hills); rocky slopes in heavily grazed dry *Acacia* bushland, 1100–1550 m. **I**: Carter & al. (2011: 615).

$\equiv$  *Aloe archeri* ssp. *tugenensis* (L. E. Newton & Lavranos) Wabuye (2006).

[13] Caulescent, branching at or near the base; stem erect or ascending to 70 cm, becoming decumbent to  $1.2 \text{ m} \times 3 \text{ cm}$   $\varnothing$ , dead leaves persistent; **L** 12–20, rosulate, lanceolate-attenuate, to  $61 \times 12$  cm, dull green, tinged brownish-red in sun, with several scattered whitish spots on seedlings and young shoots only, surface slightly rough, exudate yellow, drying brownish-yellow, **marginal teeth** to 5 mm, firm, uncinat, brown-tipped, 6–15 mm apart; **Inf** 95–130 cm, with up to 12 **Br**, lower ones sometimes rebranched; racemes cylindrical, 10–24 cm, subdense; **Bra** linear,  $11 \times 4$  mm, densely imbricate in bud stage; **Ped** 7–9 mm; **Fl** pale pink, tepals with whitish margin, 22 mm, base shortly attenuate, 5 mm  $\varnothing$  across the ovary, narrowed to 4.5 mm above, then enlarging to 7 mm at the mouth; **OTep** free for 14–15 mm; **St** and **Sty** exerted 4–6 mm.

**A. turkanensis** Christian (J. South Afr. Bot. 8 (2): 173–174, t. 6, 1942). **Type**: Kenya, Rift Valley Prov. (*Erens* 1610 [SRGH, PRE]). — **Lit**: Newton & Lavranos (1990: with ills.). **Distr**: Kenya, NE Uganda; usually in the shade of shrubs in arid areas on stony-sandy ground or lava, 915–1500 m. **I**: Carter & al. (2011: 610); Cole & Forrest (2017: 120–123).

[12] Caulescent, branching sparsely at the base forming clumps to 2 m  $\varnothing$ ; stem ascending, to 45 cm, becoming decumbent to 70 cm; **L** 14–18, densely rosulate, lanceolate-attenuate, to  $70 \times 9$  cm, dull green, sometimes with slight bluish bloom, with a few elongated pale green spots,

often more numerous and in  $\pm$  transverse bands on the lower face, surface smooth, exudate drying yellow, **marginal teeth** 2 mm, whitish, 12–18 mm apart; **Inf** to 1 m, with up to 8 **Br**, lower ones rebranched; racemes with secund flowers, 15–26  $\times$  6 cm, subdense; **Bra** ovate-cuspidate, 5–7  $\times$  3 mm; **Ped** 8–9 mm; **Fl** red to orange-red, tipped slate-grey, 25 mm, base shortly attenuate, 8–9 mm  $\varnothing$  across the ovary, narrowed to 6.5–7 mm above; **OTep** free for 9–11 mm; **St** and **Sty** exerted 3–6 mm.

*A. turkanensis* sensu Reynolds (1966) is based on *A. scabrifolia*, and his illustrations are of the latter species.

**A. tweedieae** Christian (J. South Afr. Bot. 8(2): 175–176, t. 7, 1942). **Type:** Uganda, Northern Prov. (*Tweedie* 262 [SRGH, K, PRE]). — **Distr:** W Kenya, South Sudan, E Uganda; dry sandy bushland, 1340–1800 m. **I:** Reynolds (1966: 269–270); Carter & al. (2011: 350); Cole & Forrest (2017: 124–131).

$\equiv$  *Aloe secundiflora* var. *tweedieae* (Christian) Wabuyele (2006).

[5] Acaulescent or shortly caulescent, simple or suckering to form small groups; stem rarely to 50 cm; **L**  $\pm$ 20, densely rosulate, lanceolate-attenuate,  $\pm$ 50  $\times$  13 cm, dull to glossy green, usually with many pale green spots, surface smooth, exudate yellow, drying brownish, **marginal teeth**  $\pm$ 4 mm, pungent, reddish-brown, 10–15 mm apart; **Inf** 1.2–1.5 m, with 15–20 **Br**, lower ones sometimes rebranched; terminal racemes cylindrical, laterals with secund flowers, to 15  $\times$  5 cm, lax; **Bra** ovate-acute, 2  $\times$  2 mm; **Ped**  $\pm$ 7 mm; **Fl** coral-pink, paler becoming yellowish towards the mouth,  $\pm$ 24 mm, base rounded, 8 mm  $\varnothing$  across the ovary, narrowed slightly above; **OTep** free for 16 mm; **St** and **Sty** exerted 3–4 mm.

Reynolds (1966) states that the leaf exudate dries deep purple, but this is not evident on herbarium specimens, and was not the case on specimens collected by the present author near the type locality on the Kenyan side of the border.

Natural hybrids with other species have been reported (Reynolds 1966).

**A. ukambensis** Reynolds (J. South Afr. Bot. 22(1): 33–35, 1956). **Type:** Kenya, Eastern Prov. (Reynolds 7651 [EA, K, PRE]). — **Distr:** Kenya (SE highlands); gneissic rock faces and rocky slopes on hills, 520–1400 m. **I:** Reynolds (1966: 264–266); Carter & al. (2011: 427); Laius (2014: 70–71).

[7] Acaulescent, branching at the base to form dense groups; **L** 30–40, densely rosulate, lanceolate-attenuate, to 50  $\times$  10–12 cm, grey-green tinged reddish, with conspicuous longitudinal striations, sometimes with a few scattered oval white spots near the base, on the lower face the spots H-shaped when present, surface smooth, exudate drying pale orange-brown, **marginal teeth** 3–4 mm, reddish-brown, 8–10 mm apart; **Inf** 50 cm, with 2–3 **Br**; racemes capitate or subcapitate, 4–6  $\times$  6 cm, dense; **Bra** ovate-deltoid, 5  $\times$  2.5 mm; **Ped** 18–20 mm; **Fl** bright glossy red,  $\pm$ 40 mm, base shortly attenuate, 7 mm  $\varnothing$  across the ovary, slightly narrowed above, then enlarging to the mouth; **OTep** free for 20 mm; **St** and **Sty** exerted 3–5 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. umfoloziensis** Reynolds (J. South Afr. Bot. 3(1): 42–45, t. 2, 1937). **Type:** RSA, KwaZulu-Natal (Reynolds 2011 [PRE]). — **Distr:** RSA (E KwaZulu-Natal); low-lying subtropical parkland, 800–1000 m. **I:** Reynolds (1950: 223–224); Carter & al. (2011: 167); Wyk & Smith (2014: 272–273).

[5,7] Acaulescent or shortly caulescent, simple or usually suckering to form groups; stem to 30 cm; **L**  $\pm$ 20, densely rosulate, lanceolate-attenuate, 20–25  $\times$  8–9 cm, green to brownish-green, with many dull white oblong spots scattered or  $\pm$  in interrupted transverse bands, lower face paler green with or without spots, usually somewhat lineate, **marginal teeth** 3–5 mm, pungent, 10–15 mm apart; **Inf** 1–1.5 m, with 5–8 **Br**, lower ones sometimes rebranched; racemes capitate, 7–9  $\times$  7–9 cm, subdense; **Bra** deltoid-acuminate, shorter than the pedicels; **Ped** 10–15 mm; **Fl** coral-red, 33–38 mm, base truncate, 8–9 mm  $\varnothing$  across the ovary, abruptly narrowed to 5–6 mm above, then enlarging to the mouth; **OTep** free for 8–9 mm; **St** and **Sty** exerted 0–1 mm.

Included in *A. maculata* by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011) and Wyk & Smith (2014).

**A. uncinata** L. E. Newton & Wabuye (CactusWorld 36(3): 185–187, ills., 2018). **Type:** Kenya, Homa Bay County (*Powys* 1411 [EA, K]). — **Distr:** W Kenya; rocky cliff, ±1250 m.

[13] Caulescent, pendulous; stem to 114 cm, branching at or near the base, with dead leaves persistent; **L** to 15, loosely rosulate, lanceolate-attenuate, tips recurved, 18 × 3.5 cm, brownish-green, surface smooth with light waxy sheen, exudate yellow, slowly drying purple, **marginal teeth** deltoid, 3 mm, with red tip, 9–11 mm apart; **Inf** 35 cm, erect, with 0–2 **Br**; racemes cylindrical, to 12 cm, lateral ones to 9 cm, semi-lax; **Bra** triangular-attenuate, 4 × 3 mm, whitish with a single brown vein; **Ped** 9 mm, coral-red; **Fl** coral-red, lobes yellow with red midrib, completely yellow at the apex, 30 mm, base shortly attenuate, 7–8 mm Ø across the ovary, narrowed to 5–6 mm above, widening to 7 mm at the mouth; **OTep** free for 10 mm; **St** exerted 0–1 mm; **Sty** exerted 10 mm.

**A. vacillans** Forsskål (Fl. Aegypt.-Arab., 74, 1775). **Type:** Yemen (*Forsskål* s.n. [C †]). — **Lit:** Wood (1983). **Distr:** Saudi Arabia (Asir Prov.), Yemen; rocky slopes and eroded grassland, 1300–3000 m. **I:** Reynolds (1966: 156); Collenette (1999: 30); Carter & al. (2011: 367).

**Incl.** *Aloe audhalica* Lavranos & D. S. Hardy (1965); **incl.** *Aloe dhalensis* Lavranos (1965).

[4,5] Acaulescent or shortly caulescent, simple or rarely suckering to form small groups; stem erect or decumbent, to 50 cm; **L** 15–20, rosulate, ensiform-attenuate, ±30–60 × 7–13 cm, glaucous, lower face sometimes with a few median prickles near the tip, surface rough, **marginal teeth** 2–3 mm, brown or reddish-brown, 6–10 mm apart; **Inf** to 1–2 m, simple or with up to 3 **Br**; racemes cylindrical, 35–40 cm, subdense; **Bra** ovate-acuminate, 10–15 × 6 mm; **Ped** 5–12 mm; **Fl** red or yellow, ±30 mm, base rounded, 8 mm Ø across the ovary, very slightly narrowed above, then slightly enlarging to the mouth; **OTep**

free for 6 mm; **St** and **Sty** exerted 3–4 mm. — **Cytology:** 2n = 14 (Wood 1983).

Red-flowered plants are predominant at the N end of the range, and yellow-flowered plants are predominant in the S (Wood 1983). The same author reports a natural hybrid with *A. inermis*.

**A. vallis** L. C. Leach (J. South Afr. Bot. 40 (2): 111–115, ills., 1974). **Type:** Angola, Huíla [Namibe ?] (*Leach & Cannell* 14651 [LISC, BM, BR, K, LUAI, M, MO, PRE, SRGH, WIND, ZSS]). — **Distr:** SW Angola (Namibe: W escarpment of the Serra de Chela); sandstone ledges and cliffs, ±1230 m. **I:** Carter & al. (2011: 565).

[15] Caulescent, branching at the base; stem to 50 cm; **L** densely rosulate, ovate-attenuate, 22–34 × 4–5 cm, greyish or greenish-blue to bluish-green, with a few small oval or round whitish spots near the base, lower face with more spots, with narrow yellowish margin, exudate frothy, drying as opaque crystalline yellow crust, **marginal teeth** 2–2.5 mm, pungent, yellowish, orange- or brown-tipped, 10–12 mm apart; **Inf** ≥ 50–60 cm, oblique or suberect, simple or with 1 **Br**; racemes cylindrical-acuminate, 17–45 × ±4 cm, lax; **Bra** ovate-acute, to 4.5 × 2.5 mm; **Ped** 4–4.5 mm; **Fl** bright scarlet, yellowish at the mouth, 20–25 mm, base rounded, ±5 mm Ø across the ovary, narrowed to 4.5 mm above, then enlarging to 5.5 mm at the mouth; **OTep** free for 4.5–6 mm; **St** and **Sty** exerted 0–1 mm.

**A. vanbalenii** Pillans (South Afr. Gard. 24: 25, 1934). **Type:** RSA, KwaZulu-Natal (*Van Balen* s.n. [BOL]). — **Distr:** RSA (N KwaZulu-Natal, SE Mpumalanga), Swaziland: Lebombo Range; in shade on flat rocks or rocky slopes in bushland, 300–600 m. **I:** Reynolds (1950: 420–421, t. 41); Carter & al. (2011: 431); Wyk & Smith (2014: 104–105).

[7] Acaulescent or shortly caulescent, branching to form dense groups; stem to 30 cm; **L** densely rosulate, lanceolate-attenuate, strongly recurved, 70–80 × 12–15 cm, green to copper-red, usually obscurely lineate, with horny reddish to reddish-brown margin, **marginal teeth** ±3–5 mm, pungent, reddish, 10–15 mm apart; **Inf** ±1



m, with 2–3 **Br**; racemes conical, 25–30 × 8–10 cm, subdense; **Bra** ovate-acute, 15 × 7 mm; **Ped** to 20 mm; **Fl** usually buff-yellow, sometimes dull red, ±35 mm, base shortly attenuate, not narrowed above the ovary, enlarging slightly to the mouth; **OTep** free to the base; **St** and **Sty** exerted 10–12 mm.

Natural hybrids with *A. marlothii* have been reported (Reynolds 1950).

**A. vandermerwei** Reynolds (Aloes South Afr. [ed. 1], 268–270, ills., 1950). **Type:** RSA, Limpopo (*van der Merwe* s.n. [PRE 21288]). — **Lit:** Smith & al. (2012c). **Distr:** RSA (SE Limpopo); grassy clearings in bushland, 200–700 m. **I:** Groenewald (1938: as *A. angustifolia*); Wyk & Smith (2014: 274–275).

≡ *Aloe angustifolia* Groenewald (1938) (*nom. illeg.*, ICN Art. 53.1).

[7] Acaulescent, suckering to form dense groups; **L** 15–20, rosulate, linear-attenuate, to 60 × 3.5 cm, dark green with large whitish spots ± in interrupted transverse bands, exudate drying deep purple, **marginal teeth** 3–4 mm, firm, pale brownish, 10–15 mm apart; **Inf** ±1 m, with 6–10 **Br**; racemes cylindrical, slightly acuminate, 10–20 cm, lax, with ±25 flowers; **Bra** deltoid-acuminate, to 10 × 3 mm; **Ped** 10 mm; **Fl** flesh-pink to pale pinkish-red, 30 mm, base rounded, 7–8 mm Ø across the ovary, abruptly narrowed to 5 mm above, then enlarging to 9 mm at the mouth; **OTep** free for 9–10 mm; **St** exerted 1–2 mm; **Sty** exerted 2 mm.

Included in *A. zebrina* by some authors, e.g. Carter & al. (2011).

**A. vanrooyenii** Gideon F. Smith & N. Crouch (Bothalia 36(1): 73–74, ills., (2): 174, 2006). **Type:** RSA, KwaZulu-Natal (Crouch & Smith 2 [NH]). — **Distr:** RSA (C KwaZulu-Natal); thornveld savanna, 1200–1800 m. **I:** Carter & al. (2011: 158); Wyk & Smith (2014: 276–277).

[4] Acaulescent or with a short stem to 8 cm, suckering to form small groups; **L** densely rosulate, deltoid-lanceolate, 12–15 × 6–8 cm, pale green with whitish spots often in transverse bands, exudate drying purple, **marginal teeth** pungent, 3–4 mm, orange-brown, 3–4 mm

apart; **Inf** 50–80 cm, erect, with 1–2 **Br**, lower-most rebranched; racemes cylindrical-conical, 25–47 cm, lax; **Bra** linear, 8–10 mm; **Ped** 8–10 mm; **Fl** orange or red, cream at the mouth, 33–38 mm, 8–10 mm Ø across the ovary, abruptly constricted above, widening to 8 mm at the mouth; **OTep** free for 8–15 mm; **St** and **Sty** exerted 0–1 mm.

**A. vaombe** Decorse & Poisson (Recherch. Fl. Mérid. Madagascar, 96, 1912). **Type:** Madagascar, Toliara (*Anonymous* s.n. [not located]). — **Distr:** Madagascar. **I:** Castillon & Castillon (2010: 196–199); Carter & al. (2011: 663).

**A. vaombe** var. **poissonii** Decary (Bull. Écon. Trimestriel [Madagascar] 18: 23, 1921). **Type:** Madagascar, Toliara (*Anonymous* s.n. [not located]). — **Distr:** S Madagascar (Toliara); on gneiss. **I:** Carter & al. (2011: 663).

[9] Differs from var. *vaombe*: Stem to 5 m, more slender; **L** more densely rosulate, more deflexed; **Inf** with **Br** more spreading.

**A. vaombe** var. **vaombe** — **Distr:** S & SW Madagascar (Toliara); dry thorn-bush, widespread, 50–500 (–1200) m. **I:** Reynolds (1966: 509–511); Castillon & Castillon (2010: 196–199); Carter & al. (2011: 663).

[9] Caulescent, simple; stem erect, to 3 m × 20 cm Ø, dead leaves persistent; **L** 30–40, densely rosulate, lanceolate-attenuate, 80–100 × 15–20 cm, dull green, exudate drying deep purple, **marginal teeth** 5–6 mm, subpungent, 15–20 mm apart; **Inf** ±90 cm, with ±12 **Br**, lower ones rebranched; racemes cylindrical, slightly acuminate, to 15 × 6 cm, subdense; **Bra** triangular, 8 × 5 mm; **Ped** ±12 mm; **Fl** bright crimson, ±28 mm, base rounded, 6–7 mm Ø across the ovary, narrowed above, then enlarging to the mouth; **OTep** free for 14 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Brandham 1971).

**A. vaotsanda** Decary (Bull. Écon. Trimestriel [Madagascar] 18: 23, 1921). **Type:** Madagascar, Toliara (*Decary* s.n. [P]). — **Distr:** Madagascar (Toliara); dry bush on limestone outcrops along a narrow coastal belt, 0–100 m. **I:** Reynolds (1966:



512); Castillon & Castillon (2010: 270–271); Carter & al. (2011: 668).

[9] Caulescent, simple; stem erect, to 4 m × 15 cm Ø, dead leaves persistent; **L** 30–40, densely rosulate, lanceolate-attenuate, strongly deflexed, to 1 m × 15 cm, green tinged reddish, exudate drying yellowish-brown, **marginal teeth** ±5–6 mm, pungent, 15 mm apart; **Inf** ±50 cm, with many **Br**; racemes dense, with ±50–70 secund flowers; **Bra** triangular-attenuate, 7–8 × 3 mm; **Ped** 4–6 mm; **Fl** orange-yellow, ±22 mm, base rounded, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for ±13 mm; **St** and **Sty** exerted 5 mm.

**A. variegata** Linné (Spec. Pl. [ed. 1], 1: 321, 1753). **Type**: [lecto — icono]: Commelin, Hort. Med. Amstelod. Pl. Rar., t. 47, 1706. — **Distr**: SW Namibia, RSA (Northern Cape, NE Western Cape, NW Eastern Cape, Free State); in the shade of bushes on hard or stony ground; 100–1800 m. **I**: Reynolds (1950: 206–209); Carter & al. (2011: 406); Wyk & Smith (2014: 294–295). — Fig. 67.

≡ *Gonialoe variegata* (Linné) Boatwright & J. C. Manning (2014) ≡ *Tulista variegata* (Linné) G. D. Rowley (2014); **incl.** *Aloe punctata* Haworth (1804); **incl.** *Aloe variegata* var. *haworthii* A. Berger (1908); **incl.** *Aloe ausana* Dinter (1931).

[6] Acaulescent, suckering to form groups; **L** to 24, trifarious, lanceolate-deltoid, ±10–15 × 4–6 cm, green with oblong white spots in irregular

transverse bands, with whitish horny crenate-dentate margin; **Inf** ±30 cm, simple or with 1–2 **Br**; racemes cylindrical, 10–20 cm, lax, with ±20–30 flowers; **Bra** ovate-acuminate, to 15 × 7 mm; **Ped** 4–7 mm; **Fl** flesh-pink to dull scarlet, 35–45 mm, base truncate, slightly narrowed above the ovary, then enlarging to the mouth; **OTep** free for 5–7 mm; **St** not exerted; **Sty** exerted 1–2 mm. — **Cytology**: 2n = 14 (Kondo & Megata 1943).

Natural hybrids with other species have been reported (Reynolds 1950).

**A. varimaculata** T. A. McCoy (Cact. Succ. J. (US) 88(6): 277–280, ills., 2016). **Type**: Angola, Namibe (McCoy 4269 [FT]). — **Distr**: SW Angola (Namibe); amongst rocks on a mountain pass, ±1600 m, known only from the type locality.

[11] Caulescent, branching at the base forming dense clumps; stem to 30 cm, erect to procumbent, with dried leaves persistent; **L** loosely rosulate and cauline-dispersed, lanceolate-attenuate, tips strongly recurved, 25 × 2–2.5 cm, glossy green, usually white-spotted, sheaths 8–15 mm apart, with white lines and elliptic spots, exudate clear, drying clear, **marginal teeth** deltoid, 3–4 mm, brown-tipped, 4–6 mm apart; **Inf** 30 cm, erect, with up to 2 **Br**; racemes cylindrical-conical, to 15 cm, subdense; **Bra** lanceolate-acute, 4–5 × 2.5 mm, scarios, orange-white, with 3–5 brown

**Fig. 67** *Aloe variegata*.  
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nerves; **Ped** 10–12 mm, orange; **Fl** orange to pinkish-orange, lobe tips cream with 3 greenish-brown nerves, 25 mm, base slightly rounded, 4.5 mm  $\varnothing$  across the ovary, slightly narrowed above, enlarging to 6 mm at the mouth; **OTep** free for 12 mm; **St** exerted 1 mm; **Sty** exerted 1.5 mm.

**A. vera** (Linné) Burman *fil.* (Fl. Indica, 83, 1768). **Type:** [lecto — icono]: Rheede, Hort. Malab. 11: 7, t. 3, 1692. — **Lit:** Newton (1979). **Distr:** Origin uncertain, probably Arabia; widely cultivated in warm countries, esp. around the Mediterranean (since ancient times), India, and the West Indies, and frequently naturalised. **I:** Reynolds (1966: 146–149, as *A. barbadensis*); Carter & al. (2011: 425). — Fig. 68.

≡ *Aloe perfoliata* var. *vera* Linné (1753); **incl.** *Aloe barbadensis* Miller (1768) ≡ *Aloe perfoliata* var. *barbadensis* (Miller) Aiton (1789); **incl.** *Aloe vulgaris* Lamarck (1783); **incl.** *Aloe elongata* Murray (1789); **incl.** *Aloe flava* Persoon (1805); **incl.** *Aloe barbadensis* var. *chinensis* Haworth (1819) ≡ *Aloe chinensis* (Haworth) Baker (1877) ≡ *Aloe vera* var. *chinensis* (Haworth) A. Berger (1908); **incl.** *Aloe indica* Royle (1839); **incl.** *Aloe vera* var. *littoralis* Koenig *ex* Baker (1880); **incl.** *Aloe lanzae* Todaro (1890) ≡ *Aloe vera* var. *lanzae* (Todaro) A. Berger (1908); **incl.** *Aloe vera* var. *wratislaviensis* Kostecka-Madalska (1953).

[6] Acaulescent or shortly caulescent, suckering to form dense groups; stem to 30 cm; **L**  $\pm$ 16,

densely rosulate, lanceolate-attenuate, 40–50  $\times$  6–7 cm, grey-green tinged reddish, with slightly pinkish margin, surface smooth, exudate drying yellow, **marginal teeth**  $\pm$ 2 mm, firm, pale, 10–20 mm apart; **Inf** 60–90 cm, simple or with 1–2 **B**; racemes cylindrical-acuminate, 30–40  $\times$  5–6 cm, dense; **Bra** ovate-acute, deflexed, 10  $\times$  5–6 mm; **Ped**  $\pm$ 5 mm; **Fl** yellow,  $\pm$ 28–30 mm, slightly ventricose, base rounded, 7 mm  $\varnothing$  across the ovary, enlarged above, then narrowing to the mouth; **OTep** free for 18 mm; **St** and **Sty** exerted 3–5 mm. — **Cytology:**  $2n = 14$  (Sutaria 1932).

Linné did not publish the combination *Aloe vera* as a numbered species. Reynolds (1966) argued that the name should be *A. barbadensis*, but he had overlooked the combination published by N. L. Burman (not later than April 6, 1768), which has priority over Miller's (April 16, 1768) name (Newton 1979).

Wood (1983) suggested that this is conspecific with *A. officinalis*, which he treated as a doubtfully distinct variety. As *A. vera* is not known as naturally occurring populations anywhere, it seems best to maintain it as a separate species at present. Plants from the Sumail Gap (Oman) reported by Lavranos (1965) need further investigation, though Jonkers (2009) argues that the Oman population cannot be considered a natural occurrence because the plants are few in number and are always found in association with human-populated places; moreover, they are not mentioned at all by early travellers. It is possible that

**Fig. 68** *Aloe vera*.  
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the plants now cultivated are the result of selection over 2000 years or more, and perhaps they should have the status of cultivars. *A. indica* is probably a red-flowered variant introduced to India (Reynolds 1966). Plants on the Maltese Island of Gozo could represent an ancestral population because they are known to set seed (Breuer 2003).

*A. vera* is the best known species outside the circle of succulent plant enthusiasts because of frequent advertisement of medicinal and cosmetic products based on the leaf extracts. The species has been used as a medicinal plant since ancient times. Chinchilla & al. (2013) report baked clay tablets from Sumeria from 2100 BCE that appear to be the oldest written account of the laxative properties of the species, and thus of its medicinal use. Other early accounts are in the codices of Emperor Shong-Nung ( $\pm 1800$  BCE) and the Ebers papyrus (1550 BCE). Grace & al. (2015) found that *A. vera* is part of a clade of species from the Arabian peninsula, in a subclade with *A. purpurea* and *A. yemenica* and — oddly enigmatic! — the Madagascan *A. acutissima* and *A. bakeri*. Lodé (2016) argues that plants from Petra (Jordan) sometimes referred to as representing *A. vera* in fact are *A. koeneni*.

Reynolds (2004) presents a comprehensive summary of the chemistry and medicinal use of *A. vera*. Upton & al. (2012) provide a detailed compendium of standards and preparations currently used in the contemporaneous Aloe industry, and also provide an overview of the history of main products derived from *A. vera*. *A. vera* drinks are now seen frequently in supermarkets. Little is known about safety aspects of *A. vera* taken orally, and Chen & al. (2009) found that drug absorption in the intestinal system can be enhanced, with possible unexpected influence on the uptake of drugs to above-normal levels. Boudreau & Beland (2006) and Guo & Mei (2016) review available evidence for toxicity and summarize adverse clinical effects. In more recent time, gel derived from *A. vera* leaves has been used in the fruit-growing industry as a coating preserve to prolong the shelf-life of, e.g., table grapes (Serrano & al. 2006) or nectarine fruits (Ahmed & al. 2009). Jothi (2009) reports on the use of a gel extract as coating for cotton fabric

because of its antimicrobial activity. *A. vera* extracts have also been used in soap, washing powder, and even toilet paper, though the value of this addition is doubtful (Newton 2008). The enormous demand for propagation material for large-scale industrial plantations has led to the development of a micropropagation protocol (Oliveira & al. 2009).

**A. verecunda** Pole-Evans (Trans. Roy. Soc. South Africa 5: 703, 1917). **Type:** RSA, Limpopo (*Pienaar* s.n. [PRE]). — **Distr:** RSA (North-West Prov., Limpopo, Gauteng, Mpumalanga); grassland on rocky slopes, 1000–1900 m. **I:** Reynolds (1950: 134–135); Craib (2006: 114–118); Carter & al. (2011: 134); Wyk & Smith (2014: 338–339).

[4] Acaulescent or shortly caulescent, simple or usually suckering to form groups; **R** fusiform; stem to 20 × 2 cm; **L** 8–10, usually distichous, sometimes subrosulate, linear, 25–35 × 0.8–1 cm, dull green, lower face with many small white spots near the base, **marginal teeth** minute, soft, white, 2–7 mm apart; **Inf** 25 cm, simple; raceme capitate, dense; **Bra** ovate-acute, 20 × 15 mm; **Ped** 25–30 mm; **Fl** rich peach-red to scarlet, greenish-tipped, 26–30 mm, base shortly attenuate, 12 mm  $\varnothing$  across the ovary, not narrowed above; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology:** 2n = 14 (Müller 1945).

Natural hybrids with *A. zebrina* (as *A. transvaalensis*) have been reported (Reynolds 1950). Craib (2006) suggests that *A. fouriei*, *A. verecunda* and *A. vossii* might be mere ecotypes of one species. Further field work is required.

Fritz (2012) reports that young inflorescences are browsed by antelope, and stem and leaves are eaten by baboons in years of food shortage.

**A. versicolor** Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 21: 723, 1950). **Type:** Madagascar, Toliara (*Humbert* 20617 [P]). — **Lit:** Lüthy (2006: 57–58, conservation, with ill.). **Distr:** Madagascar (Toliara).

**A. versicolor** var. **stefanicana** (Rauh) J.-B. Castillon & J.-P. Castillon (Aloe Madagascar, 28, 2010). **Type:** Madagascar, Toliara (*Razafindratsira* s.n. in *BG Heidelberg* 73599

[HEID]). — **Distr:** S Madagascar (Toliara: Tolanaro); on bare granite rocks near the sea,  $\pm 50$ –100 m. **I:** Castillon & Castillon (2010: 219); Carter & al. (2011: 254, as *A. steffanieana*).

≡ *Aloe steffanieana* Rauh (2000) ≡ *Aloe versicolor* ssp. *steffanieana* (Rauh) J.-B. Castillon & J.-P. Castillon (2016) (*nom. inval.*, ICN Art. 41.5).

[6] Differs from var. *versicolor*: Caulescent; stem to  $15 \times 2$ –3 cm  $\emptyset$ , unbranched; **L** lanceolate, to  $35 \times 3.5$  cm, green; **Inf** to 80 cm; **Bra**  $10 \times 7$  mm; **Ped** 4 mm; **Fl** reddish at the base, cream-white above, 35 mm, 8–10 mm  $\emptyset$  across the ovary; **OTep** free for 15.5 mm; **St** and **Sty** exerted  $\pm 10$  mm.

Probably a hybrid according to Carter & al. (2011: 254). Castillon & Castillon (2016: 115) argue that this could be the hybrid *A. schomeri*  $\times$  *A. versicolor*.

**A. versicolor** var. **versicolor** — **Distr:** S Madagascar (Toliara); soil pockets on silicate rocks,  $\pm 50$ –70 m. **I:** Reynolds (1966: 422–423); Castillon & Castillon (2010: 218); Carter & al. (2011: 404).

[6] Acaulescent or very shortly caulescent, suckering to form dense groups; **L**  $\pm 15$ , densely rosulate,  $15 \times 2$  cm, almost linear, tip rounded with 3–5 white teeth 1 mm long, dull bluish-green with a bloom, exudate drying deep brown, **marginal teeth** 1.5–2 mm, firm, white, 5–6 mm apart; **Inf** 30–40 cm, simple; raceme cylindrical, subcapitate,  $\pm 5$  cm, subdense; **Bra** ovate-acute,  $7 \times 4$  mm; **Ped** 15–20 mm; **Fl** coral-red to pale scarlet at the base, paler above, yellowish at the tip,  $\pm 25$  mm, base rounded, 7 mm  $\emptyset$  across the ovary, not narrowed above; **OTep** free almost to the base; **St** and **Sty** exerted 3–4 mm.

**A. veseyi** Reynolds (J. South Afr. Bot. 25(4): 315–317, t. 32, 1959). **Type:** Zambia, Northern Prov. (Reynolds 8659 [PRE, K, SRGH]). — **Distr:** SW Tanzania, N Zambia (Northern Prov.); pendulous from cliffs, 840–1500 m. **I:** Reynolds (1966: 168–169); Carter & al. (2011: 510).

**Incl.** *Aloe enotata* L. C. Leach (1972).

[13] Caulescent, branching at the base; stem pendulous, to  $40 \times 2$  cm  $\emptyset$ ; **L**  $\pm 12$ , rosulate, lanceolate-falcate, attenuate,  $40$ – $50 \times 3$  cm, dull grey-green tinged reddish, with many scattered dull white spots, **marginal teeth** 1–2 mm, firm, to 20 mm apart; **Inf**  $\pm 60$  cm, pendulous with racemes ascending, with 2–4 **Br**; racemes cylindrical-conical,  $12 \times 7$  cm, lax, with  $\pm 30$  flowers; **Bra** lanceolate-attenuate,  $6 \times 3$  mm; **Ped** 14 mm; **Fl** pale yellow, 25 mm, base rounded, 5 mm  $\emptyset$  across the ovary, slightly narrowed above, then enlarging to 10 mm at the mouth; **OTep** free for 5–6 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Brandham 1971).

**A. viguieri** H. Perrier (Bull. Acad. Malgache, n.s. 10: 20, 1927). **Type:** Madagascar, Toliara (Perrier 17592 [P, K]). — **Distr:** S Madagascar (Toliara); limestone slopes and cliffs, 60–350 m. **I:** Reynolds (1966: 441–442); Castillon & Castillon (2010: 278–279); Carter & al. (2011: 502).

[4] Acaulescent or caulescent, simple or branching to form small groups; stem decumbent to 30 cm or pendulous to 1 m, dead leaves persistent; **L** 12–16, densely rosulate, lanceolate-attenuate,  $\pm 30$ – $40 \times 8$ –9 cm, light green, lineate, with 1 mm white cartilaginous margin, **marginal teeth** 0.5–1 mm, firm, white, 1–2 mm apart; **Inf**  $\pm 45$  cm, simple; raceme cylindrical, 20–25 cm, lax, with  $\pm 22$  flowers; **Bra** ovate-acute, 1.5 mm; **Ped** 11 mm; **Fl** scarlet, 22 mm, slightly clavate, base shortly attenuate, 4 mm  $\emptyset$  across the ovary, enlarging above; **OTep** free for 11 mm; **St** and **Sty** exerted 1–2 mm.

The leaf sap is poisonous due to the presence of hemlock alkaloids (Dring & al. 1984).

**A. virginiae** J.-P. Castillon (CactusWorld 30 (3): 164–165, ill., 2012). **Type:** Madagascar, Antananarivo (Castillon 54 [TAN, TAN]). — **Distr:** Madagascar (Antananarivo); quartzitic rocks, 2200 m.

[10] Caulescent, suckering at the base; stem to 30 cm; **L** 5–8, almost distichous, linear,  $10$ – $13 \times 0.5$ –0.8 cm, green, **marginal teeth**  $< 0.5$  mm, white, 2.5 mm apart; **Inf** 30–40 cm, erect, simple; raceme cylindrical, to 10 cm, lax; **Bra**  $6 \times 2$  mm;



**Ped** 7–8 mm; **Fl** bright red, yellow-green at the mouth, 20 mm; **OTep** free to the base; **St** and **Sty** not exerted.

**A. viridiana** Gideon F. Smith & Figueiredo (*Bradleya* 36: 216, ills. (pp. 213, 215), 2018). **Type:** Cult. RBG Kew (*Anonymous* s.n. [K]). — **Lit:** Smith & Crouch (1995: as *A. greenii*). **Distr:** RSA (C to NE KwaZulu-Natal), S Moçambique; below shrubs in hot valleys, 0–1000 m. **I:** Carter & al. (2011: 192); Wyk & Smith (2014: 236–237); both as *A. greenii*.

≡ *Aloe greenii* Baker (1880) (*nom. illeg.*, ICN Art. 53.1).

[7] Acaulescent, stoloniferous and forming dense groups; **L** 12–16, densely rosulate, linear-lanceolate, attenuate,  $\pm 40\text{--}45 \times 7\text{--}8$  cm, bright green, obscurely lineate, with many confluent oblong whitish spots in irregular transverse bands, more pronounced on the lower face, with pale brownish margin, **marginal teeth** 3–4 mm, pale brown to pink, 8–10 mm apart; **Inf** 1–1.3 m, with 5–7 **Br**; racemes oblong-cylindrical, 15–25 cm, subdense; **Bra** lanceolate-deltoid, acuminate, 10 mm; **Ped** 10 mm; **Fl** light to dark pink with a bloom, lobes with white border, 28–30 mm, base truncate, 7 mm  $\varnothing$  across the ovary, abruptly narrowed to 4 mm above, enlarging to the mouth; **OTep** free for 10 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology:**  $2n = 14$  (Müller 1945: as *A. greenii*).

Described (as *A. greenii* Baker) from an undocumented plant cultivated at Kew.

**A. viridiflora** Reynolds (*J. South Afr. Bot.* 3 (4): 143–145, t. 23, 1937). **Type:** Namibia, Windhoek (*Reynolds* 1626 [PRE]). — **Distr:** C Namibia (Windhoek: Khomas Hochland); in sparse grassland on rocky slopes, 1500–1800 m. **I:** Reynolds (1950: 322–323); Carter & al. (2011: 331).

[3] Acaulescent, simple; **L** 50–60, densely rosulate, lanceolate-attenuate, to  $40 \times 8$  cm, glaucous, obscurely lineate, **marginal teeth** 2 mm, pungent, pinkish-brown, 2–5 mm apart; **Inf**  $\pm 1.5$  m, with 6 **Br**; racemes capitate,  $10 \times 8$  cm, dense, with  $\pm 50\text{--}60$  flowers; **Bra** ovate-acute,  $15 \times 7$  mm; **Ped** 20 mm; **Fl** green, lemon-tinged

about the middle, 33 mm, clavate, base attenuate, enlarged above the ovary to 9–10 mm near the mouth; **OTep** free to the base; **St** exerted 10 mm; **Sty** exerted 10–12 mm.

**A. vituensis** Baker (in Thiselton-Dyer & al., *Fl. Trop. Afr.* 7: 458, 1898). **Type:** Kenya, Coast Prov. (*Thomas* 113 [B]). — **Lit:** Leach (1970: with ills.). **Distr:** N Kenya, South Sudan; usually in the shade below large shrubs or in grass on rocky slopes, 290–1525 m. **I:** Carter & al. (2011: 498).

[11] Caulescent, branching sparingly; stem erect at first, becoming decumbent later, to 40 cm; **L** scattered along the stem for 15–20 cm, lanceolate-attenuate, to  $35 \times 4$  cm, yellow-green near the base, becoming bronze to brown above, obscurely striatulate, with many lenticular or H-shaped whitish spots, more numerous on the lower face, surface smooth, exudate none but internal tissue with fibres, esp. at the base and in the sheath, **marginal teeth** 3–4 mm, pungent, orange-brown, 5–10 mm apart, leaf sheath to 3 cm, brown-striatulate; **Inf**  $\pm 50\text{--}60$  cm, simple; raceme cylindrical, slightly acuminate,  $7\text{--}8 \times 6$  cm, subdense; **Bra** ovate-acute, usually with a small tooth on one or both sides, markedly convex and appearing fleshy,  $\pm 7\text{--}9 \times 6$  mm; **Ped** 4–7 mm; **Fl** coral-pink, greenish-tipped, 27–29 mm, base shortly attenuate,  $\pm 5$  mm  $\varnothing$  across the ovary, narrowed above, then enlarging to 8–10 mm at the mouth; **OTep** free for 6–8 mm; **St** and **Sty** exerted 0–1 mm.

The type specimen was collected on an expedition that started from Witu, but it was collected further north. Sebsebe Demissew & Nordal (2010: 108–109) hypothesize that the species should also be present in S Ethiopia.

**A. vogtsii** Reynolds (*J. South Afr. Bot.* 2(3): 118–120, t. 15, 1936). **Type:** RSA, Limpopo (*Reynolds* 1488 [PRE, BOL]). — **Distr:** RSA (Limpopo: Soutpansberg); in long grass or among shrubs on rocky slopes in the mist belt, 1400–1700 m. **I:** Reynolds (1950: 257–258); Carter & al. (2011: 164); Wyk & Smith (2014: 280–281).



[7] Caulescent, suckering to form small groups; stem to 20 cm; **L** 16–20, densely rosulate, lanceolate-attenuate, tip a pungent spine, 20–25 × 5–6 cm, cress-green, obscurely lineate, with many small white H-shaped spots, scattered or ± in wavy interrupted transverse bands, lower face dull green, with a few pale brown median prickles near the tip, **marginal teeth** ±3 mm, pungent, pale brown, 10–15 mm apart; **Inf** ±66 cm, with ±7 **Br**, lower ones rebranched; racemes cylindrical, slightly acuminate, ±20 × 8 cm, subdense, with 30–40 flowers; **Bra** ovate-acuminate, 10–15 mm; **Ped** to 18 mm; **Fl** scarlet, paler at the mouth, 34 mm, base truncate, 9 mm Ø across the ovary, abruptly narrowed to 5 mm above, then enlarging to the mouth; **OTep** free for 9 mm; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Müller 1945).

Included in *A. swynnertonii* by Glen & Hardy (2000) but treated as distinct by Carter & al. (2011). Natural hybrids with other species have been reported (Reynolds 1950).

**A. volkensii** Engler (Pfl.-welt Ost-Afr., Teil C, 141, 1895). **Type**: Tanzania, Moshi Distr. (*Volkens* 406 [B, BM]). — **Distr**: Kenya, Rwanda, Tanzania, Uganda. **I**: Carter & al. (2011: 691–692).

**A. volkensii** ssp. **multicaulis** S. Carter & L. E. Newton (Fl. Trop. East Afr., Aloaceae, 56, 1994). **Type**: Tanzania, Musoma Distr. (*Greenway* 10351 [K, EA]). — **Distr**: SW Kenya, NW Tanzania, Rwanda, SE Uganda; rocky bushland, 1150–1920 m. **I**: Carter & al. (2011: 692); Cole & Forrest (2017: 132–137).

[9] Differs from ssp. *volkensii*: Branching at the base with ≥3 main stems; **L** marginal teeth ±15 mm apart; **Fl** brick-red, 30–35 mm.

Natural hybrids with *A. ngongensis* have been reported (Carter 1994).

**A. volkensii** ssp. **volkensii** — **Distr**: SE Kenya, NE Tanzania; dry forest on steep rocky slopes, 10–1800 m. **I**: Reynolds (1966: 328–329); Carter & al. (2011: 691).

**Incl.** *Aloe stuhlmannii* Baker (1898).

[17] Caulescent, simple or branching above the base with a single basal trunk; stem erect, to 9 m × 30 cm Ø, dead leaves persistent; **L** densely rosulate, lanceolate-attenuate, to 1 m × 10 cm, glaucous-green to olive-green, surface smooth, exudate drying yellow, **marginal teeth** 4 mm, pungent, brown-tipped, 8–15 mm apart; **Inf** 70–85 cm, with ±10 **Br**; racemes subcapitate, becoming cylindrical, 8–12 × 8–9 cm, dense; **Bra** ovate-acute, ±5 × 5 mm; **Ped** ±15 mm; **Fl** reddish-orange to pale scarlet, yellow at the mouth, ±35 mm, base rounded, 7–8 mm Ø across the ovary, very slightly narrowed above, then slightly enlarging to the mouth; **OTep** free for 15 mm; **St** and **Sty** exerted 5–6 mm.

**A. vossii** Reynolds (J. South Afr. Bot. 2(2): 65–68, t. 4, 1936). **Type**: RSA, Limpopo (*Reynolds* 557 [PRE]). — **Lit**: Lüthy (2006: 59–60, conservation, with ills.). **Distr**: RSA (Limpopo: Soutpansberg); among rocks on grassy slopes in the mist belt, 1200–1800 m. **I**: Reynolds (1950: 136–137); Craib (2006: 119–122); Carter & al. (2011: 136); Wyk & Smith (2014: 340–341).

[6] Acaulescent or very shortly caulescent, suckering to form small groups; **L** 14–20, multifarious, long-attenuate, to 50 × 3 cm, deep green with several scattered elongate white spots, the spots occasionally subtuberculate and spinulescent, lower face with many spots near the base, the spots frequently with a firm white prickle, margin very narrow, white, cartilaginous, **marginal teeth** 2 mm, firm, white, 2–4 mm apart; **Inf** to 50 cm, simple; raceme capitate, ±8 × 7 cm, dense; **Bra** ovate-acute, 16 × 11 mm; **Ped** 30 mm; **Fl** scarlet, 28 mm, base rounded, 8–9 mm Ø across the ovary, slightly narrowed above towards the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm. — **Cytology**: 2n = 14 (Müller 1941).

Some populations are virtually indistinguishable from *A. verecunda* and Craib (2006: 119–122) suggests that *A. fouriei*, *A. verecunda* and *A. vossii* might be mere ecotypes of one species. Further field work is required.

**A. vryheidensis** Groenewald (Tydskr. Wetensk. Kuns 15: 129–131, 1937). **Type**: RSA,

KwaZulu-Natal (*van der Merwe* 266 [PRE]). — **Distr:** RSA (KwaZulu-Natal, Limpopo, Mpumalanga); rocky slopes and dolomite outcrops, 900–1800 m. **I:** Reynolds (1950: 429–431, and 434–435 as *A. dolomitica*); Carter & al. (2011: 655); Wyk & Smith (2014: 82–83).

**Incl.** *Aloe dolomitica* Groenewald (1938).

[4] Acaulescent or caulescent, simple or sometimes 2- to 4-branched at the base; stem decumbent, suberect or erect, to 2 m × 20 cm Ø; **L** 20–50, densely rosulate, lanceolate-attenuate, to 65 × 13 cm, dark green to glaucous-green tinged bluish, with reddish margin, surface smooth, exudate drying yellow, **marginal teeth** 2–3 mm, pungent, reddish to brownish-red, 10–15 mm apart; **Inf** 60–150 cm, oblique with raceme erect, simple; raceme cylindrical, 30–40 × 5–7 cm, dense; **Bra** ovate-acute, 8–15 × 5–10 mm; **Ped** absent; **Fl** rose or greenish-yellow to yellowish, 12–20 mm, campanulate, base obconical, 5 mm Ø across the ovary, enlarged above to 12 mm at the mouth; **OTep** free to the base; **St** and **Sty** exerted 12–17 mm.

*A. vryheidensis* was described as acaulescent or very shortly caulescent, and *A. dolomitica* as having a stem to 2 m high and occurring further north. Glen & Hardy (1995) reported that the 2 taxa are not disjunct, and they reported having found a variable population with every possible intermediate between the two, and they concluded that they are conspecific.

Natural hybrids with other species have been reported (Reynolds 1950). Hargreaves & al. (2012) report that short-billed birds and *Xylocopa* bees and honey bees are important flower visitors. Bee visitors only collect pollen and avoid the phenolic-rich nectar. Bird-exclusion experiments reduce seed production by 45%.

**A. wanalensis** T. C. Cole & T. G. Forrest (Cact. Succ. J. (US) 83(1): 34–37, ill., 2011). **Type:** Uganda, Mbale Distr. (Cole & Forrest 440 [MHU, EA]). — **Distr:** Uganda; steep rock faces, 1580–1800 m. **I:** Cole & Forrest (2017: 138–143).

[13] Caulescent, solitary or suckering from the base to form small groups; stem to 3 m, pendulous, apex turning up; **L** 20–28, rosulate, narrowly

lanceolate-attenuate, 65 × 6 cm, mid-green, surface smooth, exudate drying pale yellow, **marginal teeth** 2 mm, 10–14 mm apart; **Inf** 70–80 cm, descending and turning up towards the apex, with 3–9 **Br**; racemes cylindrical, to 18 cm, lax; **Bra** deltoid-acute, 4 × 2 mm, brown with 3 nerves; **Ped** 19–21 mm; **Fl** coral-red, becoming yellow at the mouth, 29–31 mm, base obtuse, 6 mm Ø across the ovary, very slightly narrowed above, enlarging to 8 mm at the mouth; **OTep** free for 11 mm; **St** and **Sty** exerted 2–3 mm.

Very close to *A. tartarensis* and possibly conspecific. Said to be larger and more robust, having an upturned rosette with more numerous leaves, which have a different colour and only a few hanging down.

**A. welmelensis** Sebsebe & Nordal (Kew Bull. 60(1): 117, 120, fig. 4 (p. 119), 2011). **Type:** Ethiopia, Oromia Region (Sebsebe & al. 6655 [ETH, K]). — **Distr:** S Ethiopia (Oromia Region: Bale: Welmel River); vertical rock faces in valleys and on outcrops, 1050–1500 m. **I:** Sebsebe Demissew & Nordal (2010: 104–105).

[11] Caulescent, branching to form a group; stem to 60 cm, erect or decumbent; **L** 10–18, scattered along the stem, lanceolate-attenuate, 30–50 × 2–4 cm, greyish-green, surface smooth, exudate drying yellow, **marginal teeth** to 1 mm, white, reddish-tipped, 3–5 mm apart; **Inf** 50–80 cm, oblique, with 1 (rarely up to 5) **Br**; racemes cylindrical, 15–30 cm, lax, with flowers secund; **Bra** ovate-acuminate, 4–5 × 2.5 mm; **Ped** 6–7 mm; **Fl** bright scarlet, paler to almost white towards the mouth, 28–32 mm, 6–7 mm Ø across the ovary; **OTep** free for 10–12 mm; **St** exerted 1–4 mm; **Sty** disposition unknown.

**A. weloensis** Sebsebe (Kew Bull. 60(1): 117, fig. 3 (p. 118), 2011). **Type:** Ethiopia, Amhara Region (Sebsebe & al. 6275 [ETH]). — **Distr:** Ethiopia (Amhara Region: Wello); disturbed areas alongside roads, 2440–2500 m. **I:** Sebsebe Demissew & Nordal (2010: 61–62).

[5] Acaulescent, solitary or in small groups with up to 5 rosettes; **L** to 35, rosulate, lanceolate-attenuate, 20–45 × 5–10 cm, green with paler elongated spots, exudate drying yellow,

**marginal teeth** 1–2 mm, brownish-tipped, 0.8–1 mm apart; **Inf** 55–150 cm, erect, with 3–5 **Br**; racemes cylindrical, 15–25 cm, lax; **Bra** ovate-acuminate, 2–5 × 2 mm; **Ped** 10–13 mm; **Fl** pinkish-red, 21–23 mm, base truncate, 5–6 mm  $\varnothing$  across the ovary; **OTep** free for 10–11 mm; **St** and **Sty** exerted 3–5 mm. — **Cytology**:  $2n = 14$  (Fentaw & al. 2013).

**A. welwitschii** Klopper & Gideon F. Smith (Phytotaxa 76(1): 12, 2013). **Type**: Angola, Huila (*Welwitsch* 3756 [BM]). — **Distr**: Angola (Huila Plateau); grassland. **I**: Smith (1991b: 90, as *Chortolirion angolense*).

≡ *Haworthia angolensis* Baker (1878) ≡ *Chortolirion angolense* (Baker) A. Berger (1908).

[2] Acaulescent, with short subterranean bulb, usually solitary; **L** rosulate, slightly succulent, erect, grass-like, 5–7 cm, glaucous-green, margins denticulate; **Inf** 20–25 cm, simple; raceme cylindrical; **Ped** short; **Fl** cinnamon-brownish with greenish keels, base obtuse, zygomorphic, tube straight,  $\pm 12 \times 3$  mm, limb bilabiate; **Tep** free almost to the base.

**A. wernerii** J.-B. Castillon (Haseltonia 13: 23–24, ill., 2008). **Type**: Madagascar, Toliara (*Castillon* 26 [HBG, P]). — **Distr**: Madagascar (Toliara); gneissic outcrops, 100–200 m. **I**: Castillon & Castillon (2010: 226); Carter & al. (2011: 273).

[4] Acaulescent or with a very short stem, solitary or forming small groups; **L** 20–30, rosulate, lanceolate, 40–50 × 3–3.5 cm, bright green, red-tinged when exposed to sun, **marginal teeth** 1–2 mm, white, 5–10 mm apart; **Inf** to 70 cm, erect, simple or with 1 **Br**; racemes cylindrical, 7–10 cm, dense; **Bra** ovate, 5–10 × 4–6 mm; **Ped** 0–0.5 mm; **Fl** yellow, 16–20 mm, 7 mm  $\varnothing$  across the ovary, narrowed above towards the mouth; **OTep** free almost to the base; **St** and **Sty** exerted 3–5 mm.

**A. whitcombei** Lavranos (Cact. Succ. J. (US) 67(1): 30–33, ill., 1995). **Type**: Oman, Dhofar (*Collenette* 8950 [E]). — **Distr**: Oman (Dhofar); cliffs of limestone or calcareous sandstone, 900 m. **I**: Carter & al. (2011: 471).

[13] Caulescent, branching freely at the base; stem mostly pendulous, to  $\pm 30$  cm; **L** 5–8, densely rosulate, deltoid, tip rounded, 50–80 × 1.5 cm, green with many rounded whitish spots, **marginal teeth** 0.5 mm, soft, white, 1–2 mm apart; **Inf** 35–80 cm, obliquely ascending and arched downwards, or entirely pointing obliquely downwards, simple or with 1 **Br**; racemes conical, 30–60 cm, dense, with 12–50 flowers; **Bra** deltoid-acute, 4 × 2.5 mm; **Ped**  $\pm 6$  mm; **Fl** white with green veins, 14 mm, base rounded, 4 mm  $\varnothing$  across the ovary, not narrowed above; **OTep** free for 6 mm; **St** and **Sty** exerted 3–5 mm.

**A. wickensii** Pole-Evans (Trans. Roy. Soc. South Africa 5: 29, 1915). **Type**: RSA, Limpopo (*Anonymous* s.n. [PRE]). — **Distr**: RSA (Limpopo); open bushland on dolomitic slopes,  $\pm 1000$  m. **I**: Pole-Evans (1922); Carter & al. (2011: 381).

**Incl.** *Aloe wickensii* var. *lutea* Reynolds (1935).

[5] Acaulescent, solitary or forming small groups; **L**  $\pm 45$ , densely rosulate, lanceolate-attenuate, 60–80 × 11–12 cm, dull greyish-green, surface slightly rough, **marginal teeth** deltoid, 1–2 mm, dark brown, 2–10 mm apart; **Inf** 1–1.5 m, erect, with 3–4 **Br**; racemes cylindrical-conical, 20 cm, dense; **Bra** ovate-acuminate, 20 × 16 mm, imbricate in bud; **Ped** 20–25 mm; **Fl** bright yellow, often scarlet in bud, 35 mm, 9 mm  $\varnothing$  across the ovary; **OTep** free to the base; **St** and **Sty** exerted 3–5 mm.

Very close to *A. cryptopoda* and included in that species by some authors, e.g. Glen & Hardy (2000) or Wyk & Smith (2014). The var. *lutea* is a yellow-flowered variant, and it has been reported as locally naturalized in Spain by Guillot (2013).

**A. wildii** (Reynolds) Reynolds (Kirkia 4: 13, 1964). **Type**: Zimbabwe, Eastern Prov. (*Wild* 3541 [SRGH, K, PRE]). — **Distr**: Zimbabwe (Eastern Prov.)/Moçambique: Chimanimani Mts.; grassland on rocky slopes, 1350–2135 m. **I**: Reynolds (1966: 20); Carter & al. (2011: 125).  
≡ *Aloe torrei* var. *wildii* Reynolds (1961).

[1] Acaulescent, simple or branching at the base to form small groups; **L**  $\pm 6$ , distichous,

linear, 15–30 × 0.5–1 cm, dull green tinged brownish, with a few scattered small white spots near the base, lower face with spots more numerous and minutely spinulose, **marginal teeth** ±0.5 mm, soft, white, 1–2 mm apart; **Inf** ±25–30 (–50) cm, simple; raceme cylindrical, 6–7 × 5 cm, lax, with 12–16 flowers; **Bra** ovate-acute, 5 × 2–3 mm, dull pink; **Ped** 10–15 mm; **Fl** bright orange-scarlet, green-tipped, 30–40 mm, slightly ventricose, base shortly attenuate, enlarged above the ovary, slightly narrowed at the mouth; **OTep** free to the base; **St** and **Sty** exerted 0–1 mm.

**A. wilsonii** Reynolds (J. South Afr. Bot. 22(3): 137–140, 1956). **Type:** Uganda, Karamoja Distr. (*Tweedie* 1365 [PRE, EA]). — **Lit:** Newton & Kamiti (2003). **Distr:** W Kenya, E Uganda; rocky slopes on isolated hills, 1525–3000 m. **I:** Reynolds (1966: 263–264); Carter & al. (2011: 600); Cole & Forrest (2017: 144–149); Cole (2015).

[13] Caulescent, simple or in small groups; stem decumbent, usually short, sometimes to 80 × 6 cm Ø; **L** ±24, densely rosulate, lanceolate-attenuate, to 25 × 9 cm, deep green tinged yellowish, slightly glossy, lower face sometimes with a few crowded white spots near the base, with pale brown horny margin, exudate yellow drying brownish, **marginal teeth** ±3–4 mm, pungent, reddish, 10 mm apart; **Inf** 50–60 cm, with ±8 **Br**; racemes cylindrical-acuminate, 15–18 × 5–6 cm, lax; **Bra** ovate-acuminate, 5 × 3 mm; **Ped** 15 mm; **Fl** dull scarlet with a bloom, 28 mm, base shortly attenuate, 7 mm Ø across the ovary, very slightly narrowed above, then slightly enlarged to the mouth; **OTep** free for 14 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:** 2n = 14 (Cutler & al. 1980).

**A. wollastonii** Rendle (J. Linn. Soc., Bot. 38: 238, 1908). **Type:** Uganda, Toro Distr. (*Wollaston* s.n. [BM]). — **Distr:** W Kenya, NW Tanzania, S Uganda, E Democratic Republic of the Congo [Zaire]; grassland and with grass in open woodland, 1100–2285 m. **I:** Reynolds (1966: 97, as *A. lateritia*; 99, as *A. lateritia* var. *kitaliensis*); Carter & al. (2011: 191); Cole & Forrest (2017: 150–157).

≡ *Aloe macrocarpa* ssp. *wollastonii* (Rendle) Wabuye (2006); **incl.** *Aloe angiensis* De Wildeman (1921); **incl.** *Aloe bequaertii* De Wildeman (1921); **incl.** *Aloe lanuriensis* De Wildeman (1921); **incl.** *Aloe angiensis* var. *kitaliensis* Reynolds (1955) ≡ *Aloe lateritia* var. *kitaliensis* (Reynolds) Reynolds (1966).

[5] Acaulescent, usually simple; **L** 12–15, densely rosulate, lanceolate-attenuate, 40–50 × 8–10 cm, dull green, with many elongated whitish spots in irregular transverse bands, surface smooth, **marginal teeth** 4–6 mm, pungent, red-brown, 10–20 mm apart; **Inf** to 1.25 m, with 4–6 **Br**, lower ones sometimes rebranched; racemes cylindrical-conical, 10–30 × 8 cm, lax; **Bra** linear-lanceolate, 10–20 × 4 mm; **Ped** 15–20 mm; **Fl** pinkish to orange-red, rarely yellow, 30–35 mm, base truncate, 8–10 mm Ø across the ovary, abruptly narrowed to ±6 mm above, then enlarging to the mouth; **OTep** free for ±10–12 mm; **St** and **Sty** exerted 0–1 mm.

Lebrun & Stork (2012) state “probably also Burundi and Rwanda”, but without reference to their source.

**A. woodii** Lavranos & Collenette (Cact. Succ. J. (US) 72(2): 83, ills., 2000). **Type:** Saudi Arabia, Asir Prov. (*Vesey-Fitzgerald* 16076/6 [BM]). — **Distr:** S Saudi Arabia (Asir Prov.), Yemen; open stony ground or in *Juniperus* forest remnants, 2000–3000 m. **I:** Collenette (1999: 31); Carter & al. (2011: 349).

[5] Usually acaulescent, sometimes with a short procumbent stem, usually solitary, occasionally with a few suckers; **L** 15–20, densely rosulate, spreading to ascending, very rigid, lanceolate-attenuate, 45–50 × 10–15 cm, glaucous with a yellowish tinge, **marginal teeth** 2–3 mm, brown-tipped, 8–20 mm apart; **Inf** 80–100 cm, erect, with up to 6 **Br**; racemes cylindrical, subdense; **Bra** lanceolate, 15–18 × 5–10 mm; **Ped** 7–10 mm; **Fl** cream to yellow with green longitudinal stripes, usually densely white-tomentose, 26–33 mm, base rounded, ±8 mm Ø across the ovary, not constricted above; **OTep** free for ±10 mm; **St** and **Sty** exerted 0–1 mm.

**A. wrefordii** Reynolds (J. South Afr. Bot. 22 (3): 141–143, 1956). **Type:** Uganda, Northern

Prov. (*Tweedie* 659 [PRE, EA, K]). — **Distr:** NW Kenya, South Sudan, N Uganda; stony thornbush and exposed rocky slopes, 950–1430 m. **I:** Reynolds (1966: 208–209); Carter & al. (2011: 369); Cole & Forrest (2017: 158–163).

[5] Acaulescent, simple or suckering to form small groups; **L** ±24, densely rosulate, lanceolate-attenuate, ±60 × 15 cm, dull grey-green, sometimes tinged reddish-brown, obscurely lineate, tip a reddish-brown spine, surface smooth, exudate drying yellow, **marginal teeth** 4 mm, pungent, reddish-brown, 10–15 mm apart; **Inf** ±1.2 m, with up to 16 **Br**, lower ones rebranched; racemes subcapitate, 5–8 × 6 cm, dense; **Bra** ovate-acute, 9 × 4 mm; **Ped** 16 mm; **Fl** scarlet or orange, 22 mm, clavate, base shortly attenuate, 5–6 mm Ø across the ovary, enlarged above towards the mouth; **OTep** free for 13 mm; **St** and **Sty** exerted 3–5 mm.

According to Gilbert & Sebsebe Demissew (1992) the Ethiopian material referred to this species by Reynolds (1966) is *A. otallensis*.

**A. yavellana** Reynolds (J. South Afr. Bot. 20 (1): 28–30, t. 4, 1954). **Type:** Ethiopia, Sidamo Prov. (*Reynolds* 7063 [PRE, K]). — **Lit:** Newton & Kamiti (2003). **Distr:** S Ethiopia (Sidamo Region); in forest, in clearings, or on rocks, 1700–1950 m. **I:** Reynolds (1966: 345); Carter & al. (2011: 629).

[13] Caulescent, branching at the base; stem erect to 1 m, then decumbent, to 3 m × 4 cm Ø; **L** ±16–20, scattered along the stem for the top-most 20 cm, ensiform-attenuate, to 40 × 6–8 cm, bronze-brown, paler in the shade, lower face paler bronze-brown to dull brownish-green and green-lineate near the base, surface smooth, exudate drying yellow, **marginal teeth** 2–3 mm, pungent, tipped pale reddish-brown, 10–15 mm apart, leaf sheath striate; **Inf** 60–90 cm, with 8–10 **Br**, lower ones rebranched; racemes capitate or subcapitate, 2–3 cm, dense; **Bra** deltoid, 3 × 2 mm; **Ped** 10 mm; **Fl** in bud dark scarlet with longitudinal grey stripes and white flecks, at anthesis dull scarlet at the base, paler to orange above, 27 mm, base attenuate, 5–6 mm Ø across the ovary, slightly narrowed above, slightly enlarging to the slightly upturned mouth; **OTep** free for 9 mm; **St** and **Sty**

exserted 1–2 mm. — **Cytology:** 2n = 14 (Cutler & al. 1980).

**A. yemenica** J. R. I. Wood (Kew Bull. 38(1): 20–21, ills., 1983). **Type:** Yemen (*Wood* 2537 [K]). — **Distr:** Yemen; sandstone cliffs, 700–2000 m. **I:** Carter & al. (2011: 500).

[13] Caulescent, branching at the base; stem pendulous, rarely erect, to ±50 cm; **L** 6–12, scattered along the stem, narrowly lanceolate, ±35 × 3.5 cm, bright yellow-green, with spots in the juvenile stage, surface smooth, leaf sheath to 3 cm, **marginal teeth** deltoid, 2 mm, white with reddish-brown tips, 8–10 mm apart; **Inf** to 40 cm, ascending or recurved, simple or usually with up to 2 **Br**; racemes cylindrical-acuminate, to 15 cm, lax; **Bra** ovate-acute, 10 × 7 mm; **Ped** 8–10 mm; **Fl** red, rarely yellow, ±22 mm, 4 mm Ø across the ovary; **OTep** free for 8 mm; **St** exerted 2 mm; **Sty** exerted 3 mm. — **Cytology:** 2n = 14 (Wood 1983).

**A. zakamisyi** T. A. McCoy & Lavranos (Kakt. and. Sukk. 58(10): 258–59, ills., 2007). **Type:** Madagascar, Antsiranana (*McCoy* 2832 [FT]). — **Distr:** Madagascar (Antsiranana: Ankarana National Park); “tsingy” limestone, 150 m; known only from the type locality. **I:** Carter & al. (2011: 571).

[11] Caulescent, suckering to form large groups; stem to 45 cm; **L** 8–12, laxly rosulate, narrowly deltoid, 40 × 1.5 cm, dark green, slightly bluish-tinged with wax bloom, exudate pale yellow, drying almost clear, **marginal teeth** 3 mm, white, 10 mm apart; **Inf** to 28 cm, oblique to erect, simple; raceme conical-cylindrical, 12 cm, lax; **Bra** 8–10 mm; **Ped** 6 mm; **Fl** red, 24 mm, 4 mm Ø across the ovary; **OTep** free for 3 mm; **St** and **Sty** exerted 1–3 mm; **Fr** berries.

Castillon & Castillon (2010) regard this as synonym of *A. anivoranoensis*.

**A. zebrina** Baker (Trans. Linn. Soc. London, Bot. 1: 264, 1878). **Type** [lecto]: Angola, Luanda (*Welwitsch* 3721 [LISU, BM, G, K]). — **Lit:** Smith & al. (2012c). **Distr:** Angola, N Namibia, Botswana, W Moçambique, Zambia, Zimbabwe, Malawi, RSA (North-West Prov.); grassland and thickets on dry hills, 200–2000 m. **I:** Reynolds



(1966: 90); Carter & al. (2011: 166); Klopper & al. (2012: 90–91, with distribution map); Wyk & Smith (2014: 282–283).

**Incl.** *Aloe platyphylla* Baker (1878); **incl.** *Aloe constricta* Baker (1880); **incl.** *Aloe lugardiana* Baker (1901); **incl.** *Aloe baumii* Engler & Gilg (1903); **incl.** *Aloe bamangwatensis* Schönland (1904); **incl.** *Aloe laxissima* Reynolds (1936); **incl.** *Aloe transvaalensis* var. *stenacantha* F. S. Müller (1940).

[5,7] Acaulescent or shortly caulescent, solitary or usually suckering to form small or large groups; **L** 10–20, densely rosulate, lanceolate, 20–30 × 5–7 cm, dull green, striate, with oblong whitish spots scattered or usually in irregular transverse bands, lower face with few or many spots, exudate drying purplish or orange, **marginal teeth** 4–6 mm, pungent, brownish, 8–15 mm apart; **Inf** 1–1.3 m, with 5–10 **Br**, lower ones sometimes rebranched; racemes cylindrical, slightly acuminate, 20–40 × 6–7 cm, lax; **Bra** deltoid, acuminate, ±6–15 mm; **Ped** 6–15 mm; **Fl** coral-red or dull reddish, ±30 mm, base rounded or truncate, 7–10 mm Ø across the ovary, abruptly narrowed to 4–6 mm above, then enlarging to the mouth; **OTep** free for 7–11 mm; **St** and **Sty** exerted 1–2 mm. — **Cytology:** 2n = 14 (Fernandes 1930, Müller 1941: as *A. laxissima*).

Natural hybrids with *A. littoralis* (Reynolds 1966) and with *A. verecunda* (as *A. transvaalensis*) (Reynolds 1950) have been reported.

Often treated as a variable species including many other summer-flowering taxa, such as *A. ammophila*, *A. braamvanwykii*, *A. komatiensis*, *A. lettyae*, *A. transvaalensis* and *A. vandermerwei*, e.g. by Glen & Hardy (2000: 63–65). Distinguishing characters for the taxa formerly included here are presented by Smith & al. (2012c).

**A. zombitsiensis** Rauh & M. Teissier (Kakt. and. Sukk. 51(8): 201–203, ills., 2000). **Type:** Madagascar, Toliara (*Anonymous* s.n. in *BG Heidelberg* 73994 [HEID]). — **Distr:** Madagascar.

**A. zombitsiensis** ssp. **pallida** (Rauh & Mangelsdorff) L. E. Newton & Eggle (Bradleya

36: 177, 2018). **Type:** Madagascar, Toliara (*Mangelsdorff* s.n. in *BG Heidelberg* 70588 [HEID]). — **Distr:** Madagascar (Toliara); on limestone; known only from the type locality. **I:** Castillon & Castillon (2010: 190, as *A. sakarahensis* ssp.).

≡ *Aloe prostrata* ssp. *pallida* Rauh & Mangelsdorff (2000) ≡ *Aloe sakarahensis* ssp. *pallida* (Rauh & Mangelsdorff) Lavranos & M. Teissier (2004).

[2] Differs from ssp. *zombitsiensis*: **L** bright green, brownish when young; **Fl** pale red or yellow.

**A. zombitsiensis** ssp. **zombitsiensis** — **Distr:** Madagascar (Toliara); forest, 550 m.

**Incl.** *Aloe sakarahensis* Lavranos & M. Teissier (2004) ≡ *Aloe sakarahensis* ssp. *sakarahensis*.

[2] Acaulescent, solitary; **L** 10–15, rosulate, linear, apex acute, 15 × 2–2.5 cm, chocolate-brown to dull green, obscurely lineate, **marginal teeth** deltoid, 5–6 mm, 8–12 mm apart; **Inf** 11–15 cm, erect, simple; racemes shortly cylindrical, 2–4 cm, lax; **Bra** 6–8 mm; **Ped** 3–5 mm; **Fl** bright red, paler towards the mouth, bright green at the mouth, 15–20 mm, 3 mm Ø across the ovary; **OTep** free for 2–3 mm; **St** and **Sty** not exerted; **Fr** berries.

**A. zubb** T. A. McCoy & Lavranos (CactusWorld 33(1): 31, ills. (pp. 27–34); (2): 122 [erratum], 2015). **Type:** Sudan, Kassala Prov. (McCoy 4016 [FT]). — **Distr:** E Sudan (Kassala Prov.: Red Sea Hills, Erkowit); crevices on steep granite slopes, ±1200 m.

[6] Acaulescent, suckering to form dense groups; **L** 8–12, rosulate, lanceolate-attenuate, 10–15 × 2–3 cm, light green, with many white lenticular spots, lower surface lighter green, more heavily spotted, exudate clear, drying light yellow, **marginal teeth** deltoid, 1–2 mm, red, to 7 mm apart; **Inf** 20–30 cm, erect, usually simple, sometimes with 1–2 **Br**; racemes capitately-corymbose, 1–1.5 cm, dense; **Bra** ovate-acute, 4–5 × 2–3 mm, subscarious, reddish-white with 3 nerves; **Ped** 15 mm; **Fl** mostly yellow, sometimes orange or red, clavate, 20 mm, 4 mm Ø

across the ovary, slightly narrowed above, then widening to 6 mm at the mouth; **OTep** free for >10 mm; **St** exerted 2.5–3 mm; **Sty** exerted 4–5 mm.

Plants of this species are commonly encountered in cultivation under the name *A. sinkatana*, which originates from the same general area but from lower elevations.

**A. zyorabaiensis** L. E. Newton & Wabuyelee (CactusWorld 36(3): 187, ills. (pp. 186–188), 2018). **Type:** Kenya, Kilifi County (*Powys* s.n. in *Newton* 6284 [EA, K]). — **Distr:** S Kenya (Kilifi County); rocky hills, 370 m.

[16] Caulescent, shrubby; stem erect to 2 m, much branched at the base; **L** to ±15, cauline-dispersed, lanceolate-attenuate, apex a single spine, 40 × 6 cm, greyish-green, pinkish at the margin, surface smooth, exudate yellow, drying brown, **marginal teeth** pointing forward, 5 mm, whitish, 4–10 mm apart, leaf sheaths visible for 2 cm; **Inf** to 70 cm, erect, with 5–7 **Br**; racemes cylindrical, to 14 cm, lateral ones to 10 cm, semi-dense; **Bra** lanceolate-attenuate, 6 × 2 mm, whitish with 3 brown nerves; **Ped** 15 mm; **Fl** coral-red, lobes with yellow margins, 30 mm, base shortly attenuate, 8 mm Ø across the ovary, narrowed to 6.5 mm above, scarcely enlarging to the mouth; **OTep** free for 6 mm; **St** and **Sty** exerted 5 mm.

## References

- Ahmed, M. J. [& al. 2009], Singh, Z. & Khan, A. S. (2009) Postharvest *Aloe vera* gel-coating modulates fruit ripening and quality of 'Arctic Snow' nectarine kept in ambient and cold storage. *Int. J. Food Sci. Technol.* 44(5): 1024–1033. <https://doi.org/10.1111/j.1365-2621.2008.01873.x>.
- Applequist, W. L. (2017) Report of the Nomenclature Committee for Vascular Plants: 69. *Taxon* 66(2): 500–513. <https://doi.org/10.12705/662.17>.
- Arena, G. (2018) Kraalaalwyn: An oasis in the drought. *Veld Fl.* (1975+) 104(1): 26–29, ills.
- Arena, G. [& al. 2013], Symes, C. T. & Witkowski, E. T. F. (2013) The birds and the seeds: Opportunistic avian nectarivores enhance reproduction in an endemic montane *Aloe*. *Pl. Ecol.* 214: 35–47, ills. <https://doi.org/10.1007/s11258-012-0144-z>.
- Arena, G. [& al. 2015], Witkowski, E. T. F. & Symes, C. T. (2015) Growing on rocky ground: Microhabitat predictors for site-occupancy of *Aloe peglerae*, an endangered endemic species with a restricted range. *South Afr. J. Bot.* 100: 174–182, ills. <https://doi.org/10.1016/j.sajb.2015.05.022>.
- Aymerich, P. (2015) Nuevos datos sobre plantas suculentas alóctonas en Cataluña. *Bouteloua* 22: 99–116, ills.
- Aymerich, P. (2016) Notas sobre plantas alóctonas de origen ornamental en el litoral septentrional de Cataluña. *Bouteloua* 26: 78–91, ills.
- Beer, J. J. de & Wyk, B-E. van (2011) An ethnobotanical survey of the Agter-Hantam, Northern Cape Province, South Africa. *South Afr. J. Bot.* 77(3): 741–754, map. <https://doi.org/10.1016/j.sajb.2011.03.013>.
- Berger, A. (1908) *Liliaceae — Asphodeloideae — Aloineae*. In: Engler, A. (ed.): *Das Pflanzenreich* IV.38 (Heft 33). Leipzig (DE): Wilhelm Engelmann. <http://www.biodiversitylibrary.org/bibliography/72397#/>
- Bjorå, C. S. [& al. 2015], Wabuyelee, E., Grace, O. M., Nordal, I. & Newton, L. E. (2015) The uses of Kenyan Aloes: An analysis of implications for names, distribution and conservation. *J. Ethnobiol. Ethnomed.* 11 (82): 1–16, ills. <https://doi.org/10.1186/s13002-015-0060-0>.
- Blair, O. W. & Hatch, K. A. (2011) *Aloe* nectar, birds and stable isotopes: Opportunities for quantifying trophic interactions. *Ibis* 153(1): 1–3. <https://doi.org/10.1111/j.1474-919X.2010.01090.x>.
- Bosser, J. (1968) Espèces et hybrides nouveaux d'Aloes de Madagascar. *Adansonia*, n.s. [sér. 2], 8(4): 505–512, ills. <http://www.documentation.ird.fr/hor/fdi:13252>
- Boudreau, M. D. & Beland, F. A. (2006) An evaluation of the biological and toxicological properties of *Aloe barbadensis* (Miller), *Aloe vera*. *J. Environm. Sci. Health, C* 24(1): 103–154. <https://doi.org/10.1080/10590500600614303>.
- Brandham, P. E. (1971) The chromosomes of the *Liliaceae*: II. Polyploidy and karyotype variation in the *Aloineae*. *Kew Bull.* 25(3): 381–399, ills. <https://doi.org/10.2307/4103181>.
- Brandham, P. E. (1973) New hybrids in the *Aloineae*. *Nation. Cact. Succ. J.* 28(1): 16–19, ills.
- Brandham, P. E. & Carter, S. (1990) A revision of the *Aloe tidmarshii/A. ciliaris* complex in South Africa. *Kew Bull.* 45(4): 637–645. <https://doi.org/10.2307/4113868>.
- Brandham, P. E. [& al. 1994], Carter, S. & Reynolds, T. (1994) A multidisciplinary study of relationships among the cremnophilous Aloes of northeastern Africa. *Kew Bull.* 49(3): 415–428, maps, keys. <https://doi.org/10.2307/4114465>.
- Breuer, I. (2003) *Aloe vera* am Standort. *Avonia* 21(1): 10–11, ill.
- Campbell-Barker, T. (2003) The type locality of *Aloe cameronii* Hemsley. *Haworthiad* 17(2): 47–50, ills.
- Carter, S. (1994) *Aloaceae*. In: Polhill, R. M. (ed.): *Flora of Tropical East Africa*. Rotterdam (NL)/Brookfield (US): A. A. Balkema.
- Carter, S. (1996) New *Aloe* taxa in the Flora Zambesiaca area. *Kew Bull.* 51(4): 777–785, ills. <https://doi.org/10.2307/4114465>.

- Carter, S. (2001) *Aloaceae*. In: Pope, G. V. (ed.): Flora Zambesiaca; 12(3): 48–98, key. Richmond (GB): Royal Botanic Gardens Kew.
- Carter, S. (2007) A new species of *Aloe* from northeast Somalia. *Nordic J. Bot.* 24(3): 245–247, ills. <https://doi.org/10.1111/j.1756-1051.2004.tb00837.x>.
- Carter, S. & Brandham, P. E. (1983) New species of *Aloe* from Somalia. *Bradleya* 1: 17–24, ills.
- Carter, S. & Reynolds, T. (1990) *Aloe penduliflora* and *Aloe confusa*. *Kew Bull.* 45(4): 647–651. <https://doi.org/10.2307/4113869>.
- Carter, S. [ & al. 1984], Cutler, D. F., Reynolds, T. & Brandham, P. E. (1984) A multidisciplinary approach to a revision of the *Aloe somaliensis* complex (*Liliaceae*). *Kew Bull.* 39(3): 611–633, ills. <https://doi.org/10.2307/4108600>.
- Carter, S. [ & al. 1996], Gilbert, M. G. & Sebsebe Demissew (1996) The identity of the Massawa *Aloe*. *Kew Bull.* 51(4): 775–776. <https://doi.org/10.2307/4119732>.
- Carter, S. [ & al. 2011], Lavranos, J. J., Newton, L. E. & Walker, C. C. (2011) Aloes. The definitive guide. Richmond (GB): Kew Publishing.
- Castillon, J.-B. (2005) Voyage à Madagascar, mai-juin 2004. *Succulentas* 2005(2): 29–32, ills.
- Castillon, J.-B. (2009a) *Aloe johannis-philippeii*, a new *Aloe* (*Asphodelaceae*) from the high mountains of central Madagascar. *CactusWorld* 27(1): 51–56, ills.
- Castillon, J.-B. (2009b) Corrections and description of two new taxa in the genus *Aloe* (*Asphodelaceae*) in Madagascar. *Cact.-Avent. Int.* 83: 26–32, ills., map; 84: 32, 2009 [erratum].
- Castillon, J.-B. (2009c) Rectification of a mistake by G. W. Reynolds on a Malagasy *Aloe* (*Asphodelaceae*) and description of a new species. *Bradleya* 27: 145–152, ills. <https://doi.org/10.25223/brad.n27.2009.a18>.
- Castillon, J.-B. (2010) Description of two new Madagascan taxa in the genus *Aloe* (*Asphodelaceae*); about *Aloe mandotoensis* J.-B. Castillon. *Cact.-Avent. Int.* 85: 2–8, ills.
- Castillon, J.-B. (2011) *Aloe castilloniae* J.-B. Castillon. Una magnifica specie poco conosciuta del sud ovest del Madagascar. A small, magnificent and little-known species of south-western Madagascar. *Cactus & Co.* 14(4): 56–61, ills.
- Castillon, J.-B. & Castillon, J.-P. (2008a) Identité de l'*Aloe ibitiensis* Perrier, *Asphodelaceae*, des hauts plateaux de Madagascar; espèces associées. *Succulentas* 2008(4): 3–9, ills.
- Castillon, J.-B. & Castillon, J.-P. (2010) Les *Aloe* de Madagascar. The *Aloe* of Madagascar. Etang-Salé (FR): Published by the authors.
- Castillon, J.-B. & Castillon, J.-P. (2016) A new *Aloe* (*Asphodelaceae*) from around Tôlanaro, Madagascar. Comments on *Aloe versicolor* Guillaumin subsp. *stefanieana* (Rauh). *CactusWorld* 34(2): 111–115, ills.
- Castillon, J.-P. (2012) Révision du groupe de l'*Aloe divaricata* Berger; correction d'une synonymie, combinaisons nouvelles et description d'un nouvel hybride. *Adansonia*, sér. 3, 34(1): 13–21, ills., map. <https://doi.org/10.5252/a2012n1a2>.
- Castillon, J.-P. & Castillon, J.-B. (2008b) Une nouvelle espèce d'*Aloe* (*Asphodelaceae*) des Hauts Plateaux de Madagascar. *Succulentas* 2008(2): 3–9, ills.
- Castillon, J.-P. & Nusbaumer, L. (2014) *Aloe gautieri* J.-P. Castillon & Nusb. (*Xanthorrhoeaceae*), a new species from the northeastern coast of Madagascar. *Candollea* 69(1): 75–80, ills. <https://doi.org/10.15553/c2014v691a8>.
- Chaudhary, S. A. (ed.) (2001) Flora of the Kingdom of Saudi Arabia illustrated. Volume III. Riyadh (SA): Ministry of Agriculture & Water etc.
- Chen, W. [ & al. 2009], Lu, Z., Viljoen, A. & Hamman, J. (2009) Intestinal drug transport enhancement by *Aloe vera*. *Pl. Med. (Stuttgart)* 75(6): 587–595. <https://doi.org/10.1055/s-0029-1185341>.
- Chinchilla, N. [ & al. 2013], Carrera, C., Durán, A. G., Macías, M., Torres, E. & Macías, F. A. (2013) *Aloe barbadensis*: How a miraculous plant becomes reality. *Phytochem. Rev.* 12: 581–602, map. <https://doi.org/10.1007/s11101-013-9323-3>.
- Christie, S. J. & al. (2005) *Aloe jawiyon*, a new species from Soqatra (Yemen). *Bradleya* 23: 23–30, ills.
- Cole, T. C. (2015) *Aloe lukeana*: A new, caulescent *Aloe* from Uganda. *Cact. Succ. J. (US)* 87(4): 152–159, map, ills. <https://doi.org/10.2985/015.087.0401>.
- Cole, T. C. & Forrest, T. G. (2015) Three new *Aloe* records from Uganda (*Xanthorrhoeaceae*). *Cact. Succ. J. (US)* 87(2): 76–80, ills., map. <https://doi.org/10.2985/015.087.0204>.
- Cole, T. C. & Forrest, T. (2017) Aloes of Uganda. Santa Barbara (US): Oakleigh Press.
- Collenette, S. (1999) Wildflowers of Saudi Arabia. Riad (SA): National Commission for Wildlife Conservation and Development.
- Court, D. (2000) Succulent flora of Southern Africa. Revised Edition. Rotterdam (NL)/Brookfield (US): A. A. Balkema.
- Cousins, S. R. & Witkowski, E. T. F. (2012) African *Aloe* ecology: A review. *J. Arid Environm.* 85: 1–17, map. <https://doi.org/10.1016/j.jaridenv.2012.03.022>.
- Cousins, S. R. [ & al. 2013], Witkowski, E. T. F., Pfäb, M. F., Riddles, R. E. & Mycock, D. J. (2013) Reproductive ecology of *Aloe plicatilis*, a fynbos tree aloe endemic to the Cape Winelands, South Africa. *South Afr. J. Bot.* 87: 52–65, map, ills. <https://doi.org/10.1016/j.sajb.2013.02.174>.
- Cousins, S. R. [ & al. 2014], Witkowski, E. T. F. & Pfäb, M. F. (2014) Elucidating patterns in the population size structure and density of *Aloe plicatilis*, a tree aloe endemic to the Cape fynbos, South Africa. *South Afr. J. Bot.* 90: 20–36, map. <https://doi.org/10.1016/j.sajb.2013.09.012>.
- Cousins, S. R. [ & al. 2016], Witkowski, E. T. F. & Pfäb, M. F. (2016) Beating the blaze: Fire survival in the fan aloe (*Kumara plicatilis*), a succulent monocotyledonous tree endemic to the Cape fynbos, South Africa. *Austral*

- Ecol. 41: 466–479, map, ills. <https://doi.org/10.1111/aec.12318>.
- Craib, C. (2003) Succulents on the rise — the unexpected consequences of human activity in northwestern Sekhukhuneland. *Cact. Succ. J. (US)* 75(5): 190–193, ills.
- Craib, C. (2006) Grass Aloes in the South African Veld. Hatfield (ZA): Umdaus Press.
- Craib, C. (2007) South African Grass *Aloe* species which frequent cliff faces and an evaluation of the newly described *Aloe challsii*. *Alsterworthia Int.* 7(3): 3–8, ills.
- Crouch, N. R. [et al. 2011], Smith, G. F. & Condy, G. (2011) *Aloe nicholsii*. *Flow. Pl. Afr.* 62: 16–21, t. 2263, map.
- Crouch, N. R. [et al. 2015], Smith, G. F., Klopper, R. R., Figueiredo, E., McMurtry, D. & Burns, S. (2015) Winter-flowering maculate aloes from the Lowveld of southeastern Africa: Notes on *Aloe monteiroae* Baker (*Asphodelaceae: Alooideae*), the earliest name for *Aloe parvibracteata* Schönland. *Bradleya* 33: 147–156, ills. <https://doi.org/10.25223/brad.n27.2009.a18>.
- Cutler, D. F. [et al. 1980], Brandham, P. E., Carter, S. & Harris, S. J. (1980) Morphological, anatomical, cytological and biochemical aspects of evolution in East African shrubby species of *Aloe* L. *Bot. J. Linn. Soc.* 80(4): 293–317, ills., maps. <https://doi.org/10.1111/j.1095-8339.1980.tb01666.x>.
- Dana Sánchez, E. D. & Sanz Elorza, M. (2008) Localizaciones de especies alóctonas ornamentales asilvestradas en Andalucía. *Bouteloua* 3: 14–22, ills.
- Daru, B. H. [et al. 2013], Manning, J. C., Boatwright, J. S., Maurin, O., Mclean, N., Schaefer, H., Kuzmina, M. & Bank, M. van der (2013) Molecular and morphological analysis of subfamily *Alooideae* (*Asphodelaceae*) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62(1): 62–76, ills. <http://www.jstor.org/stable/24389313>
- Dee, R. [et al. 2018], Malakasi, P., Rakotoarisoa, S. E. & Grace, O. M. (2018) A phylogenetic analysis of the genus *Aloe* (*Asphodelaceae*) in Madagascar and the Mascarene Islands. *Bot. J. Linn. Soc.* 187: 428–440, ills. <https://doi.org/10.1093/botlinnean/boy026>.
- Dioli, M. (2008) *Aloe elkerriana* (*Asphodelaceae*), a new Ethiopian species from the type locality of *Aloe jacksonii*. *Haseltonia* 13: 34–37, ills. [https://doi.org/10.2985/1070-0048\(2007\)13\[34:AEAANE\]2.0.CO;2](https://doi.org/10.2985/1070-0048(2007)13[34:AEAANE]2.0.CO;2).
- Dring, J. V. [et al. 1984], Nash, R. J., Roberts, M. F. & Reynolds, T. (1984) Hemlock alkaloids in Aloes. Occurrence and distribution of  $\gamma$ -Coniceine. *Pl. Med. (Stuttgart)* 50(5): 442–443. <https://doi.org/10.1055/s-2007-969761>.
- Drummond, R. B. [et al. 1975], Gelfand, M. & Mavi, S. (1975) Medicinal and other uses of succulents by the Rhodesian African. *Excelsa* 5: 51–56.
- Du Puy, D. (2004a) Four miniature species of *Aloe* from Madagascar. *Curtis's Bot. Mag.*, ser. nov., 21(4): 222–228, ills. <https://doi.org/10.1111/j.1355-4905.2004.00441.x>.
- Du Puy, D. (2004b) Plant portraits. *Aloe parvula*. *Aloe compressa*. *Aloe calcairophila*. *Aloe descoingsii*. *Curtis's Bot. Mag.*, ser. nov., 21(4): 229–245, ills., tt. 505–508. <https://doi.org/10.1111/j.1355-4905.2004.00441.x>.
- Duffy, K. J. & Johnson, S. D. (2011) Effects of pollen reward removal on fecundity in a self-incompatible hermaphrodite plant. *Pl. Biol. (Stuttgart)* 13(3): 556–560, ills. <https://doi.org/10.1111/j.1438-8677.2011.00445.x>.
- Duffy, K. J. [et al. 2014], Johnson, S. D. & Peter, C. I. (2014) A temporal dimension to the influence of pollen rewards on bee behaviour and fecundity in *Aloe tenuior*. *PLoS One* 9(4): e94908, 8 pp., ills. <https://doi.org/10.1371/journal.pone.0094908>.
- Duncan, J. [et al. 2006], Hoffmann, T., Rohde, R., Powell, E. & Hendricks, H. (2006) Long-term population changes in the giant Quiver Tree, *Aloe pillansii* in the Richtersveld, South Africa. *Pl. Ecol.* 185(1): 73–84, map, ills. <https://doi.org/10.1007/s11258-005-9085-0>.
- Dyer, R. A. & Hardy, D. (1969) Addendum. In: Reynolds, G. W.: *Aloes of South Africa*, ed. 2, pp. 509–516. Rotterdam (NL): A. A. Balkema.
- Ellert, A. (2008) *Aloe mossurilensis* Ellert sp. nov. A long-overlooked species from northern Moçambique. *Alsterworthia Int.* 8(1): 24–28, ills.
- Ellert, A. (2009) *Aloe perdita*, a long-lost species from the Chimanimani Mountains on the Zimbabwe/Moçambique border. *Aloe* 45(4): 76–77, ills.
- Favell, P. (2001) *Aloe ahmarensis* and its allies. *Cact. Succ. J. (US)* 73(4): 200–203, ills., map.
- Favell, P. [et al. 1999], Miller, M. B. & Al-Gifri, A. N. (1999) Notes on two Aloes from Yemen, including the description of a new species, *A. ahmarensis*. *Cact. Succ. J. (US)* 71(5): 257–261, ills.
- Fentaw, E. [et al. 2013], Dagne, K., Rønsted, N., Sebsebe Demissew & Grace, O. M. (2013) Karyotypes in Ethiopian *Aloe* species (*Xanthorrhoeaceae: Asphodeloideae*). *Kew Bull.* 68(4): 599–607, map, ills. <https://doi.org/10.1007/S12225-013-9475-8>.
- Ferguson, N. (1926) The *Aloineae*: A cytological study, with special reference to the form and size of the chromosomes. *Philos. Trans., Ser. B*, 215: 225–253. <https://doi.org/10.1098/rstb.1927.0005>.
- Fernandes, A. (1930) Études sur les chromosomes. 4. Sur le nombre et la morphologie des chromosomes de quelques espèces du genre *Aloe* L. *Bol. Soc. Brot.*, sér. 2, 6: 300–308.
- Figueiredo, E. & Smith, G. F. (2010) What's in a name: epithets in *Aloe* L. (*Asphodelaceae*) and what to call the next new species. *Bradleya* 28: 79–102. <https://doi.org/10.25223/brad.n28.2010.a9>
- Figueiredo, E. & Smith, G. F. (2012) Clarifying the application of the long-confused name *Aloe commutata*, and the establishment of *Aloe*  $\times$  *commutata* Tod. (*Asphodelaceae*). *Bradleya* 30: 25–32, ills. <https://doi.org/10.25223/brad.n28.2010.a9>.
- Figueiredo, E. & Smith, G. F. (2016) *Aloe*  $\times$  *schimperii* Tod. (*Aloe maculata* All.  $\times$  *Aloe striata* Haw.), the earliest



- name applicable to the common and invasive nothospecies known as *Aloe* × *schoenlandii* Baker (*Asphodelaceae: Alooideae*). *Haseltonia* 22: 9–17, ills. <https://doi.org/10.2985/026.022.0103>.
- Fikre Dessalegn (2006) Taxonomic and demographic studies on three species complexes within the genus *Aloe* L. (*Aloaceae*) in Ethiopia. Addis Ababa (ET): School of Graduate Studies, Addis Ababa University; unpublished Ph.D. thesis.
- Fikre Dessalegn (2013) Study on the populations of an endemic *Aloe* species (*A. gilbertii* Reynolds) in Ethiopia. *Engin. Sci. Technol. Int. J.* 3(3): 562–576, ills., map. <http://www.estij.org/papers/vol3no32013/18vol3no3.pdf>
- Foden, W. [& al. 2007], Midgley, G. F., Hughes, G., Bond, W. J., Thuiller, W., Hoffmann, M. T., Kaleme, P., Underhill, L. G., Rebelo, A. & Hannah, L. (2007) A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity & Distrib.* 13(5): 645–653, ills., map. <https://doi.org/10.1111/j.1472-4642.2007.00391.x>.
- Forster, P. I. (2000) *Aloe delphinensis* in *Aloe* sect. *Lomatophyllum*. *Bothalia* 30(1): 43–55, key. <https://doi.org/10.4102/abc.v30i1.541>.
- Fritz, G. (2009) Branched inflorescence forms of *Aloe ecklonis* in Gauteng. *Aloe* 46(2): 28–29, ills.
- Fritz, G. (2012) Serendipitous discoveries of some interesting plants in southern Gauteng. *Aloe* 49(1): 21–23, ills.
- Germishuizen, G. & Meyer, N. L. (eds.) (2003) Plants of southern Africa: An annotated checklist. Pretoria (ZA): National Botanical Institute (= Strelitzia No. 14).
- Gilbert, M. G. & Sebsebe Demissew (1992) Notes on the genus *Aloe* in Ethiopia: Misinterpreted taxa. *Kew Bull.* 47(4): 647–653. <https://doi.org/10.2307/4110702>.
- Gilbert, M. G. & Sebsebe Demissew (1997) Further notes on the genus *Aloe* in Ethiopia and Eritrea. *Kew Bull.* 52(1): 139–152. <http://www.jstor.org/stable/4117846>
- Gildenhuis, S. (2005) *Aloe reitzii* var. *reitzii* and associates. *Aloe* 42(1–2): 8–11, ills.
- Glen, H. F. & Hardy, D. S. (1987) Nomenclatural notes on three southern African representatives of the genus *Aloe*. *South Afr. J. Bot.* 53(6): 489–492, maps, keys. <https://doi.org/10.1016/S0254-6299%2816%2931383-7>
- Glen, H. F. & Hardy, D. S. (1988a) *Aloe capitata*. *Flow. Pl. Afr.* 50: t. 1973 + text.
- Glen, H. F. & Hardy, D. S. (1988b) The identity of *Aloe penduliflora* Bak. *Kew Bull.* 43(3): 523–529, ills. <https://doi.org/10.2307/4118982>.
- Glen, H. F. & Hardy, D. S. (1990) *Aloe gerstneri*. *Aloe albida*. *Aloe cameronii* var. *bondana*. *Aloe dumetorum*. *Flow. Pl. Afr.* 51(5): tt. 2008, 2010–2012 + text, ills., maps.
- Glen, H. F. & Hardy, D. S. (1991) *Liliaceae* (*Asphodelaceae*). The type specimen of *Aloe soutpansbergensis*. *Bothalia* 21(2): 151–152, ills. <http://abcjournal.org/index.php/ABC/article/view/875>.
- Glen, H. F. & Hardy, D. S. (1992) *Aloe buchlohii*. *Aloe laeta*. *Flow. Pl. Afr.* 52(1): tt. 2047–2048 + text.
- Glen, H. F. & Hardy, D. S. (1993) *Aloe meyeri*. *Aloe veseyi*. *Flow. Pl. Afr.* 52(2): t. 2065–2066 + text, maps, key.
- Glen, H. F. & Hardy, D. S. (1995) *Aloe* section *Angualoae* and the problem of *Aloe spicata* L.f. (*Aloaceae*). *Haseltonia* 3: 92–103, ills., SEM-ills., maps, diag.
- Glen, H. F. & Hardy, D. S. (2000) *Aloaceae* (first part): *Aloe*. In: Germishuizen, G. (ed.): *Flora of Southern Africa*, Vol. 5, part 1, fascicle 1. Pretoria (ZA): National Botanical Institute.
- Glen, H. F. [& al. 1992], Hardy, D. S. & Lavranos, J. J. (1992) *Aloe guillaumetii*. *Flow. Pl. Afr.* 52(1): t. 2046 + text.
- Govaerts, R. H. A. (comp.) (2014+) World checklist of selected plant families [continuously updated]. Richmond (GB): Trustees of the Royal Botanic Gardens, Kew. <http://apps.kew.org/wcsp>
- Grace, O. M. (2011) Current perspectives on the economic botany of the genus *Aloe* L. (*Xanthorrhoeaceae*). *South Afr. J. Bot.* 77: 980–987. <https://doi.org/10.1016/j.sajb.2011.07.002>.
- Grace, O. M. [& al. 2008], Kokubun, T., Veitch, N. C. & Simmonds, M. S. J. (2008) Characterisation of a nataloin derivative from *Aloe ellenbeckii*, a maculate species from East Africa. *South Afr. J. Bot.* 74(4): 761–763. <https://doi.org/10.1016/j.sajb.2008.06.004>.
- Grace, O. M. [& al. 2009], Simmonds, M. S. J., Smith, G. F. & Wyk, A. E. (B.) van (2009) Documented utility and biocultural value of *Aloe* L. (*Asphodelaceae*). A review. *Econ. Bot.* 63(2): 167–178, ills. <https://doi.org/10.1007/s12231-009-9082-7>.
- Grace, O. M. [& al. 2011], Klopper, R. R., Figueiredo, E. & Smith, G. F. (2011) The *Aloe* names book. Pretoria (ZA): South African National Biodiversity Institute/Richmond (GB): Royal Botanic Gardens, Kew.
- Grace, O. M. [& al. 2013], Klopper, R. R., Smith, G. F., Crouch, N. R., Figueiredo, E., Rønsted, N. & Wyk, A. E. (B.) van (2013) A revised generic classification for *Aloe* (*Xanthorrhoeaceae* subfam. *Asphodeloideae*). *Phytotaxa* 76(1): 7–14, key. <https://doi.org/10.11646/phytotaxa.76.1.2>
- Grace, O. M. [& al. 2015], Buerki, S., Symonds, M. R. E., Forest, F., Wyk, A. E. (B.) van, Smith, G. F., Klopper, R. R., Björå, C. S., Neale, S., Sebsebe Demissew, Simmonds, M. S. J. & Rønsted, N. (2015) Evolutionary history and leaf succulence as explanations for medicinal use in aloes and the global popularity of *Aloe vera*. *BMC Evol. Biol.* 15: 29, 12 pp., ills., map. <https://doi.org/10.1186/s12862-015-0291-7>.
- Groenewald, B. H. (1938) *Aloe angustifolia*, *Flow. Pl. South Afr.* 18: t. 708 + text.
- Guglielmone, L. [& al. 2009], Gallo, L., Meragalli, M., Smith, G. F. & Figueiredo, E. (2009) Allioni's *Aloe* names (*Asphodelaceae*): Nomenclature and typification. *Bothalia* 39(2): 177–183, ills., maps. <https://doi.org/10.4102/abc.v39i2.243>
- Guillot, D. (2013) Nuevas citas de taxones del género *Aloe* L. para la flora alóctona Valenciana. *Bouteloua* 15: 23–27, ills.



- Guo, X. & Mei, N. (2016) *Aloe vera*: A review of toxicity and adverse clinical effects. *J. Environm. Sci. Health, C* 34(2): 77–96. <https://doi.org/10.1080/10590501.2016.1166826>.
- Hardy, D. S. (1984) *Aloe divaricata*. *Aloe vaombe*. *Aloe viguieri*. *Aloe antandroi*. *Aloe erinacea*. *Flow. Pl. Afr.* 48(1–2): tt. 1881–1885 + text.
- Hargreaves, A. L. [et al. 2008], Harder, L. D. & Johnson, S. D. (2008) *Aloe inconspicua*: The first record of an exclusively insect-pollinated *Aloe*. *South Afr. J. Bot.* 74(4): 606–612, ills. <https://doi.org/10.1016/j.sajb.2008.02.009>.
- Hargreaves, A. L. [et al. 2010], Harder, L. D. & Johnson, S. D. (2010) Native pollen thieves reduce the reproductive success of a hermaphroditic plant, *Aloe maculata*. *Ecology* 91(6): 1693–1703. <https://doi.org/10.1890/09-0792.1>.
- Hargreaves, A. L. [et al. 2012], Harder, L. D. & Johnson, S. D. (2012) Floral traits mediate the vulnerability of aloes to pollen theft and inefficient pollination by bees. *Ann. Bot. (Oxford)*, n.s. 109: 761–772, ills. <https://doi.org/10.1093/aob/mcr324>.
- Hargreaves, B. J. (1990) The succulents of Botswana: An annotated checklist. Gaborone (BW): National Museum, Monuments and Art Gallery.
- Hargreaves, B. J. (2004) The *Aloe littoralis* complex in Botswana. *Alsterworthia Int.* 4(1): 18–21, ills., map.
- Hargreaves, B. J. (2005) *Aloe marlothii* in Botswana and beyond. *Alsterworthia Int.* 5(3): 6–9, 15, ills.
- Hargreaves, B. J. (2007) Aloes with short stems in Botswana. *Alsterworthia Int.* 7(1): 6–7, ills.
- Hargreaves, B. J. (2009) *Aloe aculeata* Pole Evans in Botswana. *Alsterworthia Int.* 9(2): 23, ills.
- Hargreaves, B. J. (2010) *Aloe chabaudii* in Malawi and Botswana. *Alsterworthia Int.* 10(2): 26–27, ills.
- Hargreaves, B. J. (2011) *Aloe lutescens* Groenewald in Botswana. *Alsterworthia Int.* 11(3): 7–8, ills.
- Heath, P. V. (1994) New nothogeneric names in the *Asphodelaceae*. *Calyx* 4(4): 146–147.
- Human, H. & Nicolson, S. W. (2008) Flower structure and nectar availability in *Aloe greatheadii* var. *davyana*: An evaluation of a winter nectar source for honeybees. *Int. J. Pl. Sci.* 169(2): 263–269, ills. <https://doi.org/10.1086/524113>.
- Jaarsveld, E. J. van (2008) *Aloe tenuior* var. *viridifolia*, a new variety (series *Fruticosae*) from the Eastern Cape, South Africa. *Aloe* 44(3): 60–62, ills., key.
- Jaarsveld, E. J. van (2010) Angola botanical expedition: Succulent treasures, January 2009. *Aloe* 47(1): 4–35, ills., map.
- Jaarsveld, E. J. van (2015) *Aloe scorpioides*; a new range extension to the Sierra Das Neves, south-west Angola. *Haseltonia* 21: 68–71, ills, map. <https://doi.org/10.2985/026.021.0109>.
- Jaarsveld, E. J. van & Condy, G. (2013a) *Aloe mitriformis* subsp. *comptonii*. *Flow. Pl. Afr.* 63: 10–15, t. 2282, key, map.
- Jaarsveld, E. J. van & Condy, G. (2013b) *Aloe pavelkae*. *Flow. Pl. Afr.* 63: 16–21, t. 2283, key, map.
- Jaarsveld, E. J. van & Condy, G. (2015) *Aloe huntleyana*. *Flow. Pl. Afr.* 64: 18–25, ills., map.
- Jaarsveld, E. J. van & Judd, E. (2015) *Tree Aloes of Africa*. Cape Town (ZA): Penrock Publications.
- Jaarsveld, E. J. van & Wyk, A. E. (B.) van (2006) *Aloe challisii*, a new cliff-dwelling *Aloe* from Mpumalanga, and a checklist of the obligate cliff-dwelling Aloes in South Africa and Namibia. *Aloe* 43(2–3): 36–41, ills., map, key.
- Jaarsveld, E. J. van [et al. 2005], Wyk, A. E. (B.) van & Condy, G. (2005) *Aloe omavandae*. *Flow. Pl. Afr.* 59: 2–6, t. 2201, map.
- Jack, S. L. [et al. 2016], Hoffinan, M. T., Rohde, R. F. & Durbach, I. (2016) Climate change sentinel or false prophet? The case of *Aloe dichotoma*. *Diversity & Distrib.* 22: 745–757. <https://doi.org/10.1111/ddi.12438>.
- Jacobsen, H. & Rowley, G. D. (1973) Some name changes in succulent plants. Part 5. *Nation. Cact. Succ. J.* 28(1): 4–7.
- Jankowitz, W. J. (1975) *Aloen von Südwestafrika*. Windhoek (NA): Abteilung Naturschutz und Fremdenverkehr.
- Johnson, M. A. T. & Brandham, P. E. (1997) New chromosome numbers in petaloid monocotyledons and in other miscellaneous angiosperms. *Kew Bull.* 52(1): 121–138. <https://doi.org/10.2307/4117845>.
- Johnson, S. D. [et al. 2006], Hargreaves, A. L. & Brown, M. (2006) Dark, bitter-tasting nectar functions as a filter of flower visitors in a bird-pollinated plant. *Ecology* 87(11): 2709–2716.
- Jonkers, B. (2009) What is the homeland of *Aloe vera*? Not Oman! *CactusWorld* 27(2): 113–122, ills., map.
- Jonkers, B. (2014) Hybridising with *Aloe jucunda*. *CactusWorld* 32(2): 109–110, ills.
- Jothi, D. (2009) Experimental study on antimicrobial activity of cotton fabric treated with aloe gel extract from *Aloe vera* plant for controlling the *Staphylococcus aureus* (bacterium). *Afr. J. Microbiol. Res.* 3(5): 228–232.
- Keay, R. W. J. (1963) The Nigerian species of *Aloe*. *Kew Bull.* 17(1): 65–69, ill. <https://doi.org/10.2307/4118696>.
- Kemble, B. (2005) Miniature Aloes. *Alsterworthia Int.* 5(2): 14–16, ills.
- Kemble, B. (2014) *Aloe humilis* hybrids: The spiny dwarf series. *Cact. Succ. J. (US)* 86(5): 229–231, ills. <https://doi.org/10.2985/015.086.0507>.
- King, E. G. (2008) Facilitative effects of *Aloe secundiflora* shrubs in degraded semi-arid rangelands in Kenya. *J. Arid Environm.* 72(4): 358–369. <https://doi.org/10.1016/j.jaridenv.2007.08.001>.
- King, E. G. & Stanton, M. L. (2008) Facilitative effects of *Aloe* shrubs on grass establishment, growth, and reproduction in degraded Kenyan rangelands: Implications for restoration. *Restorat. Ecol.* 16(3): 464–474. <https://doi.org/10.1111/j.1526-100X.2007.00310.x>.
- Kirkbright, D. (2010) *Aloe polyphylla* from seed: An update. *Haworthiad* 24(1): 4–5, ills.

- Klopper, R. R. & Smith, G. F. (2008) The genus *Aloe* (*Asphodelaceae: Alooideae*) in Namaqualand, South Africa. *Haseltonia* 13: 38–51, ills., maps, key. [https://doi.org/10.2985/1070-0048\(2007\)13\[38:TGA AAI\]2.0.CO;2](https://doi.org/10.2985/1070-0048(2007)13[38:TGA AAI]2.0.CO;2).
- Klopper, R. R. & Smith, G. F. (2009) *Aloe hahnii*, a new species in the section *Pictae*, in the Soutpansberg Centre of Endemism, Limpopo Province, South Africa. *Bothalia* 39(1): 98–100, ills., map. <https://doi.org/10.4102/abc.v39i1.233>.
- Klopper, R. R. & Smith, G. F. (2010a) Notes on African plants. *Asphodelaceae: Alooideae*. Reinstatement of *Aloe spectabilis*. *Bothalia* 40(1): 91–93, ill., maps. <http://abcjournal.org/index.php/ABC/article/view/197>
- Klopper, R. R. & Smith, G. F. (2010b) The genus *Aloe* L. (*Asphodelaceae: Alooideae*) in the Eastern Cape Province of South Africa. *Haseltonia* 16: 16–53, ills. <https://doi.org/10.2985/1070-0048-16.1.16>.
- Klopper, R. R. [et al. 2008], Preez, P. J. du & Smith, G. F. (2008) *Asphodelaceae: Alooideae*. New evidence in support of a disjunct distribution of *Aloe karasbergensis*. *Bothalia* 38(1): 82, map. <http://abcjournal.org/index.php/ABC/article/view/269>
- Klopper, R. R. [et al. 2009a], Matos, S., Figueiredo, E. & Smith, G. F. (2009) *Aloe* in Angola (*Asphodelaceae: Alooideae*). *Bothalia* 39(1): 19–35, maps, keys. <http://abcjournal.org/index.php/ABC/article/view/228>
- Klopper, R. R. [et al. 2009b], Retief, E. & Smith, G. F. (2009) The genus *Aloe* L. (*Asphodelaceae: Alooideae*) in the Free State Province of South Africa. *Haseltonia* 15: 41–52, ills., maps, key. <https://doi.org/10.2985/026.015.0105>.
- Klopper, R. R. [et al. 2010], Zietsman, P. C., Preez, P. J. du & Smith, G. F. (2010) A first record of a South African *Aloe*, *Aloe spectabilis*, becoming naturalized elsewhere in the country. *Bradleya* 28: 37–38, ill., map. <https://doi.org/10.25223/brad.n28.2010.af>
- Klopper, R. R. [et al. 2011], Grace, O. M., Smith, G. F. & Figueiredo, E. (2011) Reinstatement of *Aloe gracilliflora* Groenew. (*Asphodelaceae*), a maculate *Aloe* from north-east South Africa. *Bradleya* 29: 125–130, ills., map. <https://doi.org/10.25223/brad.n29.2011.a15>
- Klopper, R. R. [et al. 2012], Lane, S. S., Msekandiana-Mkwapatira, G. & Smith, G. F. (2012) The genus *Aloe* L. (*Asphodelaceae: Alooideae*) in Malawi. *Bradleya* 30: 65–92, ills., maps, key. <https://doi.org/10.25223/brad.n30.2012.a10>
- Klopper, R. R. [et al. 2013], Smith, G. F., Figueiredo, E., Grace, O. M. & Wyk, A. E. (B.) van (2013) The correct name for species of *Aloe* sect. *Chortolirion* (*Asphodelaceae: Alooideae*). *Taxon* 62(6): 1266–1267. <https://doi.org/10.12705/626.5>.
- Klopper, R. R. [et al. 2014], Smith, G. F., Grace, O. M. & Crouch, N. R. (2014) Reinstatement of *Aloe barbertoniae* Pole-Evans (*Asphodelaceae: Alooideae*) from northeastern South Africa. *Bradleya* 32: 70–75, ills., map. <https://doi.org/10.25223/brad.n32.2014.a21>
- Klopper, R. R. [et al. 2015], Crouch, N. R. & Smith, G. F. (2015) (2399) Proposal to conserve the name *Aloe parvibracteata* against *A. monteiroae* (*Asphodelaceae: Alooideae*). *Taxon* 64(6): 1320. <https://doi.org/10.12705/646.21>.
- Klopper, R. R. [et al. 2016], Smith, G. F., Figueiredo, E. & Wyk, A. E. van (2016) Proposals to reject the names *Aloe perfoliata*, *A. obscura*, *A. picta*, and *A. perfoliata* var. *saponaria* (*A. saponaria*) (*Asphodelaceae: Alooideae*). *Taxon* 65(5): 1173–1175. <https://doi.org/10.12705/655.22>.
- Kolm, L. & Newton, L. E. (2011) Phenotype variation of *Aloe lateritia* var. *graminicola*. *Haworthiad* 25(1): 18–21, ills.
- Kondo, N. & Megata, M. (1943) Chromosome studies in *Aloineae*. *Rep. Kihara Inst. Biol. Res.* 2: 69–82.
- Koshy, T. K. (1937) Number and behaviour of chromosomes in *Aloe litoralis*. *Ann. Bot. (Oxford)*, n.s. 1(1): 43–58. <http://aob.oxfordjournals.org/content/1/1/43.full.pdf+html>
- Kuiper, T. R. [et al. 2015], Smith, D. L., Wolmarans, M. H. L., Jones, S. S., Forbes, R. W., Hully, P. E. & Craig, A. J. F. K. (2015) Importance of winter-flowering *Aloe ferox* for specialist and generalist nectar-feeding birds. *Emu* 115(1): 49–57. <https://doi.org/10.1071/MU14054>.
- Laius, A. (2014) Aloes in Kenya. *Haworthiad* 28(3): 63–73, ills.
- Lane, S. (2004) The Aloes of Malawi. Hatfield (ZA): Umदाus Press.
- Lavranos, J. J. (1965) Notes on the Aloes of Arabia, with descriptions of six new species. *J. South Afr. Bot.* 31: 55–81, ills.
- Lavranos, J. J. (1969) The genus *Aloe* L. in the Socotra Archipelago, Indian Ocean. A revision. *Cact. Succ. J. (US)* 41(5): 202–207, ills.
- Lavranos, J. J. (1970) *Aloe rubroviolacea*. *Aloe squarrosa*. *Flow. Pl. Afr.* 41(1–2): tt. 1610–1611 + text.
- Lavranos, J. J. (1973) Three new Aloes from Somalia. *Cact. Succ. J. (US)* 45(3): 114–119.
- Lavranos, J. J. (1992) *Aloe inermis* Forsk. and its relatives. With description of a new species. *Cact. Succ. J. (US)* 64(4): 206–208, ills.
- Lavranos, J. J. (1995) *Aloaceae*. In: Thulin, M. (ed.): *Flora of Somalia*, 4: 35–42, ills. (incl. t. 2), key. Richmond (GB): Royal Botanic Gardens Kew.
- Lavranos, J. J. (2004) *Aloe striata* Haworth and its associates: Reflections on consistency in taxonomic treatment. *Aloe* 41(2–3): 50–51, ills., key.
- Lavranos, J. J. & McCoy, T. A. (2002) Yemeni Aloes: A new species and a synonymized variety. *Cact. Succ. J. (US)* 74(5): 237–240, ills.
- Lavranos, J. J. & McCoy, T. A. (2007) The identity of *Aloe steudneri* Schweinfurth and a new species, *Aloe neo-steudneri*, from Mt. Saber, Eritrea. *Bradleya* 25: 9–16, ills. <https://doi.org/10.25223/brad.n25.2007.a3>
- Lavranos, J. J. & Newton, L. E. (1976) Three new Aloes from East Africa and an amplified description of a fourth. *Cact. Succ. J. (US)* 48(6): 273–280.

- Lavranos, J. J. [ & al. 2004], McCoy, T. A. & Al-Gifri, A. N. (2004) *Aloe irafensis*. A beautiful new distichous species from the Yemen. *Cact. Succ. J. (US)* 76(3): 134–138, ills.
- Leach, L. C. (1970) The identity of *Aloe vituensis* Baker. *J. South Afr. Bot.* 36(2): 57–62, ills.
- Leach, L. C. (1971) Two new species of *Aloe* (*Liliaceae*) from South Tropical Africa. *J. South Afr. Bot.* 37(4): 249–266, ills.
- Leach, L. C. (1977) Notes on *Aloe* (*Liliaceae*) species of the Flora Zambesiaca area. *Kirkia* 10(2): 385–389, ill.
- Lebrun, J.-P. & Stork, A. L. (2012) Tropical African flowering plants. Ecology and distribution. Volume 7: Monocotyledons 1 (*Limnocharitaceae* – *Agavaceae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Jack, S. L. [ & al. 2014], Hoffman, M. T., Rohde, R. F., Durbach, I. & Archibald, M. (2014) Blow me down: A new perspective on *Aloe dichotoma* mortality from windthrow. *BMC Ecology* 14(7): 12 pp., ills., map. <https://doi.org/10.1186/1472-6785-14-7>.
- Lodé, J. (2016) *Aloe porphyrostachys* ssp. *koenenii* should be *Aloe* of the Bible? *Int. Cact.-Advent.* 111–112: 52–53, ills.
- Loots, S. & Mannheimer, C. (2003) The status of *Aloe pillansii* L. Guthrie (*Aloaceae*) in Namibia. *Bradleya* 21: 57–62, ills. <https://doi.org/10.25223/brad.n21.2003.a12>
- Lubia, I. K. [ & al. 2008], Kyalo, S. N., Mukonyi, K. W., Lusweti, A. M. & Situma, C. A. (2008) Strategy for conservation and management of commercial *Aloe* species in Kenya. Nairobi (KE): Kenya Wildlife Service. <https://www.kws.go.ke/download/file/fid/1405>
- Lüthy, J. M. (2006) The Aloes and Euphorbias of CITES Appendix I and the genus *Pachypodium*. Bern (CH): Bundesamt für Veterinärwesen.
- Manning, J. C. [ & al. 2014a], Boatwright, J. S., Daru, B. H., Maurin, O. & Bank, M. van der (2014) A molecular phylogeny and generic classification of *Asphodelaceae* subfamily *Aloioideae*: A final resolution of the prickly issue of polyphyly in the Alooids. *Syst. Bot.* 39(1): 55–74, key. <https://doi.org/10.1600/036364414X678044>.
- Manning, J. C. [ & al. 2014b], Boatwright, J. S. & Daru, B. H. (2014) *Aloe* and goodbye: A new evolutionary classification of the Alooids. *Alsterworthia Int.* 14(2): 7–15, key.
- Marais, W. (1975) A further note on *Lomatophyllum* (*Liliaceae*). *Kew Bull.* 30(4): 601–602. <https://doi.org/10.2307/4102902>.
- Marais, W. (1978) Famille 183: Liliacées: *Aloe*, *Lomatophyllum*. In: Bosser, J. & al. (eds.): Flore des Mascareignes, 177–188. Richmond (GB): Royal Botanic Gardens Kew etc.
- Marx, G. (2014) *Tulista* (*Aloe*) *aristata* in habitat. *Cactus & Co.* 17(2/3): 114–119, ills.
- Mays, H. (2009) Hybrids & cultivars of the succulent *Asphodelaceae*. Volume 1. *Aloe*, *Astroloba*, *Bulbine*, *Gasteria* & nothogenera. St. Michaels on Wyre (GB): Harry Mays.
- McCoy, T. A. (2007) *Aloe djiboutiensis* and *Aloe ericahenriettae*, two new species from Djibouti and the mystery of *Aloe eumassawana*'s natural habitat solved. *Cact. Succ. J. (US)* 79(6): 269–273, ills. [https://doi.org/10.2985/0007-9367\(2007\)79\[269:ADAAET\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2007)79[269:ADAAET]2.0.CO;2).
- McCoy, T. A. (2014) A report of a new discovered species of *Aloe* from the Haroni Gorge. *Ingens Bull.* 51: 12–13, ills.
- McCoy, T. A. (2018) Die taxonomische Wiedererrichtung von *Aloe termetophila* (De Wild. 1921) als gültiges Taxon mit einer erweiterten Beschreibung dieser zentralafrikanischen Art. The taxonomic reinstatement of *Aloe termetophila* De Wild. (1921) as a valid taxon with an amplified description of this Central African species. *Avonia* 36(3): 196–202, ills. (incl. back-cover).
- McCoy, T. A. (2019) The Aloes of Arabia. Temecula (US): McCoy Publishing.
- McCoy, T. A. & Lavranos, J. J. (2010) Nomenclatural notes on certain Arabian aloes. *CactusWorld* 28(1): 29–30, ills. <https://www.jstor.org/stable/42795127>
- McCoy, T. A. & Lavranos, J. J. (2015) A new species of *Aloe* from the Sudan, and the answer to a long-standing mystery. *CactusWorld* 33(1): 27–34, ills.; (2): 122 [erratum]. <https://www.jstor.org/stable/44082472>.
- McDonald, D. J. (1994) Notes on *Aloe gracilis* var. *decumbens*. *Aloe* 31(2): 46–47, ills., map.
- Medhanie, G. & Dioli, M. (2006) Observations on three poorly known Aloes from Eritrea. *Aloe schoelleri*, *Aloe steudneri* & *Aloe eumassawana*. *Cact. Succ. J. (US)* 78(1): 36–41, ills. [https://doi.org/10.2985/0007-9367\(2006\)78\[36:OOTPKA\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[36:OOTPKA]2.0.CO;2).
- Meer, M. H. J. van der (2019) Nomenclatural novelties in *Aloaceae*. *Cact. Phantast.* 2: 1–8. <https://doi.org/10.5281/ZENODO.2544155>.
- Midgley, J. J. [ & al. 1997], Cowling, R. M., Hendricks, H., Desmet, P. G., Esler, K. & Rundel, P. (1997) Population ecology of tree succulents (*Aloe* and *Pachypodium*) in the arid Western Cape: Decline of keystone species. *Biodivers. & Conservation* 6(6): 869–876, map. <https://doi.org/10.1023/B:BIOC.00001010407.65612.27>.
- Moltano, S. (2017) A second population of *Aloiampelos juddii* (van Jaarsv.) Klopper & Gideon F. Sm., with some observations on soil and climate. *Alsterworthia Int.* 17(2): 14–19, ills.
- Moore, J. (2016) Aloes & Agaves in cultivation. Solana Beach (US): Solana Succulents.
- Mottram, R. (2013) Typification and application of the name *Aloe perfoliata* L. *Cactician* 1: 1–15, ills.
- Müller, F. S. (1941) 'n sitologiese studie van 'n aantal *Aloe*-soorte. I. Gromosoomgetalle. *Tydskr. Wetensk. Kuns, n.s.*, 2: 99–104.
- Müller, F. S. (1945) 'n chromosoomstudie van 'n aantal spesies van die genus *Aloe* Linn. Met spesiale verwysing na die morfologie en betenkenis van die somatiese chromosome. *Publ. Univ. Pretoria* 2(8): 1–157.

- Ndhkala, A. R. [et al. 2009], Amoo, S. R., Stafford, G. I., Finnie, J. F. & Staden, J. van (2009) Antimicrobial, anti-inflammatory and mutagenic investigation of the South African Tree Aloe (*Aloe barberae*). *J. Ethnopharmacol.* 124(3): 404–408. <https://doi.org/10.1016/j.jep.2009.05.037>.
- Nel, P. (2017) Beobachtungen an *Aloe modesta* Reynolds. *Avonia* 35(2): 102–103, ills.
- Nepi, M. [et al. 2006], Human, H., Nicolson, S. W., Cresti, L. & Pacini, E. (2006) Nectary structure and nectar presentation in *Aloe castanea* and *A. greatheadii* var. *davyana* (*Asphodelaceae*). *Pl. Syst. Evol.* 257: 45–55, ills. <https://doi.org/10.1007/s00606-005-0376-7>.
- Newton, D. J. & Vaughan, H. (1996) South Africa's *Aloe ferox* plant, parts and derivatives industry. Johannesburg (ZA): South African National Office.
- Newton, L. E. (1970) Chromosome numbers of West African Aloes. *J. South Afr. Bot.* 36(2): 69–72, ill.
- Newton, L. E. (1976) The taxonomic status of *Aloe keayi* Reynolds. *Nation. Cact. Succ. J.* 31(3): 49–53, ills., maps.
- Newton, L. E. (1979) In defence of the name *Aloe vera*. *Cact. Succ. J. Gr. Brit.* 41(2): 29–30. <https://www.jstor.org/stable/42786287>.
- Newton, L. E. (1980) Phytogeographical associations of the succulent plant flora of southwest Arabia and the Horn of Africa. *Nation. Cact. Succ. J.* 35(4): 83–88. <https://www.jstor.org/stable/42791025>.
- Newton, L. E. (1991) On the identity of *Aloe penduliflora* Baker (*Liliaceae/Aloaceae*). *Taxon* 40(1): 53–60, ills. <https://doi.org/10.2307/1222922>.
- Newton, L. E. (1992) The identity of *Aloe archeri* Lavranos (*Liliaceae/Aloaceae*). *Taxon* 41(1): 25–34, ills. <http://www.jstor.org/stable/1222482>
- Newton, L. E. (1996) *Aloe chrysostachys* and *Aloe meruana* (*Aloaceae*). *Cact. Succ. J. (US)* 68(3): 126–129, ills.
- Newton, L. E. (1998a) Natural hybrids in the genus *Aloe* (*Aloaceae*) in East Africa. *J. East Africa Nat. Hist. Soc.* 84: 141–145, ill.
- Newton, L. E. (1998b) Two new succulent plant records for East Africa. *Bradleya* 16: 109–114, ills. <https://doi.org/10.25223/brad.n16.1998.a8>.
- Newton, L. E. (2004) Succulent plant utilisation and conservation in Eastern Tropical Africa / Usi e conservazione delle piante succulente nell'Africa orientale tropicale. In: Russo, L. (ed.): *The succulent plants of East Africa/Le piante succulente dell'Africa Orientale*; pp. 84–95, ills. Roma (IT): Associazione Italiana Amatori delle Piante Succulente.
- Newton, L. E. (2007) Goodbye to the type locality of *Aloe ballyi*. *CactusWorld* 25(Suppl.): 45–46, ills. <https://www.jstor.org/stable/42795441>.
- Newton, L. E. (2008) Coming clean with *Aloe* soap. *CactusWorld* 26(4): 250. <https://www.jstor.org/stable/42794967>.
- Newton, L. E. (2011) Uses of succulent plants in East Africa. Nairobi (KE): Succulenta East Africa/Nature Kenya.
- Newton, L. E. & Kamiti, A. (2003) *Aloe wilsonii*. *Aloe elata*. *Aloe yavellana*. *Flow. Pl. Afr.* 58: 2–15, tt. 2181–2183, maps.
- Newton, L. E. & Lavranos, J. J. (1990) Two new Aloes from Kenya, with notes on the identity of *Aloe turkanensis*. *Cact. Succ. J. (US)* 62(5): 215–221, ills., map.
- Nkuna, L. A. (2017) The ex situ seed conservation of threatened *Aloe gerstneri*. *Samara* 31: 8–9, ills.
- O'Brien, C. [et al. 2011], Wyk, B-E. van & Heerden, F. R. van (2011) Physical and chemical characteristics of *Aloe ferox* leaf gel. *South Afr. J. Bot.* 77(4): 988–995. <https://doi.org/10.1016/j.sajb.2011.08.004>.
- Oakman, N. A. [et al. 2002], Christie, S. J. & Hannon, D. P. (2002) Conservation status of two succulent endemics of Soqotra Island, Yemen. *Bradleya* 20: 23–28, ills. <https://doi.org/10.25223/brad.n20.2002.a6>
- Oliveira, E. T. de [et al. 2009], Crocorno, O. J., Farinha, T. B. & Gallo, L. A. (2009) Large-scale micropropagation of *Aloe vera*. *HortScience* 44(6): 1675–1678. <http://hortsci.ashspublications.org/content/44/6/1675.full>
- Oliver, I. (1986) Natal's *Aloe spectabilis* Reynolds finds itself at home in the eastern OFS. *Veld Fl.* (1975+) 72(1): 7–9.
- Payne, S. [et al. 2016], Symes, C. T. & Witkowski, E. T. F. (2016) Of feathers and fur: Differential pollinator roles of birds and small mammals in the grassland succulent *Aloe peglerae*. *Austral Ecol.* 41(8): 952–963, ills. <https://doi.org/10.1111/aec.12387>.
- Perrier, H. (1926) *Les Lomatophyllum* et les *Aloe* de Madagascar. *Mém. Soc. Linn. Normandie, Bot.* 1(1): 1–58, 8 tt., map.
- Perrier, H. (1938) 40e famille. Liliacées (*Liliaceae*). In: Humbert, H. (ed.): *Flore de Madagascar*. Tananarive (MG): Imprimerie Officielle. <http://biodiversitylibrary.org/page/12247520>
- Pfäb, M. F. & Scholes, M. A. (2004) Is the collection of *Aloe peglerae* from the wild sustainable? An evaluation using stochastic population modelling. *Biol. Conservation* 118(5): 695–701. <https://doi.org/10.1016/j.biocon.2003.10.018>.
- Phama, J. O. [et al. 2014], Panagos, M. D., Myburgh, W. J. & Pfäb, M. F. (2014) The population status of the endangered endemic plant *Aloe peglerae*: Area of occupancy, population structure, and past population trends. *South Afr. J. Bot.* 93: 247–251. <https://doi.org/10.1016/j.sajb.2014.04.015>.
- Pole-Evans, I. B. (1922) *Aloe wickensii* Pole-Evans. *Flow. Pl. South Afr.* 2: t. 41 + text.
- Powell, E. [et al. 2003], Hendriks, B. & Clark, B. (2003) Could *Aloe pillansii* face extinction? *Brit. Cact. Succ. J.* 21(1): 33–37, ills., map. <https://www.jstor.org/stable/42793835>.
- Ratsirarson, J. (1995) Pollination ecology of *Aloe divaricata* Berger (*Liliaceae*): an endemic plant species of south-west Madagascar. *South Afr. J. Bot.* 61(5): 249–252, ills., diags. [https://doi.org/10.1016/S0254-6299\(15\)30531-7](https://doi.org/10.1016/S0254-6299(15)30531-7).
- Rauh, W. (1995) Succulent and xerophytic plants of Madagascar. Vol. 1. Mill Valley (US): Strawberry Press.



- Rauh, W. (1998) Three new species of *Lomatophyllum* and one new *Aloe* from Madagascar. *Bradleya* 16: 92–100, ills., key. <https://doi.org/10.25223/brad.n16.1998.a12>
- Rebelo, A. G. [& al. 1989], Holmes, P. M., Hilton-Taylor, C., Samper, C., Knight, R. S., Kurtzweil, H. & Bapst, P. (1989) Branching patterns in *Aloe dichotoma* — is *Aloe ramosissima* a separate species? *Madoqua* 16(1): 23–26, maps.
- Rebmann, N. (2009) Two new subspecies of *Aloe* from Madagascar: *Aloe deltoideodonta* Baker ssp. *amboahangyensis* N. Rebmann ssp. nov., *Aloe deltoideodonta* Baker ssp. *esomyensis* N. Rebmann ssp. nov. *Cact.-Avent. Int.* 84: 24–31, ills.
- Resende, F. (1937) Über die Ubiquität der SAT-Chromosomen bei den Blütenpflanzen. *Planta* 26(5): 757–807. <https://doi.org/10.1007/BF01915460>.
- Reynolds, G. W. (1950) The Aloes of South Africa. Johannesburg (ZA): Aloes of South Africa Book Fund.
- Reynolds, G. W. (1957) The identity of *Aloe deltoideodonta* Baker with notes on Perrier's varieties, and with descriptions of three new species. *J. South Afr. Bot.* 23: 65–73.
- Reynolds, G. W. (1958) Les Aloés de Madagascar. Revision. Tananarive (MG): Institut de Recherche Scientifique de Madagascar.
- Reynolds, G. W. (1959) A new *Aloe* from Tanganyika Territory. *J. South Afr. Bot.* 25: 211–213, ills.
- Reynolds, G. W. (1966) The Aloes of tropical Africa and Madagascar. Mbabane (SZ): Aloes Book Fund.
- Reynolds, T. (1996) Chemotaxonomy of *Aloe turkanensis* and *A. scabrifolia* from Kenya. *Biochem. Syst. Ecol.* 24(4): 347–352. [https://doi.org/10.1016/0305-1978\(96\)00012-9](https://doi.org/10.1016/0305-1978(96)00012-9).
- Reynolds, T. (ed.) (2004) Aloes. The genus *Aloe*. Boca Raton (US) etc.: CRC Press. <http://www.crcnetbase.com/isbn/9780203476345>
- Riley, H. P. (1959) Chromosome numbers in *Aloe*. *J. South Afr. Bot.* 25(3): 237–246.
- Riley, H. P. & Majumdar, S. K. (1979) The *Aloineae*. A biosystematic survey. Lexington (US): University Press of Kentucky.
- Riley, S. (1993) New *Aloe* hybrids from John Bleck. *Cact. File* 1(11): 22–23, ills.
- Rothmann, S. (2004) Aloes, aristocrats of Namibian flora. A laymen's photo guide to the *Aloe* species of Namibia/ Aloes, die Aristokraten der namibischen Flora. Ein Handbuch der verschiedenen Aloes Namibias. Swakopmund (NA): ST Promotions.
- Rowley, G. D. (1982) Intergeneric hybrids in succulents. *Nation. Cact. Succ. J.* 37(1): 2–6, (2): 45–49, (3): 76–80, (4): 119, ills. <https://www.jstor.org/stable/42791373>.
- Rowley, G. D. (1996) The berried aloes: *Aloe* section *Lomatophyllum*. *Excelsa* 17: 59–62.
- Rowley, G. D. (2013a) Generic concepts in the *Aloioideae* — part 3. The phylogenetic story. *Alsterworthia Int. Spec. Issue* 10: 3–6.
- Rowley, G. D. (2013b) Generic concepts in the *Aloioideae* — part 4. *Haworthiopsis* and *Tulista* — old wine in new bottles. *Alsterworthia Int.* 13(3): 6–13, ills., keys.
- Rowley, G. D. (2014a) Intergeneric hybrids in the *Asphodelaceae* subfamily *Aloioideae* — 2014 update. *Alsterworthia Int.* 14(2): 16–23, ills.
- Rowley, G. D. (2014b) *Tulista* and the Partridge-Breasted *Aloe*. *Alsterworthia Int.* 14(3): 3–8, ills., map.
- Rowley, G. D. (2017) Succulents in cultivation — breeding new cultivars. Hornchurch (GB): British Cactus & Succulent Society.
- Satô, D. (1937) Analysis of karyotypes in *Aloinae* with special reference to the SAT-chromosomes. *Cytologia Fujii Vol.*: 80–95.
- Sebsebe Demissew & Gilbert, M. G. (1997) *Aloaceae*. In: Edwards, S. & al. (eds.): *Flora of Ethiopia and Eritrea* 6: 117–135, ills., keys. Addis Ababa (ET): Addis Ababa University/Uppsala (SE): Uppsala University.
- Sebsebe Demissew & Nordal, I. (2010) Aloes and lilies of Ethiopia and Eritrea. Ed. 2. Addis Ababa (ET): Shama Books.
- Senior, R. (2002) *Aloe polyphylla* growing outdoors in the UK. *Brit. Cact. Succ. J.* 20(4): 184–185, ills. <https://www.jstor.org/stable/42794250>
- Serrano, M. [& al. 2006], Valverde, J. M., Guillén, F., Castillo, S., Martínez-Romero, D. & Valero, D. (2006) Use of *Aloe vera* gel coating preserves the functional properties of table grapes. *J. Agric. Food Chem.* 54(11): 3882–3886. <https://doi.org/10.1021/jf060168p>.
- Shackleton, C. M. & Gambiza, J. (2007) Growth of *Aloe ferox* Mill. at selected sites in the Makana region of the Eastern Cape. *South Afr. J. Bot.* 73(2): 266–269. <https://doi.org/10.1016/j.sajb.2006.12.003>.
- Silva, V. [& al. 2015], Figueiredo, E. & Smith, G. F. (2015) Alien succulents naturalized and cultivated on the central west coast of Portugal. *Bradleya* 33: 58–81, map, ills. <https://doi.org/10.25223/brad.n33.2015.a10>.
- Smith, G. F. (1990) Nomenclatural notes on the subsection *Bowiea* in *Aloe* (*Asphodelaceae*). *South Afr. J. Bot.* 56(3): 303–308.
- Smith, G. F. (1991a) Additional notes on the taxonomic status and habitat of *Aloe bowiea* (*Asphodelaceae: Aloioideae*). *Aloe* 28(1): 9–17, ills.
- Smith, G. F. (1991b) Historical review of the taxonomy of *Chortolirion* Berger (*Asphodelaceae: Aloioideae*). *Aloe* 28(3–4): 90–95, ills.
- Smith, G. F. (2018) Proposal to conserve the name *Aloe glauca* (*Asphodelaceae: Aloioideae*) with a conserved type. *Taxon* 67(6): 1214. <https://doi.org/10.12705/676.23>.
- Smith, G. F. & Correia, R. I. de S. (1992) Establishment of *Aloe greatheadii* var. *davyana* from seed for use in reclamation trials. *Landscape Urban Planning* 23: 47–54. [https://doi.org/10.1016/0169-2046\(92\)90063-6](https://doi.org/10.1016/0169-2046(92)90063-6).
- Smith, G. F. & Craib, C. (2005) *Aloe craibii* and its environment. *Cact. Succ. J. (US)* 77(4): 202–204, ills. [https://doi.org/10.2985/0007-9367\(2005\)77\[202:ACAIE\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[202:ACAIE]2.0.CO;2).
- Smith, G. F. & Crouch, N. R. (1995) Notes on *Aloe pruinosa* Reyn. (*Aloaceae*), a rare and little-known



- maculate from the midlands of KwaZulu-Natal, South Africa. *Aloe* 32(3–4): 66–69, ills., map.
- Smith, G. F. & Crouch, N. R. (2001) *Aloe suffulta*. *Flow. Pl. Afr.* 57: 16–22, t. 2163, map.
- Smith, G. F. & Figueiredo, E. (2009) *Aloe arborescens* Mill. (*Asphodelaceae*) is spreading in Portugal. *Bradleya* 27: 165–167, ills. <https://doi.org/10.25223/brad.n27.2009.a4>.
- Smith, G. F. & Figueiredo, E. (2011a) *Aloe palmiformis*, an endemic krantz *Aloe* from Angola. *Cact. Succ. J. (US)* 83(1): 22–27, ills., map. <https://doi.org/10.2985/0007-9367-83.1.22>.
- Smith, G. F. & Figueiredo, E. (2011b) Provenance of the material on which the name *Aloe mendesii* Reynolds (*Asphodelaceae*), a cliff-dwelling species from Angola, is based. *Bradleya* 29: 61–66, ills. <https://doi.org/10.25223/brad.n29.2011.a7>.
- Smith, G. F. & Figueiredo, E. (2015) Notes on *Aloe × nobilis* Haw. (*Asphodelaceae: Alooideae*). *Haseltonia* 21: 72–76, ills. <https://doi.org/10.2985/026.021.0110>.
- Smith, G. F. & Figueiredo, E. (2018a) The nomenclature of *Aloe ferox* Mill. (*Asphodelaceae: Alooideae*), an iconic medium-sized to large aloe from southern South Africa. *Haseltonia* 25: 128–132. <https://doi.org/10.2985/026.025.0112>.
- Smith, G. F. & Figueiredo, E. (2018b) Proposal to conserve the name *Aloe melanacantha* against *A. muricata* (*Asphodelaceae: Alooideae*). *Taxon* 67: 1215. <https://doi.org/10.12705/676.24>.
- Smith, G. F. & Mössmer, M. (1995) The correct orthography of *Aloe micracantha* (*Aloaceae*). *Haseltonia* 3: 9.
- Smith, G. F. & Steyn, E. M. A. (2005) Notes on the phenology, natural geographical distribution range and taxonomy of *Aloe dichotoma* (*Aloaceae*). *Bradleya* 23: 17–22, ills., map. <https://doi.org/10.25223/brad.n23.2005.a4>.
- Smith, G. F. [et al. 1994], Wyk, B-E. van & Glen, H. F. (1994) *Aloe barberae* to replace *A. bainesii*. *Bothalia* 24(1): 34–35. <http://abcjournal.org/index.php/ABC/article/view/749>
- Smith, G. F. [et al. 2003], Steyn, E. M. A. & Crouch, N. R. (2003) *Aloe camperi* (*Asphodelaceae*): The first record of an exotic *Aloe* naturalised in South Africa. *Bradleya* 21: 17–20, ills. <https://doi.org/10.25223/brad.n21.2003.a5>.
- Smith, G. F. [et al. 2005], Steyn, E. M. A. & Crouch, N. R. (2005) *Aloe affinis*. *Curtis's Bot. Mag.*, ser. nov., 22(2): 95–99, ills., t. 524. <https://doi.org/10.1111/j.1355-4905.2005.00472.x>.
- Smith, G. F. [et al. 2011], Crouch, N. R., Klopper, R. R. & Condy, G. (2011) *Aloe neilcrouchii*. *Flow. Pl. Afr.* 62: 10–15, t. 2262, map.
- Smith, G. F. [et al. 2012a], Figueiredo, E., Klopper, R. R. & Crouch, N. R. (2012) *Aloe maculata* All. (*Asphodelaceae*) in the Free State Province, South Africa, and resurrection of 'var. *ficksburgensis*'. *Bradleya* 30: 13–18, ills., map. <https://doi.org/10.25223/brad.n30.2012.a5>.
- Smith, G. F. [et al. 2012b], Klopper, R. R., Figueiredo, E. & Crouch, N. R. (2012) Aspects of the taxonomy of *Aloe arborescens* Mill. (*Asphodelaceae: Alooideae*). *Bradleya* 30: 127–137, ills., map. <https://doi.org/10.25223/brad.n30.2012.a15>.
- Smith, G. F. [et al. 2012c], Figueiredo, E., Klopper, R. R. & Crouch, N. R. (2012) Summer-flowering species of maculate *Aloe* L. (*Asphodelaceae: Alooideae*) in the *Aloe zebrina*-complex from South Africa: Reinstatement of four names, and description of *A. braamvanwykii* Gideon F. Sm. & Figueiredo. *Bradleya* 30: 155–166, ills., map. <https://doi.org/10.25223/brad.n30.2012.a19>.
- Smith, G. F. [et al. 2016a], Figueiredo, E., Crouch, N. R., Oosthuizen, D. & Klopper, R. R. (2016) *Aloe × inopinata* Gideon F. Sm., N. R. Crouch & Oosth., (*Asphodelaceae*) [*Aloe arborescens* Mill. × *Aloe chortolirioides* A. Berger var. *chortolirioides*]: A nothospecies from the Barberton Centre of Endemism, Eastern South Africa. *Haseltonia* 22: 55–63, ills., map. <https://doi.org/10.2985/026.022.0111>.
- Smith, G. F. [et al. 2016b], Klopper, R. R., Crouch, N. R. & Figueiredo, E. (2016) Reinstatement of *Aloe candellabrum* A. Berger (*Asphodelaceae: Alooideae*), a tree-like *Aloe* of KwaZulu-Natal province, South Africa. *Bradleya* 34: 59–69, map, ills. <https://doi.org/10.25223/brad.n34.2016.a21>.
- Smith, G. F. [et al. 2017], Figueiredo, E., Klopper, R. R., Crouch, N. R. & Condy, G. (2017) *Aloe braamvanwykii*. *Flow. Pl. Afr.* 65: 14–24, t. 2323, ills., map.
- Smith, G. F. [et al. 2018], Figueiredo, E. & Molteno, S. (2018) ×*Gonimara* Gideon F. Sm. & Molteno (*Asphodelaceae*): A new nothogenus name for the artificial hybrid, ×*Gonimara corderoyi* (A. Berger) Gideon F. Sm. & Molteno, the alooid species *Gonialoe variegata* and *Kumara plicatilis*, two southern African endemics. *Bradleya* 36: 53–61, ills. <https://doi.org/10.25223/brad.n36.2018.a7>.
- Smith, G. F. & Figueiredo, E. (2019) The nomenclature and taxonomy of *Aloe glauca* Mill. (*Asphodelaceae: Alooideae*). *Bradleya* 37: 46–59, ills. <https://doi.org/10.25223/brad.n37.2019.a27>
- Smith, G. F. & Molteno, S. (2019) *Aloestrela* Molteno & Gideon F. Sm. (*Asphodelaceae: Alooideae*), a new alooid genus with *A. suzannae* (Decary) Molteno & Gideon F. Sm. as the only species. *Bradleya* 37: 3–7, ills. <https://doi.org/10.25223/brad.n37.2019.a2>
- Snoad, B. (1951) Chromosome numbers of succulent plants. *Heredity* 5(2): 279–283, ills. <https://doi.org/10.1038/hdy.1951.25>.
- Solichon, J. M. (2013) *Aloe rauhii* (*Asparagaceae*) [sic!]. *Cact. Succ.* 5(1): 31–33, ills., map.
- Spath, J. & Griffin, K. (2013) Suzanne takes you down to her place near the river — Leonard Cohen. *Cact. Succ. J. (US)* 85(6): 244–249, ills. <https://doi.org/10.2985/015.085.0604>.
- Starha, R. (2013) [Czech:] *Aloe somaliensis* W. Watson — a group of significantly variable plants. *Cactaceae* etc. 23(4): 132–136, ills.

- Starha, R. (2014a) [Czech:] *Aloe ankoberensis* Gilbert & Sebsebe. *Cactaceae etc.* 24(2): 43–46, ills.
- Starha, R. (2014b) [Czech:] Three names for one thing? *Adenium* 27: 30–33, ills.
- Stokes, C. J. & Yeaton, R. I. (1995) Population dynamics, pollination ecology and the significance of plant height in *Aloe candelabrum*. *Afr. J. Ecol.* 33(2): 101–113. <https://doi.org/10.1111/j.1365-2028.1995.tb00786.x>.
- Sutaria, R. N. (1932) Somatic cell division in *Aloe vera* L. *J. Indian Bot. Soc.* 11: 132–136.
- Symes, C. T. (2012) Seed dispersal and seed banks in *Aloe marlothii* (*Asphodelaceae*). *South Afr. J. Bot.* 78: 276–280, ills. <https://doi.org/10.1016/j.sajb.2011.06.008>.
- Symes, C. T. (2017) Notes on the flowering and pollination of the endemic grassland *Aloe reitzii* var. *reitzii* (*Asphodelaceae*). *Bothalia* 47(1): a2215, 5 pp., ills. <https://doi.org/10.4102/abc.v47i1.2215>.
- Symes, C. T. [ & al. 2008], Nicolson, S. W. & McKechnie, E. (2008) Response of avian nectarivores to the flowering of *Aloe marlothii*: A nectar oasis during dry South African winters. *J. Ornithol.* 149: 13–22. <https://doi.org/10.1007/s10336-007-0206-5>.
- Symes, C. T. [ & al. 2011], McKechnie, A. E., Nicolson, S. W. & Woodborne, S. M. (2011) The nutritional significance of a winter-flowering succulent for opportunistic avian nectarivores. *Ibis* 153(1): 110–121. <https://doi.org/10.1111/j.1474-919X.2010.01072.x>.
- Taylor, W. R. (1925) Cytological studies on *Gasteria*. II. A comparison of the chromosomes of *Gasteria*, *Aloe*, and *Haworthia*. *Amer. J. Bot.* 12(4): 219–223, ills. <http://www.jstor.org/stable/2435418>
- Teissier, M. & Lavranos, J. J. (2004) Sur l'identité de *Aloe prostrata* (H. Perrier) L. E. Newton & G. D. Rowley (*Lomatophyllum prostratum* H. Perrier) et sujets apparentés. *Succulentas* 2004(3): 14–20, ills.
- The Plant List (2013) The Plant List. Version 1.1. Published on the internet, <http://www.theplantlist.org>.
- Thiede, J. [ & al. 2015], Campbell-Barker, T. P., Clare, R., Downs, P. E. & Hargreaves, B. J. (2015) *Aloe arborescens* (*Asphodelaceae*): Arborescent forms on Mount Mulanje (Malawi). *Bradleya* 33: 136–146, maps, ills. <https://doi.org/10.25223/brad.n33.2015.a19>
- Titus, J. H. [ & al. 2012], Titus, P. J., Laituri, M. & Sethebe, B. (2012) Population structure of an arborescent aloe (*Aloe marlothii*) in Botswana. *Afr. J. Pl. Sci.* 6(12): 328–336. <https://doi.org/10.5897/AJPS11.313>.
- Upton, R. [ & al. 2012], Axentiev, P. & Swisher, D. (2012) *Aloe vera* leaf. *Aloe vera* leaf juice. *Aloe vera* inner leaf juice. *Aloe vera* (L.) Burm.f. Standards of identity, analysis, and quality control. *Scotts Valley (US): American Herbal Pharmacopoeia*.
- Verdcourt, B. & Trump, E. C. (1969) Common poisonous plants of East Africa. London (GB): Collins.
- Viljoen, A. M. [ & al. 1996], Wyk, B.-E. van, Bank, H. van der, Smith, G. F. & Bank, M. van der (1996) A chemotaxonomic and biochemical evaluation of the identity of *Aloe candelabrum* (*Aloaceae*). *Taxon* 45(3): 461–471, map, diags. <https://doi.org/10.2307/1224138>.
- Vorster, P. (1983) *Aloe meyeri* Van Jaarsveld and *A. richtersveldensis* Venter & Beukes. *J. South Afr. Bot.* 49(2): 175.
- Vosa, C. G. (1982) Chromosome studies in the southern African flora: 30–37. *J. South Afr. Bot.* 48(3): 409–424, ills.
- Wabuye, E. (2006a) Studies on Eastern African Aloes: Aspects of taxonomy, conservation and ethnobotany. Oslo (NO): Faculty of Mathematics and Natural Sciences, University of Oslo.
- Wabuye, E. (2006b) *Aloe kilifiensis* (*Aloaceae*) newly recorded for Tanzania. *J. East Africa Nat. Hist. Soc.* 95(2): 227–229, ills. [https://doi.org/10.2982/0012-8317\(2006\)95\[227:AKANRF\]2.0.CO;2](https://doi.org/10.2982/0012-8317(2006)95[227:AKANRF]2.0.CO;2).
- Wabuye, E. [ & al. 2006], Nordal, I., Grayer, R., Sebsebe Demissew & Newton, L. E. (2006) The maculate *Aloe* complex (Series *Saponariae* Berger) in Eastern Africa. In: Wabuye, E.: *Studies on Eastern African Aloes: Aspects of taxonomy, conservation and ethnobotany; paper 2: 1–39*. Oslo (NO): Faculty of Mathematics and Natural Sciences, University of Oslo.
- Walker, C. C. (2005) A tale of two Arabian Aloes. *Brit. Cact. Succ. J.* 23(4): 175–179, ills. <https://www.jstor.org/stable/42794034>.
- Walker, C. C. (2014) *Aloe hardyi* — a rare South African cremnophyte. *CactusWorld* 32(4): 289–292, ills. <https://www.jstor.org/stable/44082363>.
- Walker, C. C. (2016) *Aloe tomentosa* — a species with unusual hairy flowers from the Yemen. *CactusWorld* 34(3): 153–158, ills.
- Walker, C. C. (2017) *Aloe pulcherrima* — a beautiful Ethiopian endemic. *CactusWorld* 35(2): 131–135, ills.
- Walker, C. C. [ & al. 2015], Klopper, R. R., Smith, G. F. & Condy, G. (2015) *Aloe succotrina*. *Flow. Pl. Afr.* 64: 26–40, map, ills.
- Weisser, P. J. & Deall, G. B. (1989) *Aloe petricola*: Ecological notes and effect of fire near Sabie. *Aloe* 26(1–2): 27–30, ills., map.
- Williamson, G. (1998) The ecological status of *Aloe pillansii* (*Aloaceae*) in the Richtersveld with particular reference to Cornelskop. *Bradleya* 16: 1–8, maps, ills. <https://doi.org/10.25223/brad.n16.1998.a1>.
- Williamson, G. (2003a) Notes on Zambian Aloes. *Aloe* 39(3–4): 83–91, ills., map.
- Williamson, G. (2003b) The rediscovery of the extremely obscure, rare *Aloe fimbrialis* S. Carter. *Excelsa* 20: 21–25, ills. (p. 33).
- Williamson, G. (2005) The rediscovery of *Aloe fimbrialis* and an amplified description. *Cact. Succ. J. (US)* 77(6): 313–317, ills., map. [https://doi.org/10.2985/0007-9367\(2005\)77\[313:TROAFA\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[313:TROAFA]2.0.CO;2).
- Wilson, A. L. [ & al. 2009], Ward, D., Brown, M. & Johnson, S. D. (2009) Seed production in a threatened *Aloe* is not affected by bird exclusion or population size. *Pl. Ecol.* 203(2): 173–182. <https://doi.org/10.1007/s11258-008-9524-9>.

- Wilson, K. L. (2017) Report of the General Committee: 18. *Taxon* 66(3): 742–744. <https://doi.org/10.12705/663.15>.
- Wiseman, R. [ & al. 2004], Page, B. R. & O'Connor, T. G. (2004) Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South Afr. J. Wildlife Res.* 34(1): 25–37.
- Wood, J. R. I. (1983) The Aloes of the Yemen Arab Republic. *Kew Bull.* 38(1): 13–31, ills., maps, keys. <http://www.jstor.org/stable/4107955>.
- Wyk, B-E. van (2008) A broad review of commercially important southern African medicinal plants. *J. Ethnopharmacol.* 119: 342–355, ills. <https://doi.org/10.1016/j.jep.2008.05.029>.
- Wyk, B-E. van (2013) Uses of aloe in traditional and modern medicine. *Aloe* 50(1–2): 53–57, ills.
- Wyk, B-E. van & Smith, G. F. (1996) *Guide to the Aloes of South Africa*. Pretoria (ZA): Briza Publications.
- Wyk, B-E. van & Smith, G. F. (2004) *Guide to the Aloes of South Africa*. Ed. 2. Pretoria (ZA): Briza Publications.
- Wyk, B-E. van & Smith, G. F. (2014) *Guide to the Aloes of South Africa*. Ed. 3. Pretoria (ZA): Briza Publications.
- Zonneveld, B. J. M. (2002) Genome size analysis of selected species of *Aloe* (*Aloaceae*) reveals the most primitive species and results in some new combinations. *Bradleya* 20: 5–12. <https://doi.org/10.25223/brad.n20.2002.a3>.
- Zonneveld, B. J. M. (2003) *Aloe mitrififormis*, de echte en de hybride. *Succulenta* 82(4): 161–163, ills.
- Zonneveld, B. J. M. & Fritz, G. P. J. (2010) Three species accepted in *Chortolirion* Berger (*Xanthorrhoeaceae: Asphodeloideae*). *Bradleya* 28: 27–36, ills. <https://doi.org/10.25223/brad.n28.2010.a5>.



## × *Aloloba* ASPHODELACEAE

U. Eggli

× *Aloloba* G. D. Rowley (Nation. Cact. Succ. J. 22 (3): 74, 1967). — *Alooiideae* — **Lit:** Cumming (1999).

**Incl.** × *Chamaeloba* D. M. Cumming (1974).

**Incl.** × *Lomatoloba* D. M. Cumming (1974).

= *Aloe* × *Astroloba*. None of these hybrids have been formally named, but see Rowley (1982) for a list of known crosses.

### References

- Cumming, D. M. (1999) New nothogenera proposed for four trigeneric hybrids within *Aloaceae*. *Haworthiad* 13(1): 20–21.
- Rowley, G. D. (1982) Intergeneric hybrids in succulents. *Nation. Cact. Succ. J.* 37(1): 2–6, (2): 45–49, (3): 76–80, (4): 119, ills.

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## × *Alworthia* ASPHODELACEAE

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× **Alworthia** G. D. Rowley (Nation. Cact. Succ. J. 28(1): 7, 1973). — *Alooiidae* — **Lit:** Cumming (1999).

≡ *Aloe* × *Haworthia*. No formally named hybrids are known, and Rowley (1982: 46) lists only a single known cross between an unidentified *Aloe* and *H. cymbiformis*.

× **A. 'Fantasy'** G. D. Rowley (Teratopia, 142–143, 280, ill., 2006).

A variegated hybrid *Aloe bellatula* × *Haworthia* sp.

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### References

- Cumming, D. M. (1999) New nothogenera proposed for four trigeneric hybrids within *Aloaceae*. *Haworthiad* 13(1): 20–21.
- Rowley, G. D. (1982) Intergeneric hybrids in succulents. *Nation. Cact. Succ. J.* 37(1): 2–6, (2): 45–49, (3): 76–80, (4): 119, ills.

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## Astroloba ASPHODELACEAE

N. L. Meyer and G. F. Smith

**Astroloba** Uitewaal (Succulenta 1947 (5): 53, 1947). **Type:** *Aloe spiralis* var. *pentagona* Aiton. — **Alooiideae** — **Lit:** Pilbeam (1983: ill. synopsis); Groen (1986: ill. synopsis); Groen (1987: ill. synopsis). **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape). **Etym:** Gr. ‘aster, astros’, star; and Gr. ‘lobos’, lobe; for the stellately spreading perianth lobes.

**Incl.** *Apicra* Haworth (1819) (*nom. illeg.*, Art. 53.1). **Type:** *Aloe pentagona* (Aiton) Haworth [G. D. Rowley, Nation. Cact. Succ. J. 31(3): 54, 1976.].

Small herbaceous leaf-succulent slow-growing perennials, proliferating from the base or with subterranean stolons to form small or large clusters, caulescent, erect or creeping; **R** succulent, terete; **L** numerous, alternate, spirally arranged, imbricate, basally amplexicaul, erectly spreading, deltoid-acuminate, triangular, leathery, light to

dark green to glaucous green, upper face plane or convex, sometimes with reddish striations, lower face convex, usually with a distinct asymmetric keel extending for  $\frac{2}{3}$  of the length, margins and keel acute or slightly rounded, smooth or denticulate, tip acute, sometimes terminating in a mucro, surface smooth or tuberculate, green or brownish; **Inf** laxly flowered racemes or panicles, 10–40 cm, occasionally with accessory branchlets or buds in the axils; peduncle smooth, simple or branched, lower sterile parts bracteate; **Bra** membranous, persistent, triangular to long-acuminate, keeled with 1–3 brownish-green or pinkish central veins; **Ped** short, erect; **Fl** erect, tubular, regular,  $\pm$  straight, sometimes with inflated tissue on the sides of the perianth; **Te** 6, connate below, free but contiguous above, usually monochrome with dull colours, often drab greenish-white, rarely cream, beige, yellow or pink, distinctly veined, lobes short; **St** 6, shorter than the perianth, included or barely exerted; **Fil** yellowish-white, filiform; **Anth** yellow, dorsifixed, dehiscing longitudinally, introrse; **Ov** superior, green, sessile, oblong,  $\pm 4 \times 3$  mm  $\emptyset$ ; **Sty** whitish, straight, capitate,  $\pm 4$  mm, subulate; **Sti** minute, apical; **Fr** 3-locular capsules, cylindrical, oblong to obtuse or ovoid to acuminate, dehiscing loculicidally,  $\pm 12 \times 5$ – $6$  mm  $\emptyset$ ; **Se** angled, dark brown to black, laterally compressed, angles obscurely winged,  $\pm 4$  mm.

The genus has been revised in an unpublished thesis by Roberts Reinecke (1965). Another revision was done by Groen (1986) and Groen (1987),

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but the present authors prefer a compromise between these treatments. *Astroloba* has floral affinities with representatives of *Haworthia* subgen. *Robustipedunculares* (= *Tulista*), and the molecular phylogenetic analyses of Daru & al. (2013) and Manning & al. (2014) indeed show a placement as sister to this taxon. The suggestion that *Astroloba* should be included in *Tulista* (provisionally treated as synonym of *Haworthia* s.l. in this Handbook) is not accepted here. *Astroloba* is retained as separate mainly for its shortly caulescent habit, regular flowers (not bilabiate as in typical haworthias, i.e. subgen. *Haworthia*), and the leaves which are  $\pm$  arranged in 5 distinct ranks. A report on crossing experiments between *Astroloba* species and representatives of other Alooid genera and hybrids also supports the recognition of *Astroloba* as a separate genus (Cumming 2014).

The designations '*A. smutsiana*' and '*A. hallii*' (= *Haworthia hallii* (Roberts Reinecke) M. Hayashi) have been proposed by Roberts Reinecke (1965) for newly discovered taxa in the genus. These proposed names are not validated here. The entity for which Roberts Reinecke proposed the combination *A. foliolosa* ssp. *robusta* was recently published at species rank as *A. robusta*.

For the moment *Poellnitzia* is kept separate from *Astroloba*, pending resolution of a number of nomenclatural issues.

The genus name *Astroloba* has been proposed for conservation against the name *Poellnitzia* Uitewaal (Uitewaal 1940: 61), when these two genera are treated as a single genus (Smith & al. 2018: 206). After completion of the present handbook entry, Molteno & Smith (2018) and Molteno & Smith (2019) have clarified the identity of, and nomenclature that should be applied to, *A. pentagona* and *A. spirella*, respectively. The correct application of these two names disposes with the designations '*Astroloba smutsiana*' and '*Astroloba hallii*'. An updated treatment of *Astroloba* that recognises subgenera and sections in the genus was recently published (Molteno & al. 2018).

**A. bullulata** (Jacquin) Uitewaal (Succulenta 1947 (5): 53, 1947). **Type**: [lecto — icono]: Jacquin, *Fragm. Bot.* t. 109, 1809. — **Distr**: RSA (Western

Cape: Ceres & Laingsburg; Northern Cape: Sutherland); karroid vegetation, 500–1800 m. **I**: Pilbeam (1983: 149, as *A. bicarinata*).

$\equiv$  *Aloe bullulata* Jacquin (1809)  $\equiv$  *Apicra pentagona* var. *bullulata* (Jacquin) Baker (1880)  $\equiv$  *Haworthia bullulata* (Jacquin) Parr (1971)  $\equiv$  *Apicra bullulata* (Jacquin) Willdenow (1811) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Tulista bullulata* (Jacquin) G. D. Rowley (2013); **incl.** *Astroloba bullata* hort. (s.a.) (*nom. inval.*, Art. 61.1); **incl.** *Apicra egregia* Von Poellnitz (1930)  $\equiv$  *Astroloba egregia* (Von Poellnitz) Uitewaal (1947)  $\equiv$  *Haworthia egregia* (Von Poellnitz) Parr (1971); **incl.** *Astroloba egregia* var. *fardeniana* Uitewaal (1948)  $\equiv$  *Haworthia egregia* var. *fardeniana* (Uitewaal) Parr (1971).

**L** in 5 straight rows or rarely imbricate, spiral angle usually 0–10°, dull greenish-brown, usually suberect, tips curved upwards, frequently to the keeled side, keel forming a margin at the apex, 23–40  $\times$  13–26 mm, mucro 0.3–2 mm, vein lines absent, surface of some or all leaves tuberculate, tubercles fairly prominent,  $\pm$ 1 mm  $\varnothing$ , few and irregularly scattered or more numerous and grouped in transverse rows; **Inf** lax racemes, 14–30 cm; **Fl** erect, greenish-brown with yellow lobes; **Ped** 3–6 mm; **Per** tube straight, 8–11  $\times$   $\pm$  3 mm  $\varnothing$ , lobes  $\pm$ 2 mm. — **Cytology**: 2n = 14 (Roberts Reinecke 1965).

Along with *A. corrugata*, this species has the W-most distribution range in the genus. It occurs in an exceedingly cold and arid part of the interior of RSA, in the Tanqua Karoo, around Sutherland (Northern Cape), and in a southerly direction towards Laingsburg, and slightly beyond (Western Cape) in the W Great Karoo.

**A. congesta** (Salm-Dyck) Uitewaal (Succulenta 1947(5): 54, 1947). **Type**: [lecto — icono]: Salm-Dyck, *Monogr. Gen. Aloes & Mesembr.*, sect. 6: Fig. 1, 1854. — **Distr**: RSA (Eastern Cape: Albany, Bedford and Cradock Distr.); karroid and valley bushveld vegetation, 500–900 m. **I**: Bayer (2005: 15, as *A. foliolosa* ssp.).

$\equiv$  *Aloe congesta* Salm-Dyck (1854)  $\equiv$  *Apicra congesta* (Salm-Dyck) Baker (1880)  $\equiv$  *Astroloba foliolosa* ssp. *congesta* (Salm-Dyck) Roberts Reinecke (1965) (*nom. inval.*, Art. 29.1)  $\equiv$  *Haworthia congesta* (Salm-Dyck) Parr (1971)  $\equiv$  *Tulista*

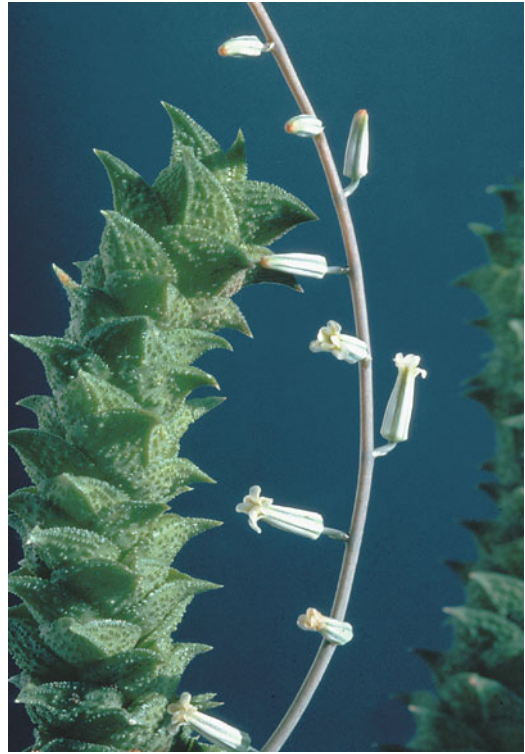
*congesta* (Salm-Dyck) G. D. Rowley (2013); **incl.** *Aloe deltoidea* Hooker fil. (1873)  $\equiv$  *Apicra deltoidea* (Hooker fil.) Baker (1880)  $\equiv$  *Astroloba deltoidea* (Hooker fil.) Uitewaal (1947)  $\equiv$  *Haworthia deltoidea* (Hooker fil.) Parr (1971); **incl.** *Apicra turgida* Baker (1889)  $\equiv$  *Apicra deltoidea* var. *turgida* (Baker) A. Berger (1908)  $\equiv$  *Astroloba deltoidea* var. *turgida* (Baker) H. Jacobsen (1954) (*nom. inval.*, Art. 33.3)  $\equiv$  *Astroloba turgida* (Baker) H. Jacobsen (1960) (*nom. inval.*, Art. 33.3?)  $\equiv$  *Haworthia deltoidea* var. *turgida* (A. Berger) Parr (1971) (*nom. inval.*, Art. 34); **incl.** *Apicra deltoidea* var. *intermedia* A. Berger (1908)  $\equiv$  *Astroloba deltoidea* var. *intermedia* (A. Berger) Uitewaal (1947)  $\equiv$  *Haworthia deltoidea* var. *intermedia* (A. Berger) Parr (1971); **incl.** *Haworthia shieldsiana* Parr (1971) (*nom. inval.*, Art. 34.1).

**L** in 5 straight rows or rarely imbricate, spiral angle 10–20°, light to dark green with a glossy sheen, erect to patent, tips curved upwards to outwards, keel not forming a margin at the apex, 20–47  $\times$  14–28 mm, mucro 0.5–1.3 mm, tubercles absent, but rarely small elongated, very slightly raised concolorous patches present on some leaves; **Inf** lax racemes, 6–31 cm, sometimes branched; **Fl** green with a creamy tinge with white or cream lobes (never yellow); **Ped** 0.7–4 mm; **Per** tube straight, 6–9  $\times$   $\pm$  3 mm  $\varnothing$ , lobes recurved, 1.4–3 mm. — **Cytology**: 2n = 14 (Majumdar 1968); doubtfully also 2n = 18 (Marshak 1934: as *Apicra*).

The species has the E-most distribution range in the genus. It occurs in the Eastern Cape, from near Middelburg and Graaff-Reinet in the N, in a SE direction to Cradock and Grahamstown.

**A. corrugata** N. L. Meyer & G. F. Smith (Bothalia 28(1): 61–62, ill., 1998). **Type**: RSA, Western Cape (*Van Jaarsveld* 13913 [PRE]). — **Distr**: RSA (Western Cape); karroid vegetation, 500–1300 m. **I**: Pilbeam (1983: 148–149, as *A. aspera*). — Fig. 1.

$\equiv$  *Haworthia corrugata* (N. L. Meyer & G. F. Smith) M. Hayashi (2000)  $\equiv$  *Tulista corrugata* (N. L. Meyer & G. F. Smith) G. D. Rowley (2013); **incl.** *Aloe aspera* Salm-Dyck (1854) (*nom. illeg.*, Art. 53.1)  $\equiv$  *Haworthia aspera* (Salm-Dyck) Parr (1971) (*nom. illeg.*, Art. 53.1);



**Fig. 1** *Astroloba corrugata*. (Copyright: U. Egli)

**incl.** *Astroloba rugosa* Roberts Reinecke (1965) (*nom. inval.*, Art. 29.1); **incl.** *Astroloba muricata* L. E. Groen (1987) (*nom. inval.*, Art. 36.1).

**L** in 5 straight rows or imbricate, spiral angle usually 0° - 10°, light to dark green, usually sub-erect, tips curved outwards, keel not forming a margin at the apex, 14–25  $\times$  11–18 mm, mucro 0.4–1 mm, surface always tuberculate, tubercles tending to be arranged in longitudinal lines, 0.5 mm  $\varnothing$ , concolorous; **Inf** lax racemes, 10–43 cm, unbranched; **Fl** white or cream with faint pink or greenish tinge, lobes cream or whitish, midrib green with beige or pink tinge; **Ped** 2–9 mm; **Per** tube 7–12  $\times$  2.5–3.5 mm  $\varnothing$ , lobes  $\pm$  1.5  $\times$  2 mm, tissue on either side of the **OTep** sometimes slightly inflated. — **Cytology**: 2n = 14 (Roberts Reinecke 1965: as *A. rugosa*).

Differing from the other tuberculate-leaved species by the non-marginate leaf tips and a more even, denser distribution of the tubercles, as well as smaller leaves. The names *Astroloba aspera* (Haworth) Uitewaal and *A. aspera* var.



*major* have been misapplied to this species, but seem to apply to a species of *Haworthia* on the base of the original descriptions.

Along with *A. bullulata*, this species has the W-most distribution range in the genus. The distribution range spans part of the arid interior of the Western Cape, from Touwsrivier, E of the Worcester-Robertson Karoo in the W, into the Little Karoo, to near Ladismith. The occurrence of the species further E, towards Graaff-Reinet in the Eastern Cape, has yet to be substantiated.

**A. cremnophila** Van Jaarsveld (Bradleya 33: 177, ills. (pp. 172–177), 2015). **Type:** RSA, Western Cape (*Van Jaarsveld* 25535 [PRE]). — **Distr:** RSA (Western Cape: Klein Karoo: Groot Swartberg); pendent from cliff faces in thicket vegetation, 600–800 m.

**L** in 5 spirally twisted rows, densely imbricate, glaucous-green turning reddish-green, suberect, tips curved upwards, frequently to the keeled side, keel forming a margin at the apex, 22–25 × 12–15 mm, faint vein lines present, faces (esp. the lower) tuberculate, tubercles prominent, irregularly scattered; **Inf** lax racemes, 12–46 cm; **Fl** subsecund, greyish-green with white stripes, tube lacking inflations; **Ped** 3 mm; **Per** tube straight, 11 × 2.5 mm Ø, lobes ±1.5 mm.

This species is restricted to cliffs around Buffelspoort in the W Groot Swartberg. It has morphological affinities with, and is allied to, *A. bullulata*. — [G. F. Smith].

**A. foliolosa** (Haworth) Uitewaal (Succulenta 1947 (5): 54, 1947). **Type:** [neo — icona]: Curtis's Bot. Mag., 1811: t. 1352. — **Distr:** RSA (Western Cape: Ladismith; Eastern Cape: Graaf-Reinet and slightly further E); karroid and valley bushveld vegetation, 100–1500 m. **I:** Pilbeam (1983: 151); Bayer (2005: 15, printed upside down).

≡ *Aloe foliolosa* Haworth (1804) ≡ *Apicra foliolosa* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia foliolosa* (Haworth) Haworth (1812) ≡ *Astroloba spiralis* ssp. *foliolosa* (Haworth) Groen (1987) ≡ *Tulista foliolosa* (Haworth) G. D. Rowley (2013).

**L** 5-ranked or imbricate, spiral angle 10° - 40°, light to grey-green with a glossy sheen, erect to

patent, tips curved upwards to outwards, keel not forming a margin at the apex, 14–40 × 9–24 mm, mucro 0.4–1.5 mm, margins and keels concolorous, paler or whitish, surface smooth or with small elongate slightly raised concolorous patches, lower face sometimes with whitish flecks or darker green lines; **Inf** lax racemes, 5–29 cm, sometimes branched; **Fl** greenish-white or pale cream with white or cream lobes; **Ped** 0.8–3.8 mm; **Per** tube straight, 6–9 × ± 3 mm Ø, lobes recurved, 1.5–3 mm, midrib green with glaucous or beige tinge. — **Cytology:** 2n = 14 (Majumdar 1968; Brandham 1971; Resende 1937: as *Apicra*).

The distribution range of the species spans the E-C parts of the arid interior of the Western Cape, from Ladismith in the Little Karoo in an easterly direction to Graaff-Reinet, and slightly further E, in the Eastern Cape.

**A. herrei** Uitewaal (Desert Pl. Life 20: 37–39, ills., 1948). **Type:** RSA, Western Cape (*Herre* 5703 [WAG]). — **Lit:** Molteno & al. (2017). **Distr:** RSA (Western Cape: Prince Albert and Uniondale Distr.); karroid vegetation, 600–1200 m. **I:** Bayer (1975); Bayer (2005: 14).

≡ *Tulista herrei* (Uitewaal) G. D. Rowley (2013); **incl.** *Astroloba dodsoniana* Uitewaal (1950) ≡ *Haworthia dodsoniana* (Uitewaal) Parr (1971) ≡ *Astroloba herrei* cv. *Dodsoniana* (Uitewaal *pro sp.*) L. E. Groen (1987); **incl.** *Haworthia harlandiana* Parr (1971).

**L** in 5 straight rows or imbricate, light green, usually suberect, tips curved upwards to outwards, keel not forming a margin at the apex, 18–32 × 9–16 mm, narrowly acuminate, mucro 0.7–1.8 mm, margins and keels concolorous or paler, lamina with very fine longitudinal lines, smooth; **Inf** lax racemes, 10–30 cm, unbranched; **Fl** white with yellow lobes, midribs pale green with glaucous or beige tinge; **Ped** 3.5–10.8 mm; **Per** tube with very marked smooth or slightly undulating inflations of tissue on either side of the **OTep**, 7–9 × 2.5–4 mm Ø, lobes 1.5–3 × 1.5–3 mm. — **Cytology:** 2n = 14 (Majumdar 1968).

Differs from *A. spiralis* in chromosome number and in the smooth or slightly undulating nature of the inflated tissue of the perianth tube. Other differences are the very marked lines, frequently

occurring as fine longitudinal ridges, and the narrowly acuminate leaf tips.

The species was once thought to have a restricted and disjunct distribution range around Prince Albert in the Western Cape, and at Uniondale, further E. However, it also occurs between these two localities on the N slopes of the Swartberg in the Great Karoo (Molteno & al. 2017).

**A. robusta** Roberts Reinecke *ex* Molteno & al. (Bradleya 35: 205–207, ills. (pp. 202–208), 2017). **Type:** RSA, Western Cape (Molteno 504 [NBG]). — **Distr:** RSA (E Western Cape, W Eastern Cape); widespread in the S Great Karoo, on shale flats and rocky undulating slopes.

**L** in 5 vertical rows, spirally twisted, appearing imbricate, dark green, grey or brown infused, suberect, rarely erect, keel cartilaginous, white, not forming a margin at the apex, apex curving outwards, attenuate, mucronate, 20–40 × 12–25 mm, usually distinctly glossy, most often glabrous, sometimes with occasional white spots or tubercles; **Inf** robust lax racemes, 10–50 cm, persistent; **Fl** ascending-spreading, usually sessile or **Ped** to 0.5 mm; **Per** tube straight, 6 × 4 mm Ø, lacking inflations, lobes free, white (not yellow), midribs expressed as darker grey stripes.

*A. robusta* can be distinguished by its inflorescence that has a robust, basally flattened peduncle, as well as its glossy leaves with whitish margins and keels. It flowers in winter (May–October), while *A. foliolosa*, with which it has affinities, flowers in summer (August–March). This species occurs across an extensive range in the S Great Karoo. *A. foliolosa* is a more eastern element. — [G. F. Smith].

**A. spiralis** (Linné) Uitewaal (Succulenta 1947 (5): 53, 1947). **Type:** [lecto — icono]: Dillenius, Hort. Eltham., 16, t. 13: fig. 14, 1732. — **Distr:** RSA (Western Cape: Ladismith and Oudtshoorn; Eastern Cape: Graaff-Reinet); karroid vegetation, 400–800 m. **I:** Pilbeam (1983: 154); Bayer (2005: 14). — Fig. 2.

≡ *Aloe spiralis* Linné (1753) ≡ *Haworthia spiralis* (Linné) Duval (1809) ≡ *Apicra spiralis* (Linné) Baker (1880) ≡ *Tulista spiralis* (Linné)



**Fig. 2** *Astroloba spiralis*. (Copyright: E. J. Van Jaarsveld)

G. D. Rowley (2013); **incl.** *Aloe spiralis* var. *imbricata* Aiton (1789) ≡ *Aloe imbricata* (Aiton) Haworth (1811) ≡ *Apicra imbricata* (Aiton) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia imbricata* (Aiton) Haworth (1812); **incl.** *Aloe spiralis* var. *pentagona* Aiton (1789) ≡ *Aloe pentagona* (Aiton) Haworth (1804) ≡ *Apicra pentagona* (Aiton) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia pentagona* (Aiton) Haworth (1812) ≡ *Astroloba pentagona* (Aiton) Uitewaal (1947) ≡ *Astroloba spiralis* cv. 'Pentagona' (Aiton *pro var.*) Groen (1987); **incl.** *Aloe spiralis* Haworth (1804) (*nom. illeg.*, Art. 53.1) ≡ *Aloe pentagona* var. *spiralis* (Haworth) Salm-Dyck (1836) ≡ *Astroloba pentagona* var. *spiralis* (Haworth) Uitewaal (1947) ≡ *Haworthia pentagona* var. *spiralis* (Salm-Dyck) Parr (1971); **incl.** *Haworthia spirella* Haworth (1812) ≡ *Astroloba spirella* (Haworth) hort. (s.a.) (*nom. inval.*, Art. 29.1) ≡ *Aloe spirella* (Haworth) Salm-Dyck (1817) ≡ *Apicra pentagona* var. *spirella* (Haworth) Baker (1880) ≡ *Astroloba pentagona* var. *spirella* (Haworth) Uitewaal (1947) ≡ *Haworthia pentagona* var. *spirella* (Haworth) Parr (1971); **incl.** *Apicra pentagona* var. *torulosa* Haworth (1821) ≡ *Astroloba pentagona* var. *torulosa* (Haworth) Uitewaal (1947) ≡ *Haworthia pentagona* var. *torulosa* (Haworth) Parr (1971); **incl.** *Haworthia gweneana* Parr (1971) (*nom. inval.*, ICN Art. 41.4).

**L** in 5 straight rows or imbricate, erect to suberect, grey-green to blue-green, tips following the axis of the leaf or curved outwards, keel not forming a margin at the apex, 19–42 × 10–18 mm, mucro

0.4–1.6 mm, margins and keels concolorous or darker, leaf tips slightly reddish-brown, surface occasionally with visible lines, smooth; **Inf** lax racemes, 16–39 cm, very rarely branched; **Fl** with a marked rugose inflation of tissue on either side of the **OTep**, white with yellow lobes, midrib pale green with glaucous or beige tinge; **Ped** 1.5–8 mm; **Per** tube straight, 7–13 × 2.5–4 mm Ø, lobes 1.5 × 2 mm. — **Cytology**: 2n = 28 (Ferguson 1926: as *Apicra pentagona spiralis*).

The distribution range of the species spans the arid interior of the E part of the Western Cape, around Ladismith, Calitzdorp and Oudtshoorn in the Little Karoo. Its occurrence at Graaff-Reinet in the Eastern Cape is thus far unsubstantiated.

**A. tenax** Molteno & al. (Bradleya 35: 143–144, ills. (incl. pp. 142, 146), 2017). **Type**: RSA, Western Cape (*Molteno* 150 [NMG]). — **Distr**: RSA (Western Cape: near Prince Albert).

**A. tenax** var. **moltenoi** Gideon F. Smith & Van Jaarsveld (Bradleya 35: 241, ills. (pp. 239–240), 2017). **Type**: RSA, Western Cape (*Molteno* 112 [NMG]). — **Distr**: RSA (Western Cape: S-C Groot Karoo N and E of Prince Albert); Prince Albert Succulent Karoo vegetation.

Differs from var. *tenax*: Stem 6 cm, including the leaves 7.6 (–7.9) cm Ø; **L** (35–) 40–45 (–50) × (16–) 20–26 (–30) mm; **Inf** ± 80 cm.

Geographically var. *moltenoi* (from NE of Prince Albert) does not overlap with var. *tenax* (from W of Prince Albert). The two varieties can be easily separated on their size alone, var. *moltenoi* being much larger and more robust in all respects. — [G. F. Smith].

**A. tenax** var. **tenax** — **Distr**: RSA (Western Cape: along the lower N foothills of the Groot Swartberg Mts., near Prince Albert); Prince Albert Succulent Karoo vegetation, fully exposed or in semi-shade of karroid shrublets and rocks.

**L** in 5 vertical ranks, mostly spirally-twisted, often appearing imbricate, dark green to yellowish-green, turning orange to purplish when exposed to full sun, horizontally spreading, rarely suberect, tips curved upwards, acuminate, attenuate, mucronate, keeled, keel sometimes

double, 20–35 × 16 mm, usually glossy, glabrous, sometimes with spots, tubercles, or lines; **Inf** lax racemes or panicles, 30–60 cm; **Fl** ascending-spreading; **Ped** 3–5 mm; **Per** light grey, interspersed with darker grey, tube straight, 9–11 × 3–4 mm Ø, lacking inflations, lobes free.

The species is related to *A. bullulata*, from which it differs by its straighter, shinier, more spreading to horizontal leaves. *A. tenax* also has longer, sometimes branched, inflorescences. — [G. F. Smith].

## References

- Bayer, M. B. (1975) Notes on *Astroloba herrei* Uitewaal. *Aloe* 13(4): 99–100, ills.
- Bayer, M. B. (2005) *Astroloba* flowers. *Haworthiad* 19(1): 14–16, 25, ills.
- Brandham, P. E. (1971) The chromosomes of the *Liliaceae*: II. Polyploidy and karyotype variation in the *Aloineae*. *Kew Bull.* 25(3): 381–399, ills. <https://doi.org/10.2307/4103181>.
- Cumming, D. M. (2014) *Astroloba* Uitewaal: Inferred relationships from extensive hybridisation. *Alsterworthia Int.* 14(2): 2–5, ills.
- Daru, B. H. [& al. 2013], Manning, J. C., Boatwright, J. S., Maurin, O., Mclean, N., Schaefer, H., Kuzmina, M. & Bank, M. van der (2013) Molecular and morphological analysis of subfamily *Aloioideae* (*Asphodelaceae*) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62(1): 62–76, ills. <http://www.jstor.org/stable/24389313>.
- Ferguson, N. (1926) The *Aloineae*: A cytological study, with special reference to the form and size of the chromosomes. *Philos. Trans., Ser. B*, 215: 225–253. <https://doi.org/10.1098/rstb.1927.0005>.
- Groen, L. E. (1986) *Astroloba* Uitew. *Succulenta* 65(1): 19–23, ills.
- Groen, L. E. (1987) *Astroloba* Uitew. *Succulenta* 66(3): 51–55, (4): 82–87, (5): 110–113, (6): 162–167, (9): 171–174, (12): 261–263, key, maps, ills., SEM-ills.
- Majumdar, S. K. (1968) Morphology, cytogenetics and evolution in the *Aloineae*. Lexington (US): University of Kentucky, unpublished Ph.D. thesis.
- Manning, J. C. [& al. 2014], Boatwright, J. S., Daru, B. H., Maurin, O. & Bank, M. van der (2014) A molecular phylogeny and generic classification of *Asphodelaceae* subfamily *Aloioideae*: A final resolution of the prickly issue of polyphyly in the Alooids. *Syst. Bot.* 39(1): 55–74, key. <https://doi.org/10.1600/036364414X678044>.
- Marshak, A. (1934) Chromosomes and compatibility in the *Aloineae*. *Amer. J. Bot.* 21(9): 592–598. <http://www.jstor.org/stable/2436110>.
- Molteno, S. [& al. 2017], Smith, G. F. & Jaarsveld, E. J. van (2017) Extending the natural distribution range of *Astroloba herrei* Uitewaal (*Asphodelaceae*): Implications

- for its conservation status. *Haseltonia* 23: 39–47, ills., map. <https://doi.org/10.2985/026.023.0106>.
- Molteno, S. & Smith, G. F. (2018) The identity and typification of *Astroloba pentagona* (Haw.) Uitewaal (*Asphodelaceae: Aloioideae*), the type species of the genus *Astroloba* Uitewaal. *Haseltonia* 25: 57–71.
- Molteno, S. & Smith, G. F. (2019) The taxonomy and identity of *Astroloba spirella* (Haw.) Molteno & Gideon F.Sm. (*Asphodelaceae: Aloioideae*), a distinctive species from the western Klein Karoo, Western Cape Province, South Africa. *Bradleya* 37: in press.
- Molteno, S. [ & al. 2018 ], Smith, G.F. & Figueiredo, E. (2018) A synopsis of *Astroloba* Uitewaal (*Asphodelaceae: Aloioideae*): species, types, and infrageneric classification. *Haseltonia* 25: 72–83.
- Pilbeam, J. (1983) *Haworthia* and *Astroloba* — a collector's guide. London (GB): Batsford Ltd.
- Resende, F. (1937) Über die Ubiquität der SAT-Chromosomen bei den Blütenpflanzen. *Planta* 26(5): 757–807. <https://doi.org/10.1007/BF01915460>.
- Roberts Reinecke, P. (1965) The genus *Astroloba* Uitewaal (*Liliaceae*). Cape Town (ZA): M.Sc. thesis, unpublished. <https://open.uct.ac.za/handle/11427/12154>.
- Smith, G.F. [ & al. 2018 ], Figueiredo, E., Klopper, R. R. & Van Wyk, A. E. (2018) (2580) Proposal to conserve the name *Astroloba* against *Poellnitzia* (*Asphodelaceae: Aloioideae*). *Taxon* 67: 206.
- Uitewaal, A. J. A. (1940) Een nieuw geslacht der *Aloineae*. *Succulenta* 22(6): 61–64, ill.







## × *Astroworthia* ASPHODELACEAE

N. L. Meyer and G. F. Smith

× ***Astroworthia*** G. D. Rowley (Nation. Cact. Succ. J. 22(3): 74, 1967). — ***Aloioideae***.

**Incl.** × *Apworthia* Von Poellnitz (1943).

**Incl.** × *Astrolista* Molteno & Figueiredo (2017).

= *Astroloba* × *Haworthia*. Since the dismantling of *Haworthia* s.l. is increasingly accepted, and the parentage of the hybrid treated below involves a taxon segregated to the genus *Tulista*, the recently published × *Astrolista* is available for use (Smith & al. 2017).

In addition to the taxon treated below, Mays (2009: 45) describes and illustrates a further named cultivar of unknown parentage.

× ***A. bicarinata*** (Haworth) G. D. Rowley (Nation. Cact. Succ. J. 28(1): 7, 1973). **Type:** K [neo — icono: undated drawing by T. Duncanson]. — **Distr:** RSA (Western Cape: Montagu, Swellendam). **I:** Groen (1987: as *A. skinneri*).

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≡ *Apicra bicarinata* Haworth (1819) ≡ *Aloe bicarinata* (Haworth) Schultes & Schultes *fil.* (1829) ≡ *Astroloba bicarinata* (Haworth) Uitewaal (1947) ≡ *Haworthia bicarinata* (Haworth) Parr (1971) ≡ *Tulista* × *bicarinata* (Haworth) G. D. Rowley (2013) ≡ × *Astrolista bicarinata* (Haworth) Molteno & Figueiredo (2017); **incl.** *Apicra skinneri* A. Berger (1908) ≡ *Haworthia skinneri* (A. Berger) Resende (1943) ≡ *Astroloba skinneri* (A. Berger) Uitewaal (1947) ≡ × *Astroworthia bicarinata* nvar. *skinneri* (A. Berger) G. D. Rowley (1973) ≡ × *stroworthia skinneri* (A. Berger) Groen (1987); **incl.** *Apicra bullulata* Uitewaal (1938) (*nom. illeg.*, Art. 53.1); **incl.** *Haworthia olivettiana* Parr (1971).

To 30 cm tall; **L** in 5 straight rows to irregularly imbricate, 33–51 × 17–25 mm, dull dark green, erect to suberect, tips curved upwards to outwards, tip marginate, mucro 0.3–2 mm, keel not always distinct, occasionally doubly keeled, vein lines usually absent, tubercles present, evenly distributed or sometimes in groups, ±0.5 mm Ø, few and irregularly scattered or more numerous and grouped in transverse rows; **Inf** lax racemes, 12–36 cm; **Fl** erect, white to yellowish with pale green midribs; **Ped** 3–9 mm; **Per** tube straight, 7–13 × 2.5–4.5 mm Ø, lobes 1.5–3 mm. — **Cytology:** 2n = 14.

This is the hybrid *Astroloba corrugata* × *Haworthia margaritifera* (Linné) Haworth which occurs naturally, e.g., in the Barrydale area (Bayer 2010, Smith & al. 2017).

## References

- Bayer, M. B. (2010) *Haworthia minima* 'opalina'. *Haworthiad* 24(3): 64–65, ills.
- Groen, L. E. (1987) *Astroloba* Uitew. *Succulenta* 66(3): 51–55, (4): 82–87, (5): 110–113, (7/8): 162–167, (9): 171–174, (12): 261–263, key, maps, ills., SEM-ills.
- Mays, H. (2009) Hybrids & cultivars of the succulent *Asphodelaceae*. Volume 1. *Aloe*, *Astroloba*, *Bulbine*, *Gasteria* & nothogenera. St. Michaels on Wyre (GB): Harry Mays.
- Smith, G. F. [ & al. 2017], Figueiredo, E. & Molteno, S. (2017) × *Astroloba* Molteno & Figueiredo (*Asphodelaceae*): A new name for the South African endemic nothogenus *Astroworthia*. *Bradleya* 35: 195–200, ills. <https://doi.org/10.25223/brad.n35.2017.a22>



## × Bayerara ASPHODELACEAE

U. Eggli

× **Bayerara** D. M. Cumming (Haworthiad 13(1): 20, 1999). — *Aloioideae* — **Lit:** Cumming (1999). **Etym:** For Martin Bruce Bayer (\*1935), South African agricultural entomologist, succulent plant enthusiast and gardener, and former curator of the Karoo National Botanic Gardens, Worcester, RSA, specialist on *Haworthia*; and suffix '-ara', indicating plurigeneric hybrids.

≡ *Aloe* × *Gasteria* × *Haworthia*. The only known combination (with a *Haworthia* × *Gasteria* hybrid as one parent and a complex interspecific

*Aloe* hybrid as the other parent) is the cultivar 'Triple Chance' (Mays 2009: 46, with ills.).

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### References

- Cumming, D. M. (1999) New nothogenera proposed for four trigeneric hybrids within *Aloaceae*. *Haworthiad* 13(1): 20–21.
- Mays, H. (2009) Hybrids & cultivars of the succulent *Asphodelaceae*. Volume 1. *Aloe*, *Astroloba*, *Bulbine*, *Gasteria* & nothogenera. St. Michaels on Wyre (GB): Harry Mays.

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## Bulbine ASPHODELACEAE

E. Van Jaarsveld and P. I. Forster

**Bulbine** Wolf (Gen. Pl., 84, 1776). **Type:** *Anthericum frutescens* Linné. — **Asphodeloideae** — **Lit:** Baijnath (1977: monograph); Watson (1986a: cytology); Watson (1986b: cytology); Watson (1987: flora Australia); Kativu (1996: Flora Zambesiaca area); Kativu (2001: Flora Zambesiaca); Jaarsveld & Wyk (2005: key to cliff-dwelling species); Williamson (2016: illustrations diversity). **Distr:** S Africa (mostly RSA), Australia. **Etym:** Lat., an onion-like plant (from Lat. 'bulbus', bulb).

**Incl.** *Blephanthera* Rafinesque (1837). **Type:** not designated.

**Incl.** *Nemopogon* Rafinesque (1837). **Type:** *Nemopogon glaucum* Rafinesque.

**Incl.** *Bulbinopsis* Borzi (1897). **Type:** not designated.

**Incl.** *Jodrellia* Baijnath (1978). **Type:** *Jodrellia macrocarpa* Baijnath.

Plants perennial (rarely annual), caulescent or acaulescent, deciduous to evergreen, dwarf

succulent shrublets, often geophytic with tuberous or rhizomatous base (caudex), solitary or dividing to form dense groups; tuber very variable, depressed to rounded or oblong, often lobed; **L** very variable, terete to flattened, firm to softly succulent, glabrous or hairy, rosulate or rarely distichous, green to glaucous, sometimes with translucent lines or windows, often surrounded at the base by bristles, margin entire, ciliate or minutely denticulate, interior tissue uncoloured; **Inf** racemose, few- to many-flowered, lax or dense, cylindrical to corymbose, erect; peduncle ebracteate, smooth; fertile **Bra** small, membranous; **Fl** actinomorphic or rarely slightly zygomorphic due to the asymmetrical or divergent placement of stamens and style; **Per** stellate, spreading, rarely  $\pm$  connivent,  **Tep** 6 in 2 series, free, often becoming reflexed, mostly yellow, the outer smaller; **St** 6; **Fil** bearded, yellow, rarely orange; **Anth** dorsifixed, introrse; **Ov** ovoid to globose, 3-locular; **Sty** terete; **Sti** capitate; **Fr** 3-locular loculicidal globose capsules; **Se** blackish, flat, angular, oblong to rounded in outline.

A genus (here covered in its entirety) of 84 species occurring in Africa and Australia with the greatest diversity in the SW Cape (most species here are deciduous geophytes). The genus shows a large diversity of growth forms with leaves varying from grass-like to almost globose and highly succulent, and characters for floral bracts, flowers, stamens and esp. seeds show a surprising diversity (Williamson 2016). According to the molecular studies by Devey & al. (2006), *Jodrellia* is

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imbedded within *Bulbine* and should be included as synonym (Boatwright & Manning 2010). In a preliminary note about on-going phylogenetic studies, Boatwright & al. (2015) report that the genus is monophyletic, and that the Australian species are clearly embedded within. Some major clades retrieved by these authors are said to conform to informal groups based on morphological characters. The position of the Australian species imbedded within the genus is in line with the cytological data at hand: The basic chromosome number of the African species is  $x = 7$ , while the Australian species have  $x = 12$ , explainable by a polyploidy event followed by reduction (Moore & al. 2016).

*Bulbine* is related to *Bulbinella* (1 succulent species) and *Trachyandra*, but is distinguished from these by the presence of bearded filaments. The hairs responsible for the bearded appearance of the filaments are outgrowths of single epidermal cells, and are probably exuding volatile oils for pollinator attraction (Naidoo & al. 2011). Vaughton & al. (2008) also suppose that the bearded filaments serve for pollinator attraction, and this might be of special importance as these authors described the flowers of their study species, *B. vagans* as nectarless. Duffy & Johnson (2015) experimentally confirm the importance of the staminal hairs for pollinator attraction for *B. abyssinica*, which is pollinated by a native honeybee.

Several species are traditionally used as medicinal plants, and are especially valued for their wound-healing properties. Pather & al. (2011) have been able to experimentally verify these properties for *B. frutescens* and *B. natalensis*, and Coopooosamy (2011) has found antibacterial activity in four species.

*Bulbine* is a very variable group that is easily propagated by seeds or divisions. The plants are fast-growing (though somewhat delicate at least in the N hemisphere) and attractive garden and container subjects. Some species show very attractive leaf markings and  $\pm 30$  species are found cultivated (see Smale (2002) for a selection of more commonly cultivated taxa). Flowering is hysteranthous or synanthous. The caulescent *B. frutescens* is frequently cultivated as a ground cover in S Africa.

[Editorial note: The texts for most of the Australian species were authored by P. I. Forster for ed. 1, and have been updated for this revised edition by the editor, as shown in the individual authorship attributions for the species.]

The following names are of unresolved application but are referred to this genus: *Bulbine adnutans* Schultes (1829) (*nom. inval.*, Art. 34.1b); *Bulbine elongata* Schlechter ex Von Poellnitz (1944); *Bulbine nigra* Schinz (1902); *Bulbine patersoniae* Schönland (1919) (*nom. inval.*, Art. 32.1d); *Bulbine witputzii* hort. (s.a.) (*nom. inval.*, Art. 29.1).

**B. abyssinica** A. Richard (Tent. Fl. Abyss. 2: 334, t. 97, 1851). **Type:** Ethiopia (*Quartin-Dillon & Petit* 177 [holo?, K]). — **Distr:** NE Africa (Ethiopia, Somalia) to N and E RSA; grassland, savanna, and degraded bushland, 250–2000 m, flowering in early summer. **I:** Sebsebe Demissew & Nordal (2010: 121–122).

**Incl.** *Bulbine xanthobotrys* Engler & Gilg (1903); **incl.** *Bulbine asphodeloides* var. *filifolioides* De Wildeman (1909); **incl.** *Bulbine huilensis* Von Poellnitz (1943); **incl.** *Bulbine latitepala* Von Poellnitz (1943); **incl.** *Bulbine asphodeloides* var. *monticola* Von Poellnitz (1944); **incl.** *Bulbine decurvata* Peter ex Von Poellnitz (1944); **incl.** *Bulbine hamata* Peter ex Von Poellnitz (1944).

Evergreen, acaulescent, to 50 cm tall; **R** yellow, fleshy, terete; **L** rosulate, green, 15–50, linear, soft, 8–20  $\times$  0.4–0.6 cm, upper face flat, lower face convex, apex acuminate; **Inf** 1–5, densely flowered, to 35 cm tall with flowers crowded in the upper  $\frac{1}{4}$ ; peduncle terete, 3 mm  $\varnothing$ ; **Bra** linear-lanceolate, 11–12  $\times$  1.5 mm; **Ped** terete, 1.5–3 mm; **Per** spreading, stellate, yellow; **OTep** lanceolate, cymbiform, 10  $\times$  5 mm; **ITep** 9  $\times$  6 mm, obtuse; **St** 6 mm; **Fil** densely bearded in the upper  $\frac{1}{3}$ ; **Anth** 1 mm, oblong; **Ov** ovoid, 3 mm long; **Sty** erect, terete, 5 mm; **Fr** ovoid, 5 mm; **Se** grey-black, 3 mm.

Newton (2011: 4) reports that this species is used in a similar way as *Aloe vera* in East Africa to treat skin problems. According to a preliminary note by Boatwright & al. (2015), this widespread and variable species is not monophyletic in its

current circumscription and in need of further study. — [E. Van Jaarsveld]

**B. alata** Baijnath (Brunonia 1(1): 117–120, ill., 1978). **Type:** Australia, South Australia (Hill 714 [BM]). — **Distr:** Australia (Western Australia, Northern Territory, South Australia, Queensland, New South Wales, NW Victoria); flood plains, sandy soil or exposed stony hillsides. **I:** Kapitany (2007: 26–27).

≡ *Bulbinopsis alata* (Baijnath) G. M. Cunningham & al. (1981) (*nom. inval.*, Art. 33.4); **incl.** *Bulbine semibarbata* var. *depilata* J. M. Black (1932) ≡ *Bulbinopsis semibarbata* var. *depilata* (J. M. Black) H. Eichler (1965).

Annual succulent herbs without caudex; **R** fibrous; **L** 3–10, linear to subulate, channelled, 8–12 cm, 1–2.5 mm wide, glaucous; **Inf** several to many, erect, peduncle terete; **Ped** 4–17 mm at fruiting time, erect; **Tep** 3–5 mm, yellow; **St** 3 short, 3 long, ± erect and closely bunched; **Fil** with clavate hairs below the apex; **Anth** yellow, horizontally arched after dehiscence; **Ov** with 2 ovules per locule; **Sty** erect, 1–1.5 mm; **Fr** globose, 4–9 mm; **Se** with membranous wing.

The species hybridizes with *B. semibarbata* in contact zones, and *B. semibarbata* var. *depilata* (listed as synonym here) likely is based on such a hybrid, probably a back-cross with *B. alata*. — [P. I. Forster & U. Eggli]

**B. alooides** (Linné) Willdenow (Enum. Pl. Hort. Reg. Berol., 372, 1809). **Type:** [lecto — icono]: Dillenius, Hort. Eltham., 312, t. 232: fig. 100, 1732. — **Distr:** RSA (Western Cape, Eastern Cape, Limpopo, Gauteng, KwaZulu-Natal); widespread in summer- and winter-rainfall regions (grassland and Renosterveld), 10–2155 m, flowering in winter and spring.

≡ *Anthericum alooides* Linné (1753); **incl.** *Bulbine acaulis* Linné (1762); **incl.** *Anthericum aloifolium* Salisbury (1796); **incl.** *Bulbine macrophylla* Salm-Dyck (1834); **incl.** *Bulbine platyphylla* Baker (1892).

Solitary shortly caulescent geophytes 6–25 cm tall; tuber depressed, 5- to 7-lobed, brownish, to 4 cm Ø, lobes to 9 mm Ø at the base, tapering; **R** terete; stem erect to 3 cm with a ring of bristles

at the base surrounding the leaves; **L** 2–4, unequal, 6–25 × 0.8–1.2 cm, opposite, erect, light green, amplexicaul, linear-lanceolate, faintly striated, upper face channelled, lower face convex, apex acute; **Inf** 1–2, to 40 cm, synanthous, with up to 35 flowers; peduncle biconvex, to 5 mm Ø at the base; **Fil** stellate, spreading, ± 20 mm Ø, yellow; **Bra** to 4 mm, ovate-acuminate, 3–4 mm wide at the base, clasping; **Ped** 10–15 mm; **Tep** becoming reflexed; **OTep** elliptic, 10 × 2 mm, acute; **ITep** obovate, 9 × 5 mm, obtuse; **St** 7 mm; **Anth** yellow, oblong, 1 mm; **Ov** elliptic-oblong, 2 mm; **Sty** curved, yellow, 5 mm; **Fr** oblong, 10 × 4 mm; **Se** oblong, 3 × 1.5 mm, grey-black.

The **lectotype** listed above is **formally designated here**, but was previously listed as such, though ineffectively under the Code, in the first edition of this handbook. — [E. Van Jaarsveld]

**B. alveolata** S. A. Hammer (Cact. Succ. J. (US) 75(6): 251–253, ill., 2003). **Type:** RSA, Northern Cape (*Bruyns* 6015 [BOL]). — **Distr:** RSA (Northern Cape: Knersvlakte); crevices of shale.

Fast growing, acaulescent, clustering, dwarf; tuber ovoid, 10 × 10 mm, with several fat radiating finger-like extensions, interior tissue reddish-white, tunics pale pinkish-brown, shiny; **L** ± 10–20, horizontally arranged in a tight rosette appressed to the ground, 1.2 cm × 2 mm, linear-lanceolate, apex often necrotic, with a mucro, surface pale silvery-green to greyish-green or reddish-grey (in full sun), upper face concave, alveolate, sparkling, with 3–5 prominent longitudinal whitish veins, rugulose, margins glabrous, slightly repand; **Inf** 2–7, peduncle erect, to 6 cm, raceme with up to 30 flowers; **Fil** 1–2 open per day, strongly sweet-scented; **Bra** whitish, 1 × 1.5 mm, clasping, acute, with a brownish keel and elongate awl; **Ped** 3–8 mm; **Tep** strongly reflexed, orange-yellow; **OTep** 7 × 1.5 mm; **ITep** 9 × 2.5 mm; **St** 4 mm, bearded; **Ov** globose, 2 mm Ø; **Sty** 5 mm; **Fr** globose; **Se** black, shiny, 1.2 × 0.8 mm, rugose. — [E. Van Jaarsveld]

**B. angustifolia** Von Poellnitz (Feddes Repert. Spec. Nov. Regni Veg. 52(1): 112, 1943). **Type:**

Namibia (*Dinter* 4404 [B]). — **Lit:** Watson (1987). **Distr:** Namibia, RSA (Northern Cape, Limpopo, Gauteng, Free State), Swaziland; grassland and savanna, 850–1325 m, spring-flowering.

**Incl.** *Bulbine tortifolia* I. Verdoorn (1947).

Plants solitary, to 35 cm tall; **R** fleshy, terete; **L** rosulate, amplexicaul, to 20 per rosette, shiny green, ascending, 3.5 × 0.5 cm, linear-terete and twisted, flattened; **Inf** solitary, to 80 cm with flowers in the upper ½; peduncle terete, 6 mm Ø at the base; **Bra** 12–15 mm, membranous, linear-acuminate, clasping; **Ped** 5–10 mm; **Per** stellate, 12–14 mm Ø, yellow; all **Tep** ovate-lanceolate, 6 × 4 mm, obtuse; **St** 5 mm; **Anth** cream; **Ov** oblong-globose, 2.5 × 2 mm; **Sty** erect, yellow, 2.5 mm; **Fr** subglobose, 10 mm Ø; **Se** grey-black, 3 mm. — [E. Van Jaarsveld]

**B. annua** (Linné) Willdenow (Enum. Pl. Hort. Reg. Berol., 372, 1809). **Type:** not typified. — **Distr:** RSA (Northern Cape, Western Cape); Strandveld and coastal Fynbos vegetations, 15–775 m, winter-growing/spring-flowering.

≡ *Anthericum annuum* Linné (1753).

Acaulescent rosulate annuals or weak perennials, 6–20 cm; **R** terete, to 1 mm Ø; **L** 4–35, linear, subterete, amplexicaul at the base, ascending to spreading, 1.8–18 cm, softly succulent, upper face flat, lower face convex, apex acute; **Inf** 11–25 cm, ascending, flowers in the upper ½; peduncle terete, 3 mm Ø at the base; **Bra** ovate-acuminate, 5 × 2 mm, deltoid-acuminate, membranous; **Per** stellate, 12–13 mm Ø, yellow; **OTep** elliptic, 6 × 2 mm; **ITep** 5 × 3 mm, obtuse; **Ov** globose, 1.5 mm Ø; **Sti** 3 mm; **Fr** globose, 5–6 mm Ø; **Se** angular, 2 mm Ø. — [E. Van Jaarsveld]

**B. asphodeloides** (Linné) Sprengel (Syst. Veg. 2: 85, 1825). **Type:** LINN 432.11 [lecto, ex cult. Hort. Uppsala]. — **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape, Limpopo, North West, Gauteng, Free State, KwaZulu-Natal), Swaziland; Renosterveld (Fynbos biome), 3–2310 m, flowers in mid-winter and spring.

≡ *Anthericum asphodeloides* Linné (1753) ≡ *Phalangium asphodeloides* (Linné) Kuntze (1891); **incl.** *Anthericum altissimum* Miller

(1768) ≡ *Bulbine altissima* (Miller) Fourcade (1932); **incl.** *Anthericum longiscapum* Jacquin (1787) ≡ *Bulbine longiscapa* (Jacquin) Willdenow (1809); **incl.** *Anthericum succulentum* Salisbury (1796); **incl.** *Bulbine mettinghii* Tenore (1831); **incl.** *Bulbine pallida* Baker (1876); **incl.** *Bulbine crocea* L. Guthrie (1928); **incl.** *Bulbine dielsii* Von Poellnitz (1944).

Perennials, dividing to form dense groups 20 cm tall and Ø with up to 15 heads; **R** fleshy, brownish-orange, terete, 1.5 mm Ø, tips yellow; stem short, to 2 cm; **L** rosulate, to 10, amplexicaul, green to reddish-green, ascending, linear, firm, 8–20 cm × 3–4 mm, upper face flattened, lower face convex, surface with fine longitudinal grooves, margin minutely dentate, apex acute; **Inf** solitary, 30–45 cm, ascending to spreading with flowers in the upper ½ and 3–10 mm apart; peduncle 2 mm Ø at the base, terete; **Bra** 6–7 × 1.5 mm, membranous, deltoid-acuminate, clasping; **Ped** 10–13 mm; **Per** stellate, yellow; **OTep** elliptic-lanceolate, 8 × 3 mm, obtuse; **ITep** broadly ovate, 8 × 5 mm, obtuse; **St** 5–6 mm; **Anth** yellow, oblong; **Ov** globose, 2 mm Ø, yellowish-green, grooved; **Sty** erect, yellow, 5 mm; **Fr** ovoid-globose, 6 × 5 mm; **Se** grey-black, 2 × 1.5 mm. — [E. Van Jaarsveld]

**B. brunsvigiifolia** Baker (in Thiselton-Dyer, Fl. Cap. 6: 366–367, 1896). **Type:** RSA, Northern Cape (*Drège* 2674 [K]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo and Renosterveld vegetations.

Rosulate geophytes, solitary or forming small groups; tuber depressed, to 4.5 cm Ø and 3 cm high with numerous **Bri** to 3 cm surrounding the leaves; **R** terete, to 4 mm Ø; **L** oblong-lorate, attenuate, to 10 × 4.5 cm, flat, margin ciliate, apex obtuse, minutely cuspidate; **Inf** 30–75 cm with flowers in the upper ½; peduncle 1 cm wide at the base; **Bra** membranous, ovate-lanceolate, 8–15 × 2 mm; **Ped** 1–2 cm; **Per** stellate, yellow; **OTep** lanceolate, 10–12 × 2.5 mm; **ITep** ovate, 7 × 4 mm; **St** 7 mm; **Ov** 3 mm, ovoid; **Sty** 5 mm; **Fr** oblong, 15 × 5 mm; **Se** oblong, 4.5 × 1.5 mm.

Sometimes treated as synonym of *B. latifolia*, but a distinct winter-rainfall taxon. — [E. Van Jaarsveld]

**B. bruynsii** S. A. Hammer (Cactus & Co. 2(4): 6–7, ills., 1998). **Type:** RSA, Northern Cape (*Bruyns* 6126 [BOL]). — **Distr:** RSA (Northern Cape: Namaqualand); Succulent Karoo, to 600 m.

Deciduous erect soft succulent herbs 6–12 cm tall; tuber napiform, to 4 × 1 cm, with brown skin, producing offshoots from secondary tubers; **L** 2, soft, erect, semitranslucent, transversely banded red and green, 1–6 × 1–1.8 cm, oblong-ovate and shaped like a Chinese lantern (horizontally ridged) and tapering at the tip; second **L** subulate; **Inf** erect; peduncle slender, to 20 cm × 1–2 mm; **Fl** 8–20, sweetly scented; **Bra** triangular, membranous, <2 mm; **Ped** to 15 mm; **OTep** narrowly linear, 1.2–1.5 mm wide, bright yellow; **ITep** ovate, to 4 mm wide, yellow with a bright green midstripe, strongly crinkled, shiny; **Fil** to 6 mm; **Anth** 1 mm; **Ov** broadly pear-shaped, bright green; **Sty** 6 mm; **Sti** knob-like; **Fr** globose; **Se** 1.6 × 0.8 mm, dull black, narrowly triangular. — [E. Van Jaarsveld]

**B. bulbosa** (R. Brown) Haworth (Revis. Pl. Succ., 33, 1821). **Type:** Australia, New South Wales (*Brown* s.n. [BM]). — **Distr:** Australia (Queensland, Western Australia, New South Wales, Victoria, Tasmania); usually damp places in woodland, grassland and sclerophyll forests. **I:** Cunningham & al. (1981: 183).

≡ *Anthericum bulbosum* R. Brown (1810) ≡ *Phalangium bulbosum* (R. Brown) Kuntze (1891) ≡ *Bulbinopsis bulbosa* (R. Brown) Borzi (1897); **incl.** *Bulbine australis* Sprengel (1825); **incl.** *Blephanthera depressa* Rafinesque (1837); **incl.** *Blephanthera hookeri* Rafinesque (1837); **incl.** *Bulbine subbarbata* Steudel (1840); **incl.** *Bulbine fraseri* Kunth (1843).

Perennial succulent herbs with bulb-shaped caudex; **R** succulent; **L** 3–10, linear, channelled, 4.5–48 cm × 1.5–1.8 mm wide, green, rarely glaucous; **Inf** 1–2, 20–50 cm, terete, erect; **Ped** 10–28 mm at fruiting time, not drooping at the end; **Tep** 9–22 mm, yellow; **St** ± equal, closely bunched or spreading; **Fil** with clavate or acute hairs at the tip; **Anth** yellow, ± basifixed, all or some remaining erect after dehiscence and sometimes twisting about their vertical axis; **Ov** with 3–8 ovules per locule; **Sty** deflexed, 2.5–9 mm; **Fr**

globose to obovate, 4–7 mm; **Se** smooth, slightly tuberculate or ridged.

Vaughton & Ramsey (2010) found that the species is self-compatible, but that selfing results in fewer seeds per fruit than outcrossing (but see *B. vagans*). — [U. Eggli]

**B. capensis** Baijnath *ex* G. Williamson (Aloe 43(4): 91–92, ills., 2007). **Type:** RSA, Western Cape (*Williamson* 5982 [NBG]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo, in sandy loam with quartz pebbles.

Acaulescent solitary herbs to 55 cm tall (incl. inflorescence); tuber rounded and broadly pyramidal, 20 mm high and 35 mm broad at the base, clothed with up to 10 imbricate, semi-lunate storage scales to 10 mm broad which form a circular sheath; **R** widening at the base, arising from scale indentations; **L** 4–8 in a basal rosette, dark green, glabrous with 6 main veins, ascending, to 26 cm × 4–8 mm and 4 mm thick towards apex, base subcylindrical and surrounded by fibrous leaf remains; **Inf** 1–3, peduncle ± 29 cm, 3–4 mm Ø, raceme to 17 cm with 60–80 flowers; **Bra** 6 × 2.5 mm, base broadly ovate; **Ped** 10 mm; **Fl** porrect; **Tep** reflexed; **OTep** 10 × 2.5 mm, greenish-yellow, narrowly elliptic; **ITep** 10 × 6 mm, dark yellow, ovate, margin crenate; **St** porrect, 7 mm, with glandular hairs; **Sty** ± 7 mm; **Fr** 6 × 4 mm; **Se** 2.2–2.8 × 1.5 mm, dark brown, pyramidal. — [E. Van Jaarsveld]

**B. capitata** Von Poellnitz (Feddes Repert. Spec. Nov. Regni Veg. 53(1): 37, 1944). **Type:** RSA, Mpumalanga (*Wilms* 1508 [B]). — **Distr:** Namibia, RSA (Limpopo, Gauteng, Mpumalanga, Free State, KwaZulu-Natal), Swaziland, Botswana, Moçambique; grassland and savanna, 230–1850 m, spring-flowering.

**Incl.** *Bulbine asphodeloides* var. *otaviensis* Von Poellnitz (1943) ≡ *Bulbine otaviensis* (Von Poellnitz) Sölch (1960) (*nom. inval.*, Art. 30.5, 34.1c); **incl.** *Bulbine hydenburgensis* Von Poellnitz (1944); **incl.** *Bulbine stenophylla* I. Verdoorn (1948).

Evergreen, rosulate, clustering, short-stemmed; **R** yellow, fleshy, terete; stems to 5 cm; **L** green, 20 per stem, linear, subterete, 7–20 cm × 2 mm, upper face flat to slightly channelled, lower

face convex, attenuate, apex acute; **Inf** densely flowered to 20 cm, flowering head subcorymbose; peduncle terete, 3 mm  $\varnothing$  at the base; **Bra** triangular-lanceolate, 3  $\times$  2 mm; **Ped** terete, 15 mm; **FI** scented, spreading, stellate, yellow; **OTep** oblong-ovate, 7  $\times$  3 mm; **ITep** 7  $\times$  4 mm, obtuse; **St** 6 mm; **Fil** densely bearded in the upper  $\frac{1}{2}$ ; **Anth** 1 mm, oblong; **Ov** ovoid, 2 mm; **Sty** erect, terete, 3.5 mm; **Fr** ovoid. — [E. Van Jaarsveld].

**B. caput-medusae** G. Williamson (Aloe 32 (3–4): 80–83, ills., 1995). **Type:** Namibia, Witputz (*Williamson* 4208 [NBG]). — **Distr:** S Namibia; desert, 500–1500 m, flowers mid-winter to late spring.

Perennials, dividing to form clusters with up to 8 heads; **R** dense, fibrous, matted, to 20 cm; **L** up to 15 in dense clusters arising from dense white fibrous sheaths, 4 cm  $\times$  2 mm, channelled to 1 mm below, terete in the upper  $\frac{1}{2}$  to  $\frac{2}{3}$ , spreading, strongly circinate and contorted, shiny dark green, minutely sparsely granulate; **Inf** 1–2 per head; peduncle green, suberect to spreading, to 8 cm; raceme 4–6 cm, crowded, with up to 20 flowers; **Bra** membranous, triangular, 1.2 mm; **Ped** 15 mm; **Per** stellate; **OTep** light canary yellow, 9  $\times$  1.8 mm; **ITep** elliptic, 8  $\times$  2 mm; **Fil** bearded with **Ha** 5 mm long; **Ov** globose, dark green; **Sty** slightly curved, 5 mm; **Fr** rounded, to 12 mm long; **Se** black, oblong with contorted projecting ridges, 5  $\times$  4 mm. — [E. Van Jaarsveld]

**B. cepacea** (Burman *fil.*) Wijnands (*Bothalia* 21(2): 157, 1991). **Type:** [icono]: Hermann, Horti Acad. Lugd.-Bat. Cat. t. 467, 1687. — **Distr:** RSA (Western Cape); well-drained Renosterveld vegetation, 220–550 m, autumn-flowering.

$\equiv$  *Ornithogalum cepaceum* Burman *fil.* (1768); **incl.** *Ornithogalum tuberosum* Miller (1768)  $\equiv$  *Bulbine tuberosa* (Miller) Obermeyer (1976); **incl.** *Anthericum pugioniforme* Jacquin (1793)  $\equiv$  *Bulbine pugioniformis* (Jacquin) Link (1821); **incl.** *Anthericum latifolium* Jacquin (1793) (*nom. illeg.*, Art. 53.1); **incl.** *Bulbine bisulcata* Haworth (1827); **incl.** *Bulbine parviflora* Baker (1896); **incl.** *Bulbine cataphyllata* Von Poellnitz (1944); **incl.** *Bulbine inexpectata* Von Poellnitz (1944); **incl.**

*Anthericum bisulcata* Haworth *ex* Baijnath (1977) (*nom. inval.*, Art. 61.1).

Hysteranthous tuberous geophytes; tuber depressed, globose on top, up to 5 cm high and 10 cm  $\varnothing$ ; **R** fleshy, terete, to 8 mm  $\varnothing$ , radiating from lower margin of tuber, tapering; stem very short with bristles at the base; **L** subterete, rosulate, 4–15, unequal,  $\pm$  linear, 6–25  $\times$  0.3–1 cm  $\varnothing$ , spirally arranged, erect, green, amplexicaul, faintly striated, upper face of lower leaves flat, lower face convex, apex acute; **Inf** 1–2, 40–70 cm; peduncle 5 mm  $\varnothing$  at the base, **FI** numerous in the upper  $\frac{1}{2}$ , stellate, spreading,  $\pm$  20 mm  $\varnothing$ , yellow; **Bra** 7  $\times$  3–4 mm, triangular-acuminate, clasping; **Ped** 10–15 mm; **OTep** elliptic, 9  $\times$  2.5 mm, acute; **ITep** obovate, 8  $\times$  3.5 mm, obtuse; **St** 7 mm; **Anth** yellow, oblong, 1 mm; **Ov** globose, 2 mm  $\varnothing$ ; **Sty** 5 mm; **Fr** narrowly ovoid, 8–10  $\times$  4 mm; **Se** dark brown, oblong, winged, to 7 mm. — [E. Van Jaarsveld]

**B. coetzei** Obermeyer (*Bothalia* 9(2): 343–344, 1967). **Type:** RSA, Mpumalanga (*Coetzee* s.n. [PRE 30026]). — **Distr:** RSA (KwaZulu-Natal, Mpumalanga), Swaziland; grassland, 1240–2015 m.

Base tuberous, 2.5  $\times$  1.5 cm; **R** terete, succulent, spreading; **L** rosulate,  $\pm$  7, ascending, linear, terete, to 50  $\times$  1 cm, amplexicaul and sheathing below forming a short neck 2 cm long, upper face grooved, tip acuminate; **Inf** 1, to 50 cm, flowers in the upper  $\frac{1}{3}$ , dense; peduncle terete; **Bra** to 25 mm, membranous, linear-acuminate, aristate; **Ped** to 25 mm; **Per** stellate, to 23 mm  $\varnothing$ , yellow, reflexed; **Tep** linear-lanceolate,  $\pm$  6  $\times$  1 mm, obtuse; **Ov** ovoid, 7 mm, truncate at the apex; **Sty** erect; **Fr** obovoid, 4 mm  $\varnothing$ ; **Se** black, angled, 2 mm. — [E. Van Jaarsveld]

**B. crassa** D. I. Morris & Duretto (*Muelleria* 22: 93–96, 2006). **Type:** Australia, Tasmania (*Harris* s.n. [HO 312703]). — **Lit:** Moore & al. (2016: cytology). **Distr:** S Australia (islands of S Victoria and N Tasmania); salt-influenced coastal shrubland and tussock grassland.

Perennial tufted herb, offsetting around the flowering shoot; **R** fleshy; **L** several, erect, flat with bulging lower face or channelled, to 50 cm,



basally to 2.5 cm wide, fleshy with abundant clear mucilage, bright green, only slightly glaucous; **Inf** solitary, to 60 cm, fertile part to 30 cm; **Bra** lanceolate-acute,  $\pm 7$  mm; **Ped** to 10 mm; **Fl** stellate,  $\pm 25$  mm  $\varnothing$ , yellow; **Tep** 12–13 mm, with green midvein; outer **St**  $\pm 7$  mm, naked or with few to many hairs at the filament tip, inner **St**  $\pm 9$  mm, with a dense beard of clavate hairs near the filament tip; **Ov** globose,  $\pm 2$  mm  $\varnothing$ ; **Sty** 2–2.8 mm, slightly up-curved; **Sti** shortly 3-lobed; **Fr** 5–6.5 mm  $\varnothing$ ; **Se** 3–3.5 mm, 2–3 per locule, black, wrinkled, narrowly winged.

According to the protologue, plants were traditionally identified as a robust form of *B. semi-barbata*, but the overall appearance is more similar to *B. glauca*. On the basis of karyotype data, Moore & al. (2016: 215) argue that *B. crassa* has more affinities with *B. bulbosa*, rather than with *B. glauca*. — [U. Eggli]

**B. cremnophila** Van Jaarsveld (Aloe 36(4): 72, ills., 2000). **Type:** RSA, Eastern Cape (*Van Jaarsveld* 7238 [NBG]). — **Distr:** RSA (Eastern Cape); shady quartzitic sandstone cliff-faces, mid-summer-flowering.

Plants dwarf, rosulate, clustering, to 8 cm tall and 10 cm  $\varnothing$  with 3–8 heads; **R** grey, fleshy, terete; **L** 5–7 in rosettes, curving downwards, linear-triangular to linear-lanceolate, 6–10  $\times$  1–1.5 cm, upper face channelled above, cymbiform below, glaucous, apex acute, mucronate; **Inf** 1, to 30 cm, 17- to 35-flowered in the upper  $\frac{1}{2}$ ; peduncle 2 mm  $\varnothing$  at the base, terete; **Bra** deltoid, acuminate, 5  $\times$  1 mm, clasping; **Fl** drooping; **Per** stellate, becoming reflexed,  $\pm 8$ –10 mm  $\varnothing$ ; **Ped** 15–18 mm; **Tep** pale orange-yellow; **OTep** elliptic, 7  $\times$  2 mm; **ITep** ovate to ovate-elliptic, 6  $\times$  2.5 mm, obtuse; **St** 5 mm; **Ov** globose, 1.5 mm  $\varnothing$ ; **Sty** erect, 6 mm; **Fr** ovoid, 3  $\times$  2.5 mm; **Se** 2 mm. — [E. Van Jaarsveld].

**B. dactylopsoides** G. Williamson (Aloe 41 (2–3): 32–35, ills., 2004). **Type:** RSA, Western Cape (*Williamson & Kritzinger* 6009 [BOL, NBG]). — **Distr:** RSA (Western Cape: Knersvlakte); quartz gravel flats in Succulent Karoo, spring-flowering.

Highly succulent geophytes, to 10 cm tall (excl. inflorescence); tuber ovoid to ellipsoid-elongate, 20  $\times$  15 mm, stoloniferous with radiating runners ending in bulbils; **L** distichous, 2–4, 3–8  $\times$  2.5–3 cm, upper  $\frac{2}{3}$  narrowly oval with a narrow adaxial gutter, lower  $\frac{1}{3}$  forming a funnel, surface with minute raised shiny granules; **Inf** to 30 cm, ascending, with up to 34 flowers; **Fl** horizontal, drooping after anthesis, sweetly scented; **Bra** triangular, to 14 mm; **OTep** 11  $\times$  3 mm, elliptic, obtuse, dark orange-yellow; **ITep** 12  $\times$  7 mm, ovate, canary-yellow; **Fil** 8 mm; **Ov** ovoid, 2 mm; **Sty** 8 mm; **Fr** 9–10  $\times$  4 mm; **Se** 2.8  $\times$  1.5 mm, narrowly pyramidal, shiny brownish-black. — [E. Van Jaarsveld]

**B. dewetii** Van Jaarsveld (*Haseltonia* 23: 54–55, ills. (pp. 53–55), 2017). **Type:** RSA, Western Cape (*Van Jaarsveld & Stander* 26953 [NBG]). — **Distr:** RSA (Western Cape); Fynbos vegetation, ledges on S-facing cliffs, in rock crevices, often among moss; flowers in late spring.

Dwarf acaulescent summer-deciduous geophytes; tuber ovate, somewhat stellately lobed, 10–15  $\times$  10–15 mm wide at the truncate base, with whitish tunics; **R** terete, radiating from the lobes, pinkish-brown, succulent, to 55 mm, at the base to 3 mm  $\varnothing$ , tapering; **L** 3–5, soft and fragile, somewhat glaucous when exposed, amplexicaul, forming a neck 5–10 mm long, above spreading-pendent, 2–3.3  $\times$  0.2–0.5 cm, subterete, linear, tapering, smooth, wrinkled when withering, glabrous, upper face channelled, lower face convex, faintly striate, translucent, older leaves withering, persistent and becoming tortuous, tip acuminate with a soft mucro; **Inf** 1–2 per plant, 12–24 cm, 8- to 14-flowered in the upper  $\frac{1}{3}$ , raceme 5–11 cm; **Bra** ovate-acuminate, translucent, 2–3  $\times$  0.75 mm, clasping; **Ped** ascending-spreading, 10–11 mm; **Per** stellate,  $\pm 14$ –15 mm  $\varnothing$ ; **OTep** 8  $\times$  2 mm, linear-lanceolate, pale yellow with a green to yellowish-green median stripe, subacute, abaxial face whitish; **ITep** ovate-lanceolate, 7  $\times$  3 mm; **St** 6–6.5 mm; **Fil** sparingly bearded from close to the base to the middle, glandular hairs yellowish-green, tips clavate; **Anth**  $\pm 0.8$  mm, yellow, pollen yellow; **Ov** subglobose, 6-grooved, white, 1.5 mm; **Sty** erect, to 5–6 mm; **Sti** minute; **Fr** subglobose,

2.5 mm  $\emptyset$ , ascending; **Se** 2 × 1.5 mm, grey-brown, minutely and deeply fissured, angular. — [E. Van Jaarsveld]

**B. diphylla** Schlechter *ex* Von Poellnitz (Feddes Repert. Spec. Nov. Regni Veg. 53(1): 40–41, 1944). **Type:** RSA, Western Cape (*Schlechter* 8202 [B]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo, quartz gravel flats, 100–650 m, flowers in mid-winter. **I:** Smale (2002).

Dwarf solitary caulescent geophytes to 7 cm tall; tuber 3- to 7-lobed, brownish, lobes ovoid, 5–10 mm, obtuse; **R** terete; stem erect to 5–20 mm tall with distinct maroon striations; **L** 2, unequal, sub-opposite, erect, light green, amplexicaul; lower **L** subterete, ovate-lanceolate, 3–5 × 1.5 cm, reticulate, upper face slightly channelled, lower face convex, apex acute; upper **L** linear-terete to ovate, 1.5–3 × 1–1.5 cm, channelled; **Inf** 1, 12–17 cm, 5- to 10-flowered; **Fl** spreading, ± 15 mm  $\emptyset$ , yellow; **Bra** to 2 × 1 mm, ovate-acuminate, clasping; **Ped** 1–1.5 cm; **Per** stellate, becoming reflexed; **OTep** lanceolate, 8 × 2 mm; **ITep** elliptic, 8 × 4.2 mm, obtuse; **St** 5 mm; **Anth** yellow, oblong, 0.5 mm; **Ov** ellipsoid-oblong, 1–2.5 mm; **Sty** erect, yellow, 5 mm; **Fr** and **Se** not seen. — [E. Van Jaarsveld]

**B. dissimilis** G. Williamson (Aloe 34(3–4): 70–72, *ills.*, 1997). **Type:** RSA, Northern Cape (*Williamson & Hammer* 5710 [NBG]). — **Distr:** RSA (Northern Cape: Springbok Distr.); ± 800 m.

Solitary acaulescent perennial geophytes; tuber to 3 × 2 cm, oblong to turnip-shaped, covered with brownish to blackish imbricate papery sheaths; **R** short, fleshy, tapering downwards, deltoid, to 1.5 × 1 cm; **L** subtended by 3 triangular acute sheathing papery **Bra** to 25 × 7 mm; **L** 3, erect, 13 × 1 cm, dark glaucous-green with powdery bloom, linear-triangular, upper face grooved; **Inf** erect, solitary, to 24 cm, raceme 8 × 2 cm; **Fl** 14–20, sweetly scented; **Ped** 7 mm; **Tep** spreading, becoming reflexed, dark orange-yellow with shiny luminous surface; **OTep** obovate, 7 × 4.5 mm; **St** 7 mm; **Ov** globose, green, 1 mm  $\emptyset$ ; **Sty** slender, 6 mm; **Fr** ovoid, 2.5 mm; **Se** shiny

black, oblong and triangular in cross-section, 2 × 1.2 mm. — [E. Van Jaarsveld]

**B. erectipilosa** G. Williamson (Aloe 38(1–2): 28, 2001). **Type:** RSA, Eastern Cape (*Williamson* 5928 [NBG]). — **Lit:** Williamson (2000: 37–40). **Distr:** RSA (Eastern Cape: near Jeffreys Bay); coastal grassland, flowers early summer.

≡ *Bulbine canaliculata* G. Williamson (2000) (*nom. illeg.*, Art. 53.1).

Small solitary geophytes; tuber ovoid, 10 × 15 mm; **R** orange-brown; **L** up to 5, to 18 × 0.8 cm, rosulate, erect, linear-lanceolate, bright and shiny green, acute from a broad base, upper face canaliculate, margins hyaline, finely ciliate in the lower part; **Inf** solitary, erect, to 22 cm, to 20-flowered; peduncle 1.2 mm  $\emptyset$  at the base, terete; **Bra** deltoid-acuminate, 5 × 3 mm; **Tep** recurved, shiny yellow; **OTep** elliptic, subacute, 6 × 1.8 mm; **ITep** ovate, 6 × 3.2 mm, tips obtuse; **St** projecting forwards in a cluster; **Ov** ovoid, 1.8 mm, bright green; **Sty** erect, 6 mm; **Sti** papillate; **Fr** and **Se** not seen.

Plants are rapidly and aggressively growing, and become weeds in collections. — [E. Van Jaarsveld]

**B. erumpens** S. A. Hammer (Cact. Succ. J. (US) 77(3): 128–129, *ills.*, 2005). **Type:** RSA, Northern Cape (*Hammer* 2565 [BOL]). — **Distr:** RSA (Northern Cape: Richtersveld); quartz-topped hillocks, autumn-flowering.

Solitary dwarf winter-active geophytes; tuber carrot-shaped, yellow-skinned, ± 30 × 6–8 mm; **L** 1–3, linear-lanceolate, to 6.5 × 0.2–0.4 cm, tapering to a sharp point, firm, covered with a powdery bloom, terete in the upper ½, upper face flattened towards the base, slightly grooved, leek-green, longitudinally striate, smooth; **Inf** solitary, erect, appearing in autumn before the leaves, with 15–30 flowers; **Fl** 18 mm  $\emptyset$ , 1–3 opening at the same time, sweetly scented; **Ped** 10–15 mm; **Tep** bright yellow; **OTep** reflexed, margins undulate; **Fil** 8–10 mm, bearded; **Sti** 7–8 mm; **Fr** globose, 2 mm; **Se** 1.8 × 1.2 mm, flattened, blackish-grey. — [E. Van Jaarsveld]

**B. esterhuyseniae** Baijnath (South Afr. J. Bot. 53(6): 427–430, ill., 1987). **Type:** RSA, Western Cape (*Esterhuysen* 25,487 [BOL, K, PRE]). — **Distr:** RSA (Western Cape); Fynbos, quartzitic sandstones, 500–1000 m, flowers in mid-summer.

Dwarf solitary geophytes to 2.5 cm tall; tuber depressed, 4- to 5-lobed,  $\pm$  5 mm tall and 10–15 mm  $\varnothing$ ; **R** terete; **L** rosulate, 5–10, 0.5–3.5 cm  $\times$  0.5 mm, ascending, apex obtuse, surrounded at the base by 2–3 scales 2  $\times$  4 mm; **Inf** 1–2, 5–12 mm, 2- to 8-flowered; peduncle to 2 mm  $\varnothing$ , terete; **Fl** spreading, stellate,  $\pm$  8–10 mm  $\varnothing$ , yellow; **Bra** 2.5  $\times$  3 mm, ovate; **Ped** 10–14 mm, recurved; **OTep** elliptic, 6  $\times$  2 mm; **ITep** elliptic, 5  $\times$  2.5 mm, obtuse; **St** 4 mm; **Anth** yellow, oblong; **Ov** globose, 1 mm; **Sty** erect, yellow, 2 mm; **Fr** ovoid, 2 mm; **Se** 1.5 mm, blackish. — [E. Van Jaarsveld]

**B. fallax** Von Poellnitz (Feddes Repert. Spec. Nov. Regni Veg. 53(1): 41–42, 1944). **Type:** RSA, Northern Cape (*Schlechter* 11,019 [B]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo, quartz gravel flats, 200–600 m. **I:** Smale (2002). — Fig. 1.

Dwarf deciduous acaulescent rosulate solitary geophytes; tuber oblong, 3.5  $\times$  1.5 cm, brown, with a ring of bristles around the base of the rosette; **R** fleshy, terete; **L** densely arranged, up to 20, linear-lanceolate, to 9  $\times$  1.6 cm, green, with reticulate pattern, flat above, convex below, margin minutely ciliate, apex acute; **Inf** 1, to 25–33 cm; peduncle terete, 3 mm  $\varnothing$  at the base; **Bra** 1 cm, ovate-lanceolate, clasping; **Ped** 1.5–3 cm; **Fl** stellate, to 26 mm  $\varnothing$ , yellow; **Tep** lanceolate, 6–7 mm, obtuse; **St** 6–8 mm; **Sty** erect, terete, yellow; **Fr** oblong-ovoid, 8–12 mm; **Se** angled, black, 3 mm. — [E. Van Jaarsveld]

**B. favosa** (Thunberg) Schultes *fil.* (Syst. Veg. 7: 444, 1829). **Type:** RSA, Western Cape (*Thunberg* s.n. [K]). — **Lit:** Craib (2002). **Distr:** RSA (Western Cape, Eastern Cape, Gauteng, North West), Lesotho; flats and lower slopes in Fynbos and grassland, 50–2000 m, autumn-flowering.

$\equiv$  *Anthericum favosum* Thunberg (1800); **incl.** *Bulbine dubia* Schultes *fil.* (1829); **incl.** *Bulbine*



**Fig. 1** *Bulbine fallax*. (Copyright: E. Van Jaarsveld)

*filifolia* Baker (1876); **incl.** *Bulbine trichophylla* Baker (1876); **incl.** *Bulbine mayorii* Beauverd (1914); **incl.** *Bulbine rigidula* Schlechter *ex* Von Poellnitz (1944); **incl.** *Bulbine setifera* Von Poellnitz (1944).

Hysteranthous geophytes, solitary, to 10 cm tall (excl. inflorescence); tuber oblong, 3–3.5  $\times$  1 cm  $\varnothing$ ; **R** 1 mm  $\varnothing$ , terete; **L** 1–3, subterete, 2–10 cm  $\times$  1–1.5 mm, linear, attenuate, upper face flat, lower face convex, apex acute; **Inf** laxly flowered in the upper  $\frac{1}{3}$ , 12–27 cm; peduncle terete, 1 mm  $\varnothing$ ; **Bra** triangular-lanceolate, 2  $\times$  2.5 mm; **Ped** 6–7 mm; **Per** stellate, to 1.6 cm  $\varnothing$ , yellow; **OTep** oblong-ovate, 8  $\times$  2 mm; **ITep** 8  $\times$  3 mm, obtuse; **Fil** 6–7 mm, bearded in the upper  $\frac{1}{3}$ ; **Anth** 0.75 mm, oblong; **Ov** globose, 2.5 mm; **Sty** erect, terete, 5.5 mm; **Fr** globose, 4 mm  $\varnothing$ ; **Se** 1.5 mm  $\varnothing$ . — [E. Van Jaarsveld]

**B. fistulosa** Chiovenda (Ann. Bot. (Roma) 9: 143, 1922). **Type:** Ethiopia, Tigre (*Chiovenda* 557 [FT]). — **Distr:** Eritrea, Ethiopia, Zambia, Malawi, Tanzania, Zimbabwe; savanna and thickets or seasonally moist grassland, sometimes on termite mounds.

$\equiv$  *Jodrellia fistulosa* (Chiovenda) Baijnath (1978); **incl.** *Bulbine breviracemosa* Von Poellnitz (1944).

Solitary perennial from a short rhizome, to  $\pm$  40 cm tall; **R** fleshy, 3–5 mm  $\varnothing$ , spreading, some thin and fibrous, terete; **L** synanthous, linear to linear-lanceolate, terete, flattened or 3-angled and grooved on the upper face, 3.6  $\times$  0.2–1.2 cm, hollow, base expanding into a tubular sheath; **Inf**

peduncle 10–25 cm tall,  $\pm 3$  mm  $\varnothing$ , shorter than the leaves, raceme 1.5–3  $\times$  1.2–1.7 cm; **Bra** cuspidate, 12  $\times$  2–3 mm, attenuate, membranous; **Ped** 2–4 mm, overtopped by the bracts at anthesis, recurved after flowering; **Fl** congested, stellate, white; **OTep** 5–6  $\times$  2 mm; **ITep** 5–6  $\times$  1 mm, obtuse; **St** 3–4 mm, yellow; **Ov** globose, 1 mm  $\varnothing$ ; **Sty** erect, 4 mm, terete; **Fr** obovoid, 4.5 mm; **Se** deltoid, angled, 2 mm wide. — [E. Van Jaarsveld].

**B. flexicaulis** Baker (in Thiselton-Dyer, Fl. Cap. 6: 365, 1896). **Type:** RSA, Eastern Cape (*Pappe* 30 [K]). — **Distr:** RSA (Eastern Cape); among shrubs.

**Incl.** *Bulbine inops* N. E. Brown (1931).

Acaulescent geophytes; tuber depressed, **R** terete; **L** 4–6, linear, succulent, ascending, 6–10  $\times$  1.2 cm; **Inf** lax, flexuose to 15 cm; **Bra** triangular, minute; **Ped** 6–9 mm; **Fl** stellate,  $\pm 12$ –13 mm  $\varnothing$ , yellow; **OTep** oblong-ovate, 5–6  $\times$  1.5 mm; **ITep** 4.5  $\times$  2 mm, obtuse; **St** 6 mm; **Fil** bearded in the upper  $\frac{1}{3}$ ; **Ov** globose, 0.75 mm; **Sty** erect, terete, 3.5 mm; **Fr** globose, 4 mm  $\varnothing$ ; **Se** not seen. — [E. Van Jaarsveld].

**B. flexuosa** Schlechter (J. Bot. 36: 27, 1889). **Type:** RSA, Western Cape (*Leipoldt* s.n. [BOL]). — **Distr:** RSA (Northern Cape, Western Cape); dry Fynbos, 90–800 m, flowers in autumn. **I:** Smale (2002).

Geophytes with 1–3 heads, to 13 cm tall; **R** 1 mm  $\varnothing$ , terete; tuber depressed, to 3 cm  $\varnothing$  and 1 cm tall; **L** hysteranthous, filiform, 5.5–13 cm  $\times$  1 mm; **Inf** laxly flowered, flexuose to 14 cm; peduncle terete, 0.75 mm  $\varnothing$ ; **Bra** triangular, clasping, 1.5  $\times$  1 mm; **Ped** 12–35 mm; **Fl** stellate, to 12 mm  $\varnothing$ , yellow; **OTep** oblong-ovate, 6  $\times$  2 mm; **ITep** 6  $\times$  4 mm, obtuse; **St** 3–4 mm; **Fil** bearded in the upper  $\frac{1}{3}$ ; **Ov** globose, 1 mm  $\varnothing$ ; **Sty** erect, terete; **Fr** globose, 3 mm  $\varnothing$ ; **Se** oblong, 3  $\times$  1 mm, grey-black. — [E. Van Jaarsveld]

**B. foleyi** E. Phillips (Ann. South Afr. Mus. 1917: 352, 1917). **Type:** RSA, Western Cape (*Kensit* 10,612 [BOL]). — **Distr:** RSA (Western Cape); strandveld vegetation, flowers in spring.

Plants short-stemmed, to 15 cm tall; tuber depressed-globose, to 1.4 cm  $\varnothing$  and 1 cm tall;

**R** terete, 1 mm  $\varnothing$ ; stem to 4 cm; **L** 2–5 per stem, linear, 5.5–10 cm  $\times$  1.5–2 mm  $\varnothing$ , upper face flat, lower face convex, apex mucronate; **Inf** laxly flowered in the upper  $\frac{1}{2}$ , 9–23 cm; peduncle terete, 1 mm  $\varnothing$ ; **Bra** triangular-lanceolate, 5  $\times$  2 mm; **Ped** 6–7 mm; **Fl** spreading, stellate, 10–11 mm  $\varnothing$ , yellow; **OTep** oblong-ovate, 5  $\times$  1.5 mm; **ITep** 4  $\times$  1.5 mm, obtuse; **St** 3–5 mm; **Fil** bearded in the upper  $\frac{1}{3}$ ; **Anth** 0.5 mm, oblong; **Ov** globose, 0.5 mm  $\varnothing$ ; **Sty** erect, terete, 2.5 mm; **Fr** globose, 2.5 mm  $\varnothing$ ; **Se** grey-black, 3  $\times$  2 mm, flattened. — [E. Van Jaarsveld]

**B. fragilis** G. Williamson (Haseltonia 4: 13–15, 17, ill., 1996). **Type:** RSA, Northern Cape (*Williamson & Hammer* 5411 [NBG]). — **Distr:** RSA (Northern Cape: Richtersveld); Succulent Karoo, flowers mid-winter to spring.

Deciduous erect soft acaulescent herbs to 10 cm tall; tuber depressed-pyramidal, to 3 cm tall with up to 7 thick and fleshy decurrent **R** tapering from the tuber; **L** to 3, erect, light green, basal portion subtended by an elongated papyraceous sheath to 1 cm long; **L** linear-lanceolate, channelled or subterete to terete, to 10 cm  $\times$  4 mm, tip acute; **Inf** erect; peduncle slender, 7–28 cm, to 1.5 mm  $\varnothing$ ; raceme to 15 cm; **Fl** 3–13; **Bra** triangular-acuminate, membranous, to 1.5 mm; **Ped** to 15 mm; **Tep** luminous cadmium-yellow with green midvein, stellately spreading; **OTep** elliptic, 7  $\times$  3 mm; **ITep** obovate, 7  $\times$  5 mm; **Fil** slender-bearded; pollen green, later brown; **Ov** globose, orange, 1.8 mm; **Sty** 5 mm, decurved; **Se** flattened, deltoid, to 1.2 mm broad. — [E. Van Jaarsveld]

**B. francescae** G. Williamson & Baijnath (South Afr. J. Bot. 61(6): 312–314, ill., 1995). **Type:** Namibia (*Williamson* 4711 [NBG]). — **Distr:** S Namibia; flowers mid-winter. **I:** Williamson (2016: 4, 6).

Dwarf solitary geophytes to 10 cm tall; tuber dorsiventrally flattened-deltoid,  $\pm 1.5$  cm  $\varnothing$  and 1 cm tall; **R** succulent, terete, to 1.5 cm long; **L** 1–2, ascending, slightly dissimilar, first **L** lanceolate-acuminate, 4–10  $\times$  0.5–1 cm, translucent, pale green, upper face channelled, with 16 dark green longitudinal veins and 16 transverse



constrictions; second **L** similar to the first but lanceolate with acute tip, 1–4 cm × 1–2 mm, curved outwards; **Inf** 1, 6- to 12-flowered, to 11 cm, ascending; **Bra** 1 × 0.5 mm, membranous, deltoid-acuminate; **Ped** 8–10 mm; **Per** stellate, bright yellow; **OTep** narrowly elliptic, 10 × 3 mm; **ITep** elliptic, 10 × 6 mm, tips obtuse; **St** 7 mm; **Ov** globose, 2 mm Ø, yellowish-green, grooved; **Sty** erect, 9 mm, slightly curved; **Sti** capitate, papillate; **Fr** ellipsoid, 5 × 3 mm; **Se** deltoid, 2 × 1.5 mm, greyish-black, surface reticulate-alveolate. — [E. Van Jaarsveld].

**B. frutescens** (Linné) Willdenow (Enum. Pl. Hort. Reg. Berol., 372, 1809). **Type:** [lecto — icono]: Dillenius, Hort. Eltham. t. 231: fig. 298, 1732. — **Distr:** Namibia, RSA (Northern Cape, Western Cape, Eastern Cape, Gauteng, Mpumalanga, Free State, KwaZulu-Natal), Lesotho, Swaziland; arid savanna, to 2285 m, spring-flowering.

≡ *Anthericum frutescens* Linné (1753); **incl.** *Bulbine caulescens* Linné (1753) (*nom. inval.*, Art. 34.1c); **incl.** *Anthericum incurvum* Thunberg (1794) ≡ *Bulbine incurva* (Thunberg) Sprengel (1825) ≡ *Bulbine caulescens* var. *incurva* (Thunberg) Baker (1897) ≡ *Bulbine frutescens* var. *incurva* (Thunberg) G. D. Rowley (1973); **incl.** *Anthericum fruticosum* Salisbury (1796); **incl.** *Anthericum rostratum* Jacquin (1797) ≡ *Bulbine rostrata* (Jacquin) Willdenow (1809) ≡ *Bulbine frutescens* var. *rostrata* (Jacquin) G. D. Rowley (1973); **incl.** *Bulbine triebneri* Dinter (1943); **incl.** *Bulbine curvifolia* Von Poellnitz (1944); **incl.** *Bulbine alba* Van Jaarsveld (2002).

Plants caulescent to 15 cm tall, ± shrubby, dividing to form dense clumps to 30 cm Ø with up to 30 stems; **R** terete, brownish, apex yellow; stem short, often with stilt-roots; **L** up to 8 per stem, very variable in length, alternate, basally amplexicaul, ascending, slightly falcate, linear, 4–13 cm × 4–5 mm, lamina obscurely striate, upper face flat, lower face convex, apex acute; **Inf** racemose, solitary, 30–60 cm, ascending, densely flowered in the upper ½, flowers 2–25 mm apart; peduncle 3 mm Ø basally and triangular, terete upwards, **Bra** 5 × 1 mm, membranous, deltoid-acuminate, clasping; **Ped**

8–12 mm; **Fl** stellate, 19 mm Ø, yellow, rarely orange or white; **OTep** elliptic-lanceolate, 8–9 × 3 mm, obtuse; **ITep** broadly ovate, 8 × 4–5 mm, obtuse; **St** 5–6 mm; **Anth** yellow, oblong; **Ov** globose, 2 mm Ø; **Sty** erect, yellow, 5 mm; **Fr** ovoid, 6 × 5 mm; **Se** grey-black, 2 × 1.5 mm.

The lectotype given above is **formally designated here**, but was already previously listed as such, though ineffectively under the ICN, in the first edition of this handbook.

The leaf sap of this species (locally known as ‘kopieva’ or ‘geelkopieva’) is used to treat wounds, burns and insect bites because of its soothing antiseptic properties (G. F. Smith & E. Figueiredo, pers. comm.), and Coopoosamy (2011) has reported antibacterial activity for this and a couple of further species. It is frequently cultivated as a ground-cover in RSA. Plants with deviating flower colours have been described as cultivars, ‘Virgo’ has white flowers, and ‘Hallmark’ orange flowers. — [E. Van Jaarsveld]

**B. glauca** (Rafinesque) E. M. Watson (in George, A. S. (ed.), Fl. Austral. 45: 469, 1987). **Type:** Australia, Tasmania (*Anonymus* s.n. [K]). — **Lit:** Moore & al. (2016). **Distr:** Australia (E New South Wales, E Victoria, Tasmania); rock crevices on cliffs and summits. **I:** Curtis’s Bot. Mag. 59: t. 3129, 1832, as *Anthericum semibarbatum*; Kapitany (2007: 28–29).

≡ *Nemopogon glaucum* Rafinesque (1837); **incl.** *Bulbine suavis* Lindley (1838); **incl.** *Bulbine hookeri* Kunth (1843); **incl.** *Bulbinopsis terrae-victoriae* Von Poellnitz (1945).

Perennial succulent herbs without caudex; **R** succulent; **L** 6–16, subulate, terete towards the apex, otherwise channelled, 10–45 × 0.2–1 cm, glaucous blue-green; **Inf** 2 or more, to 90 cm, erect, peduncle terete; **Ped** 12–22 mm at fruiting time, erect; **Tep** 9–17 mm, yellow; **St** subequal, spreading or loosely grouped; **Fil** with clavate hairs; **Anth** yellow, dorsifixed, forming a convex horizontal arch after dehiscence; **Ov** with 3–4 ovules per locule; **Sty** deflexed, 3–7 mm; **Fr** globose to obovate, 4–6 mm; **Se** smooth, slightly tuberculate or ridged.

Moore & al. (2016) found considerable karyotype variation amongst the many populations



studied, involving structural rearrangements. They argue that the 6 distinctive groups that can be separated on karyological grounds also differ morphologically and should be recognized as separate species. — [P. I. Forster & U. Eggli]

**B. hallii** G. Williamson (Aloe 32(3–4): 80–81, ill. (p. 82), 1995). **Type:** RSA, Northern Cape (*Williamson & Hammer* 5421 [NBG]). — **Distr:** RSA (Northern Cape: Namaqualand); flowers early spring.

Dwarf perennial deciduous acaulescent rosulate solitary geophytes; tuber deltoid-depressed, 2 cm tall, 1.5 cm Ø, with a ring of bristles surrounding the rosette, tunics brown; **R** fleshy, terete; **L** densely arranged, up to 20, oblong-acute, ascending, 4.5 cm × 2 mm, flat to slightly channelled in the lower part, convex below, terete in the upper 1/3, dull silvery green, surface minutely granulate, margin entire, tip acute; **Inf** solitary, to 25-flowered, to 7 cm; peduncle wiry, terete, 1 mm Ø at the base; **Bra** 1.5 mm, deltoid; **Ped** to 11 mm; **Per** stellate becoming reflexed, to 16 mm Ø, light yellow with dark green central veins; **OTep** lanceolate, 8 × 2.5 mm; **ITep** 8 × 6 mm, tips obtuse; **St** 7 mm; **Ov** oblong, 2 mm; **Sty** oblique, terete, yellow, 5 mm; **Sti** capitate; **Fr** broadly ellipsoid, 3 × 2 mm; **Se** black, deltoid with contorted ridges, 1.2 × 1.2 mm, surface granular. — [E. Van Jaarsveld]

**B. haworthioides** B. Nordenstam (Bot. Not. 117: 183–187, 1964). **Type:** RSA, Western Cape (*Nordenstam* 807 [LD]). — **Distr:** RSA (Western Cape); Succulent Karoo, quartz flats, 100–615 m, flowers in late spring and early summer. **I:** Smale (2002). — Fig. 2.

Dwarf deciduous acaulescent rosulate solitary geophytes; tuber oblong to globose, 5- to 7-lobed, to 1.5 cm high and 2 cm broad, yellowish-brown; **R** yellow, fleshy, terete; **L** densely arranged, 8–14, linear-lanceolate, cymbiform, spreading, grey-green, lamina 0.7–1 × 0.25–0.3 cm, upper face flat, lower face convex, margin ciliate, apex obtuse to acute; **Inf** 1, ± 10-flowered, to 15 cm; peduncle wiry; **Bra** 1–3 mm, triangular to lanceolate, clasping; **Ped** 8–12 mm; **Fl** to 15 mm Ø,



**Fig. 2** *Bulbine haworthioides*. (Copyright: J. Trager)

yellow, 5–10 mm apart; **Tep** stellate, becoming reflexed; **OTep** lanceolate, 5–6 × 1.2–2 mm; **ITep** 6.5–7 × 3–4 mm, obtuse; **St** 4–5 mm; **Ov** oblong-globose, 1–1.5 mm; **Sty** erect, terete, yellow, 4–6 mm; **Fr** globose, 3 mm Ø; **Se** 1.5 mm, blackish. — [E. Van Jaarsveld]

**B. inamarxiae** G. Williamson & A. P. Dold (Aloe 41(2–3): 28–31, ills., 2004). **Type:** RSA, Eastern Cape (*Zeyher* 1068 [SAM in NBG, BOL, K]). — **Distr:** RSA (Eastern Cape); open grassland, inconspicuous, spring-flowering.

**Incl.** *Bulbine inaei* Baijnath ex Vanderplank (1998) (*nom. inval.*, Art. 36.1, 37.1).

Perennial, acaulescent from tuberous base; tuber napiform, 15 × 8 mm; **L** up to 3, synanthous, base with short, upright, petiole-like, membraneous extension 2 × 2 mm, lamina prostrate, suberect to erect, falcate, turgid, outer leaves ovate to narrowly ovate, ± 1 × 0.45–0.75 cm, upper face concave, lower face convex, tip acute, aristate; **Inf** solitary, ascending, peduncle to 11.5 cm,

wiry, terete, raceme 5 cm, with up to 9 flowers; **Bra** 1.6 × 1.8 mm, narrowly triangular, acuminate; **Fl** slightly nodding, yellow; **Ped** 8 mm; **Tep** reflexed; **OTep** elliptic, 6.2 × 1.8 mm; **ITep** ovate, 6.2 × 2.8 mm; **St** 4 mm; **Ov** obovoid, 1 × 0.8 mm; **Sty** 3.6 mm; **Sti** swollen; **Fr** 3 × 2.8 mm, globose; **Se** 0.8–1.5 mm, subdeltoid to deltoid, tuberculate, shiny black. — [E. Van Jaarsveld]

**B. inflata** Obermeyer (Bothalia 9(2): 342–343, t. 3, 1967). **Type:** RSA, Mpumalanga (*Codd* 9503 [PRE]). — **Distr:** RSA (Gauteng, KwaZulu-Natal, Mpumalanga), Swaziland; grassland, 220–1705 m.

Geophytes with compact rhizome; **R** spreading, terete; **L** 10–15, rosulate, ascending, linear, terete, to 50 cm, to 1 cm Ø, sheathing below forming a short neck, upper face grooved, apex subulate; **Inf** 1, to 1.25 m, densely flowered in the upper ½; peduncle terete; **Bra** to 2.5 cm, membranous, linear-acuminate, aristate; **Ped** to 25 mm; **Fl** stellate, to 23 mm Ø, yellow; **Tep** becoming reflexed, linear-lanceolate, 10 × 3 mm, obtuse; **St** 7 mm; **Ov** oblong, 7 mm, tip truncate; **Sty** erect, 7 mm; **Fr** globose, 13 mm Ø; **Se** black, angled, 2 mm. — [E. Van Jaarsveld]

**B. lagopus** (Thunberg) N. E. Brown (Bull. Misc. Inform. Kew 1931: 195, 1931). **Type:** RSA, Western Cape (*Thunberg* s.n. [K]). — **Distr:** RSA (Western Cape, KwaZulu-Natal), Lesotho; among quartzitic sandstones in Fynbos and grassland, 15–1080 m, ± 1000 m, flowers in late spring.

≡ *Anthericum lagopus* Thunberg (1800); **incl.** *Bulbine graminea* Haworth (1821); **incl.** *Bulbine caespitosa* Baker (1897); **incl.** *Bulbine asphodeloides* var. *denticulifera* Von Poellnitz (1944).

Evergreen, rosulate, clustering with 3–5 growths per plant, shortly caulescent to 12 cm tall and 15 cm Ø; **R** yellow, 2 mm Ø, terete; stems short, 2–3 × 1 cm Ø; **L** 12–15 per growth, green, curved inwards, firm, linear to linear-lanceolate, 4–16 × 0.5 cm, upper face flat, lower face convex, attenuate, margin entire, apex acute, mucronate; **Inf** 30–60 cm, densely flowered in the upper ½, peduncle terete, 3–6 mm Ø; **Bra**

triangular-lanceolate, 5 × 2 mm; **Ped** 15–25 mm; **Fl** stellate, 14 mm Ø, yellow; **OTep** lanceolate, 5 × 2 mm; **ITep** ovate, 5 × 3 mm, obtuse; **St** 6 mm; **Ov** globose; **Sty** erect, terete; **Fr** globose, 4–5 mm Ø; **Se** 2.5 × 2 mm, angled, blackish. — [E. Van Jaarsveld]

**B. lamprophylla** G. Williamson (Bradleya 14: 84–86, ill., 1996). **Type:** RSA, Northern Cape (*Williamson & Hammer* 5707 [NBSG]). — **Distr:** RSA (Northern Cape); Succulent Karoo, 600–800 m. **I:** Smale (2002).

Dwarf deciduous acaulescent rosulate solitary geophytes; tuber pinkish, deltoid, 7–13 × 5–8 mm, with several basal fleshy terete **R**; **L** 4–6, crowded and forming a tight basal cylinder to 8 × 2 mm, lamina 1.5–4 cm × 1.2–3.5 mm, oblong-acute, subterete, ascending, shiny luminescent, upper face flat to slightly channelled, lower face convex, epidermis finely tuberculate with minute trichomes towards the base, tip acute; **Inf** 1, 4–14 cm; raceme to 6 cm, 6- to 14-flowered; peduncle wiry, terete; **Fl** sweetly scented; **Ped** 10 mm; **OTep** elliptic, 7 × 2.5 mm, light orange-green, lower face apricot; **ITep** 8 × 5 mm, obovate, orange-yellow; **St** to 6 mm; **Ov** oblong, 2 mm; **Sty** 4 mm; **Fr** broadly ellipsoid, 3 × 2 mm; **Se** pyramidal, dark brown, rugose, 1.4 × 1 mm. — [E. Van Jaarsveld].

**B. latifolia** (Linné *fil.*) Sprengel (Syst. Veg. 2: 86, 1825). **Type:** [icon]: Jacquin, Icon. Pl. Rar. 2: t. 406, 1793. — **Distr:** E RSA (Western Cape, Eastern Cape, Kwazulu-Natal, Gauteng).

≡ *Anthericum latifolium* Linné *fil.* (1781); **incl.** *Bulbine ensifolia* Baker (1901); **incl.** *Bulbine transvaalensis* Baker (1904).

*B. natalensis* is superficially similar but has softer leaves and different ecological preferences. Zukulu & al. (2012: 15) report local usage for cleansing “dirty blood”, and as an emetic to remove previously applied herbal medicine. — [E. Van Jaarsveld]

**B. latifolia** var. *curvata* Van Jaarsveld (Aloe 40(1): 4–5, ill., 2003). **Type:** RSA, Eastern Cape (*Van Jaarsveld* 13,806 [NBSG]). — **Distr:** RSA (Eastern Cape); sheer quartzitic sandstone cliffs in Gamtoos Thicket vegetation, spring-flowering.

Differs from var. *latifolia*: **L** linear-lanceolate, firm and fibrous, falcately curving downwards, 15–25 × 0.8–2 cm, becoming almost subterete when fully turgid. — [E. Van Jaarsveld]

**B. latifolia** var. *latifolia* — **Distr**: E RSA (Western Cape, Eastern Cape, KwaZulu-Natal, Gauteng); pioneer in arid savannas, 35–1400 m, spring-flowering. — Fig. 3.

Plants rosulate, solitary, to 20 cm tall; **R** fleshy, terete; **L** in a dense rosette, green, obscurely striate, firm, ascending, older leaves becoming recurved, lamina triangular-lanceolate, 19–40 × 3–6 cm, upper face flat, slightly channelled towards the apex, lower face flat or somewhat convex, margin acute, minutely ciliate, apex acuminate; **Inf** 1–4, densely flowered in the upper ½, 40–100 cm, ascending to spreading; **Fl** up to 8 open at the same time, ± 7–12 mm Ø, yellow, crowded; peduncle flattened below, biconvex, to 15 mm wide and tapering to 6–8 mm; **Bra** membranous, withering, linear-lanceolate, 5–8 × 1 mm; **Ped** 12–14 mm; **OTep** lanceolate, 7 × 3 mm, obtuse; **ITep** 7 × 3.5 mm, obtuse; **St** 7 mm; **Anth** yellow, 1 mm, oblong; **Ov** globose, 1.5 mm, yellowish-green, grooved; **Sty** erect, 6 mm; **Fr** rounded, 4 × 3 mm; **Se** 2.5 × 1.5 mm, ellipsoid, grey-black. — [E. Van Jaarsveld]

**B. lavrani** G. Williamson & Baijnath (Aloe 36 (2–3): 28–30, ills., 2000). **Type**: RSA, Northern Cape (*Williamson* 5283 [NBG]). — **Distr**: RSA (Northern Cape); steep quartzitic sandstone ridges, ± 350 m.

Dwarf solitary acaulescent single-headed geophytes; tuber oblong, tapering, black, 3 × 2 cm; **R** fibrous; **L** 1, erect, basally amplexicaul, linear, subterete, glaucous, 1–1.5 × 0.2–0.4 cm, upper face channelled; **Inf** 1, erect, to 11–22 cm, up to 15-flowered; peduncle 1.5 mm Ø basally, terete; **Bra** deltoid, acuminate, 2 × 1 mm, clasping; **Fl** spreading, stellate, ± 15 mm Ø, yellow, 7–12 mm apart; **Ped** 5–7 mm; **OTep** elliptic, 7 × 2 mm; **ITep** ovate to ovate-elliptic, 6 × 2.5 mm, obtuse to subacute; **St** 6 mm; **Ov** globose, 1 mm Ø; **Sty** erect, 7 mm; **Fr** globose, 2.5 mm; **Se** angular, grey-black, 1 mm. — [E. Van Jaarsveld]



**Fig. 3** *Bulbine latifolia* var. *latifolia*. (Copyright: E. Van Jaarsveld)

**B. lolita** S. A. Hammer (Cact. Succ. J. (US) 78(2): 70–71, ills., 2006). **Type**: RSA, Western Cape (*Lavrano*s 31140 [HNT]). — **Distr**: RSA (Western Cape); Succulent Karoo, coarse-grained decomposed gneiss, flowers in mid-winter.

Plants solitary, dwarf, 6–8 mm tall (excl. inflorescence) and 15 mm Ø, from a tuberous base; tuber like a flattened pea, 6–8 mm Ø and 4–6 mm tall, with pale yellowish-brown non-peeling skin and short horizontally radiating roots; **L** synanthous, 12–16, spirally arranged, 0.3 cm long, 0.4 cm Ø, depressed-globose, pale bluish-green with central window, tessellately patterned, becoming truncate, tapering slightly towards the translucent apex, apex with soft apiculus; **Inf** with a tough, 12 cm long, tortuose, reddish-brown peduncle, raceme diffuse, with 12–20 secondly arranged strongly scented flowers; **Ped** 8–10 mm; **Tep** 8–10 × 3–4 mm, slightly reflexed, undulating, yolk-yellow; **Fil** 4–6 mm, bearded; **Fr** 2 mm,



wrinkled, blackish; **Se**  $\pm 20$ , deltoid, 0.8–1.1 mm, dull black. — [E. Van Jaarsveld]

**B. longifolia** Schinz (Bull. Herb. Boissier, sér. 2, 2: 939, 1902). **Type:** RSA, Western Cape (*Schlechter* 8715 [Z, BOL]). — **Distr:** RSA (Western Cape); dry Fynbos vegetation, 100–1220 m, flowers in winter and spring.

Small solitary geophytes to 4.5–20 cm tall; tuber depressed,  $\pm 1$  cm  $\varnothing$ ; **R** terete; **L** linear to linear-lanceolate, 2–5 per stem, 3–20 cm  $\times$  2–5 mm, flat to channelled above, convex below, attenuate, apex acute; **Inf** laxly flowered, to 15–25 cm; peduncle terete, 1 mm  $\varnothing$  at the base; **Bra** triangular-lanceolate, 3–6  $\times$  1–3 mm; **Ped** terete, 8–9 mm; **Fl** stellate, 14–15 mm  $\varnothing$ , yellow; **OTep** oblong-ovate, 7  $\times$  2 mm; **ITep** 7  $\times$  5 mm, obtuse; **St** 5 mm; **Anth** 0.5 mm, oblong; **Ov** globose, 1.5 mm; **Sty** erect, terete, 4 mm; **Fr** and **Se** not seen. — [E. Van Jaarsveld]

**B. louwii** L. I. Hall (South Afr. J. Bot. 3(6): 356–357, 1984). **Type:** RSA, Western Cape (*Hall* 4718 [NBG]). — **Distr:** RSA (Western Cape); Succulent Karoo, quartz flats,  $\pm 200$  m.

Dwarf deciduous acaulescent rosulate solitary geophytes; tuber depressed, globose above, flat below, with radiating taproots, 1 cm tall, 1.5 cm broad; **R** terete; **L** dense, to 30, spatulate, ascending, 4  $\times$  0.8–1 cm, striate, margin ciliate, apex obtuse, mucronate; **Inf** 1–2, to 12 cm, 30- to 40-flowered; peduncle reddish-brown, wiry, 1.5 mm  $\varnothing$  at the base; **Bra** to 3 mm, deltoid-cuspidate; **Ped** 10–12 mm; **Per** stellate, becoming reflexed, to 20 mm  $\varnothing$ , yellow; **OTep** lanceolate, 10  $\times$  3 mm; **ITep** 10  $\times$  7 mm, obtuse; **St** 5 mm; **Ov** oblong, 1.5 mm; **Sty** oblique, terete, yellow, 7 mm; **Fr** 4 mm; **Se** not seen. — [E. Van Jaarsveld]

**B. margarethae** L. I. Hall (South Afr. J. Bot. 3(6): 357, 1984). **Type:** RSA, Western Cape (*Hall* 5083 [NBG]). — **Distr:** RSA (Western Cape); Succulent Karoo, on limestone outcrops,  $\pm 200$  m, flowers in late spring and early summer. **I:** Smale (2002); Helme (2013). – Fig. 4.

Dwarf deciduous acaulescent rosulate clustering geophytes; tuber depressed, globose above,



**Fig. 4** *Bulbine margarethae*. (Copyright: J. Trager)

flat below, 1  $\times$  1.5 cm, lobed; **R** fibrous, terete; **L** dense, to 25, linear, 5  $\times$  0.5 cm, biconvex, upper face distinctly tessellate, apex acute; **Inf** 1,  $\pm 25$ -flowered, to 15 cm; peduncle wiry, terete, to 1.5 mm  $\varnothing$  at the base; **Bra** 2–3 mm, triangular-lanceolate, clasping; **Ped** 8–10 mm; **Per** stellate, becoming reflexed, to 18 mm  $\varnothing$ , yellow; **OTep** oblong, 9  $\times$  2.5 mm; **ITep** oblong, 8  $\times$  6 mm, obtuse; **St** 6 mm; **Anth** 1 mm; **Ov** globose, 1.5 mm; **Sty** erect, 6 mm; **Fr** ovoid, 4  $\times$  3 mm; **Se** 1.25 mm, angular, rough. — [E. Van Jaarsveld].

**B. meiringii** Van Jaarsveld (Aloe 40(1): 5–6, ill. (p. 6–7), 2003). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 12762 [NBG]). — **Distr:** RSA (Western Cape: Little Karoo, Swartberg Mtn.); on quartzitic sandstone cliffs, rock crevices, flowers in spring.

Dwarf rosulate succulents to 10 cm tall, dividing to form clusters  $\pm 20$  cm  $\varnothing$  with up to 12 heads; **R** grey, fleshy, terete; stem short,

2 cm, thickening towards the base; **L** 4–7, curving downwards, striate, linear-lanceolate, 10–15 cm × 6–8 mm, upper face flat, lower face convex, apex acute; **Inf** 1, 21–26 cm, ascending to spreading, flowers in the upper  $\frac{1}{3}$ , 4–6 mm apart; peduncle 3 mm wide at the base, biconvex, terete upwards; **Bra** 3 mm, membranous, deltoid-acuminate, clasping; **Ped** 10–12 mm; **Per** stellate, becoming reflexed; **Tep** pale yellow; **OTep** elliptic, 7 × 2 mm, obtuse; **ITep** ovate to ovate-elliptic, 6 × 2.5–3 mm, obtuse; **St** 5 mm; **Anth** yellow, oblong; **Ov** globose, 1.5 mm  $\varnothing$ ; **Sty** erect, 5 mm; **Fr** ovoid, 3 × 4 mm; **Se** grey-black, 1.5 × 1 mm. — [E. Van Jaarsveld]

**B. melanovaginata** G. Williamson (Aloe 40 (1): 16–17, ill., 2003). **Type:** RSA (Williamson 5961 [NBG]). — **Distr:** RSA (Western Cape: Olifants River valley); Succulent Karoo, spring-flowering.

Plants erect, ascending from dome-shaped tubers, tubers 2.5–3 × 2 cm high, with 6–12 basal, spreading, tapering roots, apex with a well-developed collar surrounding the developing leaf bases and peduncle; sheathing leaf remnants persistent, 2.5 × 0.4 cm, scabrous, black; **L** 6–8, hysteroanthous, dark green, with succulent margin, linear, dorsiventrally compressed with shallow adaxial groove, tapering, 6.5 × 0.4–0.5 cm, apical  $\frac{1}{3}$  curling, occasionally spring-like; **Inf** ascending, developing after the leaves have withered, peduncle to 9 cm, emerging from a pseudo-stem, raceme to 5 cm, 20- to 50-flowered; **Bra** 7–10 mm; **Ped** 8–10 mm; **Fil** drooping at midday; **Tep** light greenish-yellow to yellow; **OTep** reflexed, elliptic, 6 × 2 mm; **ITep** ovate, 6 × 4 mm; **Fil** ± 6 mm, bearded; **Anth** yellow, 0.8–1 mm; **Ov** irregularly obovate, 1.8 mm; **Fr** broadly ellipsoid, 3 × 2 mm; **Se** black, 1.2 × 0.8 mm, ovate. — [E. Van Jaarsveld]

**B. mesembryanthoides** Haworth (Philos. Mag. J. 66: 31–32, 1825). **Type:** RSA, “Cape Prov.” (*Bowie* s.n. [K [icono: Duncanson drawing], NBG [photo]]). — **Lit:** Williamson (2004: typification). **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape); mainly in Succulent Karoo vegetation, 125–1395 m.

**Incl.** *Bulbine mesembryanthemoides* Baker (1896) (*nom. inval.*, Art. 61.1).

Dwarf solitary summer-deciduous geopytes 1–2.5 cm tall; tuber globose to deltoid, depressed, 3- to 5-lobed, ± 1.2–2 cm  $\varnothing$  and 1 cm tall, lobes ovoid, tapering, flesh grey-white where exposed; **R** light yellowish-grey, fleshy, terete; **L** 1–4, erect, amplexicaul, dissimilar; larger **L** 1.5–3 × 1–2 cm, oblong, tip acute or truncate to concave (appearing scalped), pinkish-grey-green, striate, upper face grooved; younger **L** linear-lanceolate to lanceolate, 1.5 × 0.3 cm, almost terete, acute at first, withering from the top and becoming truncate or remaining acute, upper face grooved, lower face convex; **Inf** 1, 17.5–20 cm, 1- to 7-flowered, erect to ascending, flowers spreading, 5–10 mm apart; peduncle 1 mm  $\varnothing$  at the base, terete; **Bra** 1.5–2 × 1 mm, membranous, deltoid-acuminate, clasping; **Ped** 8–10 mm; **Per** stellate, 10 mm  $\varnothing$  when fully spread, yellow; **OTep** lanceolate, 6–7 × 1.5–2 mm; **ITep** ovate to ovate-elliptic to oblanceolate, 5–6 × 2–3 mm, obtuse; **St** 4–5 mm; **Anth** yellow, oblong, 0.75 mm; **Ov** globose, 1 mm  $\varnothing$ ; **Sty** erect, yellow, 5 mm; **Fr** globose, 3 mm  $\varnothing$ ; **Se** 1.5 mm. — [E. Van Jaarsveld]

**B. mesembryanthoides** ssp. *mesembryanthoides* — **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape); Succulent Karoo vegetation, rocky regions, summer-flowering. **I:** Smale (2002).

**Incl.** *Bulbine orchoides* Drège ex Von Poellnitz (1944).

Tuber globose, elongating into the roots; **L** 2–3, terete, acute even when withering; **Inf** usually 3- to 6-flowered; **Fil** with a single tuft of hairs. — [E. Van Jaarsveld]

**B. mesembryanthoides** ssp. *namaquensis* G. Williamson (Aloe 36(1): 14–15, ill., 1999). **Type:** RSA, Northern Cape (*Le Roux* 3116 [STE in NBG]). — **Distr:** RSA (Northern Cape); Succulent Karoo, rocky regions. **I:** Smale (2002).

Differs from ssp. *mesembryanthoides*: Tubers deltoid; **L** 1 normal and 1 vestigial, normal leaf truncate, terete, vestigial leaf falcate, acute; **Inf** shorter, 1- to 6-flowered; **Fil** with a double tuft of hairs. — [E. Van Jaarsveld]



**B. migiurtina** Chiovenda (Pl. Nov. Min. Not. Ethiop. 5, 1928). **Type:** Somalia (*Puccioni & Stefanini* 777 [FT]). — **Distr:** Ethiopia, Somalia, Kenya; *Commiphora-Acacia* savanna on granite rocks in red sandy loam. **I:** Whitehouse (2002, 15); Sebsebe Demissew & Nordal (2010: 124, as *Jodrellia macrocarpa*).

≡ *Jodrellia migiurtina* (Chiovenda) Baijnath (1978); **incl.** *Jodrellia macrocarpa* Baijnath (1978) ≡ *Bulbine macrocarpa* (Baijnath) Boatwright & J. C. Manning (2010).

Solitary perennial from a short rhizome, to ± 38 cm tall; **R** fibrous, terete, some fleshy, spreading and 2–5 mm Ø; **L** synanthous, linear, terete, 38 cm × 4–7 mm, hollow, base reduced to a membranous sheath; peduncle at anthesis 22 × 0.3 cm, shorter than the leaves; raceme 4 × 2 cm; **Bra** cuspidate, 10 × 2–3 mm, attenuate, tapering to a filiform apex, membranous; **Ped** 2–4 mm, overtopped by the bracts at anthesis, recurved after flowering and extending to 22 mm in fruit; **Fl** congested, stellate, white; **OTep** 5–6 × 2 mm; **ITep** 5–6 × 1 mm, obtuse; **St** 3 mm, yellow; **Ov** globose, 1 mm Ø; **Sty** erect, 4 mm; **Fr** obovoid, 8–15 mm, inflated when mature; **Se** deltoid, angled, 2 mm wide, tuberculate. — [E. Van Jaarsveld]

**B. minima** Baker (J. Linn. Soc., Bot. 15: 344, 1876). **Type:** RSA, Western Cape (*Drège* 953 [K]). — **Distr:** RSA (Western Cape); Renosterveld vegetation, 50–1430 m, summer-flowering.

**Incl.** *Bulbine concinna* Baker (1897).

Dwarf rosulate evergreen acaulescent geophytes; tuber globose-depressed, 1–1.5 cm tall and 1.5–2 cm broad with numerous bristles to 15 mm surrounding the rosette; **R** terete, 1 mm Ø; **L** filiform, curved, 15–20 per rosette, 2.5–4.5 cm × 0.75 mm; **Inf** 1–3, 13–16 cm, laxly flowered in the upper ½; peduncle terete, 1 mm Ø; **Bra** triangular, 1 × 0.75 mm; **Ped** terete, 6–7 mm; **Per** 7–8 mm Ø, stellate becoming reflexed, yellow; **OTep** oblong-ovate, 4 × 1 mm; **ITep** 3.5 × 1.5 mm, obtuse; **Fr** globose, 3 mm Ø; **Se** 1.5 × 1 mm, flattened, semicircular in outline. — [E. Van Jaarsveld].

**B. monophylla** Von Poellnitz (Feddes Repert. Spec. Nov. Regni Veg. 53(1): 45, 1944). **Type:** RSA, Western Cape (*Schlechter* 4912 [B]). — **Distr:** RSA (Western Cape); Renosterveld vegetation, 240–800 m, spring-flowering.

Solitary geophytes to 45 cm tall; tuber depressed-globose, 1–1.4 cm tall, 1.2–1.5 cm Ø; **R** terete; **L** 1, terete, synanthous, 30–45 cm × 3–7 mm Ø, apex tapering, acute; **Inf** 30–40 cm, laxly flowered in the upper ½; peduncle terete, 2–3 mm Ø at the base; **Bra** triangular-lanceolate, 5 × 2 mm; **Ped** 10–14 mm; **Per** stellate, 16–18 mm Ø, yellow; **OTep** oblong-elliptic, 9 × 2 mm; **ITep** oblong-ovate, 8 × 3 mm, obtuse; **St** 5 mm; **Ov** ellipsoid, 2 mm; **Sty** erect, terete, 6 mm; **Fr** oblong-globose, 4 × 5 mm; **Se** not seen. — [E. Van Jaarsveld]

**B. muscicola** G. Williamson (Bradleya 18: 36, ills. (p. 32, 38), 2000). **Type:** RSA, Western Cape (*Williamson* 5930 [NBG]). — **Distr:** RSA (Western Cape: lower foothills of the Cederberg); shallow quartzitic sandstone outcrops, among mosses, 150–200 m, flowers late spring.

Dwarf solitary single-headed geophytes; tuber dome-shaped, 1 × 0.8 cm, with spreading wedge-shaped roots; **L** 1, erect, amplexicaul, linear-terete becoming lanceolate, translucently light green, 3.5 × 0.4 cm, later in the season becoming shorter and truncate (2.5 × 0.5 cm); **Inf** solitary, erect, to 8 cm, raceme 4 cm, to 10-flowered; peduncle terete, 1.5 mm Ø at the base; **Bra** deltoid-acuminate, 2.5 × 0.8 mm, clasping; **Ped** 8 mm; **Tep** pale yellowish-green; **OTep** recurved, narrowly ovate, 6 × 2 mm; **ITep** ovate, 6 × 3 mm, obtuse; **Ov** ovoid, 1 mm Ø; **Sty** erect, 6 mm; **Sti** capitate; **Fr** 3 × 2 mm; **Se** narrowly pyramidal, brownish-black, 1.3 × 0.5 mm. — [E. Van Jaarsveld]

**B. namaensis** Schinz (Bull. Herb. Boissier, sér. 2, 2: 939–940, 1902). **Type:** Namibia (*Schinz* 934 [Z]). — **Distr:** Namibia, RSA (Northern Cape); Strandveld vegetation, flowers in July.

**Incl.** *Bulbine vesicularis* Dinter (1943).

Plants rosulate, clustering with 2–5 heads per plant, to 14 cm tall; tuber small, oblong 1 × 0.7 cm; **R** terete, 1–2 mm Ø; **L** 10–15, ascending,

to 14 cm × 1 mm, curved at the top, filiform with basal membranous sheaths of 2.5 cm; **Inf** 18–43 cm, densely flowered in the upper ½; peduncle terete, 3–6 mm Ø at the base; **Bra** triangular-acuminate, 7 × 1.5–2 mm; **Ped** terete, 12–15 mm; **Fl** scented, spreading, stellate, 16 mm Ø, yellow; **OTep** oblong-ovate, 8 × 2 mm; **ITep** 7 × 3 mm, obtuse; **St** 5 mm; **Anth** 1 mm, oblong; **Ov** globose, 1 mm; **Fr** globose, 1 cm; **Se** angled, oblong, 4 mm Ø. — [E. Van Jaarsveld]

**B. narcissifolia** Salm-Dyck (Hort. Dyck., 334, 1834). **Type:** not typified. — **Distr:** RSA (Eastern Cape, KwaZulu-Natal, Free State, Gauteng), Botswana, Lesotho; grassland, to 2900 m, flowers from spring to autumn.

**Incl.** *Bulbine densiflora* Baker (1876); **incl.** *Bulbine latibracteata* Von Poellnitz (1944).

Plants acaulescent, clustering, 8–15 cm tall; tuber depressed, 1 × 2 cm; **R** yellow, fusiform, terete; **L** 4–5, distichous, with slight spiral twist, amplexicaul, green, ascending, linear, 6.5–15 × 0.4–2.2 cm, lamina obscurely striate, flat, apex acute, mucronate; **Inf** 1, racemose, to 38 cm, densely flowered, capitate, flowers ±2–3 mm apart; peduncle 2–8 mm Ø at the base, terete to flattened; **Bra** 8–9 × 3 mm, membranous, lanceolate-acuminate; **Ped** 15–25 mm; **Per** stellate, 15 mm Ø, yellow, becoming reflexed; **OTep** elliptic-lanceolate, 7 × 2 mm; **ITep** lanceolate-ovate, 6 × 2.5 mm, obtuse; **St** 5 mm; **Anth** yellow, oblong; **Ov** oblong-globose, 2 mm; **Sty** erect, yellow, 3 mm; **Fr** ovoid, 6 × 5.5 mm; **Se** grey-black, 1.5 mm. — [E. Van Jaarsveld]

**B. natalensis** Baker (in Thiselton-Dyer, Fl. Cap. 6: 366, 1896). **Type:** RSA, KwaZulu-Natal (*Wood* 553 [K]). — **Distr:** RSA (Eastern Cape, KwaZulu-Natal); sandstone cliff faces, flowers in early spring and summer. **I:** Wyk & al. (1997: 64).

Plants evergreen, rosulate, with short stem, without tuber; **R** yellow, fleshy, terete; **L** 10–14, triangular-lanceolate, softly succulent, grey-green, striate, soft, spreading, 8.5–13 × 3.5–4.5 cm, upper face flat to broadly channelled, lower face flat to rounded, margin densely ciliate, apex acuminate, cilia 2 mm; **Inf** 1–3, densely

flowered, to 55 cm; peduncle flattened at the base, 6–7 mm Ø; **Bra** linear-lanceolate, 10 × 1 mm; **Ped** 9–11 mm; **Fl** spreading; **Per** stellate, to 15 mm Ø, yellow; **OTep** lanceolate, 6 × 3 mm; **ITep** 6 × 4 mm, obtuse; **St** 5 mm; **Ov** globose, 1.5 mm; **Sty** 6 mm; **Fr** globose, 3 mm; **Se** 1.5 mm, grey-black, ellipsoid.

Sometimes treated as synonym of *B. latifolia*, but with softer leaves and different ecological preferences. The leaf sap is used to treat wounds, burns and insect bites because of its soothing antiseptic properties (G. F. Smith & E. Figueiredo, pers. comm.). — [E. Van Jaarsveld]

**B. navicularifolia** G. Williamson (Aloe 40(1): 16, 18–19, ills., 2003). **Type:** RSA (*Williamson* 5956 [NBG]). — **Distr:** RSA (Western Cape); Succulent Karoo, spring-flowering.

Ascending from rounded, oblong tubers to 2 cm high and 2.5 cm wide, or ellipsoid tubers to 2 × 1.2 cm, covered in a layer of coarse, striate, reddish-brown sheaths; basal roots radiating, tapering; **L** 3, light pea-green, boat-shaped, enveloping each other in the lower ½, 2 outer leaves 12–14 × 2.2 cm; **Inf** erect, to 30 cm, 32- to 50-flowered; **Bra** ovate-acuminate, 6 × 1 mm; **Ped** 12 mm; **Fl** light yellow; **OTep** reflexed, elliptic, subacute, 8–10 × 2 mm; **ITep** ovate, subacute, 10–12 × 5–7 mm; **Fil** ± 8 mm; **Anth** green, 0.8–1 mm; **Ov** broadly ellipsoid, 1.5 mm; **Sty** 7 mm; **Fr** broadly ellipsoid, 5 × 2 mm; **Se** narrowly pyramidal to oblong, blackish-grey, 4 × 1.5 mm. — [E. Van Jaarsveld]

**B. nutans** (Jacquin) Sprengel (Syst. Veg. 2: 86, 1825). **Type:** [icono]: Jacquin, Collectanea 2: 17, t. 407, 1787. — **Distr:** RSA (Western Cape); dry Fynbos vegetation, 540–1080 m.

≡ *Anthericum nutans* Jacquin (1787); **incl.** *Bulbine bachmanniana* Schinz (1902); **incl.** *Bulbine bachmannii* Baker (1903).

Solitary rosulate geophytes to 30 cm tall (without inflorescences); tuber oblong, 4 × 3.5 cm with few radiating succulent roots to 12 mm Ø at the base and tapering, crowned with a ring of bristles and withered leaves to 4.5 cm; **L** linear to ovate-lanceolate, 5–30 × 0.6–2.2 cm, flat, keeled, spreading, amplexicaul at the base, margins

ciliate, apex acuminate; **Inf** 1–2, 25–40 cm, flowers in the upper  $\frac{1}{3}$ ; peduncle terete, 2–5 mm  $\varnothing$  at the base; **Bra** triangular to triangular-lanceolate, 3  $\times$  1 mm; **Ped** terete, 11–15 mm; **Fl** spreading, stellate, 12–13 mm  $\varnothing$ , yellow; **Tep** 6  $\times$  1.5 mm, oblong-ovate, obtuse; **Fr** oblong-ovate, 6 mm; **Se** oblong, 2–3  $\times$  1 mm. — [E. Van Jaarsveld]

**B. ophiophylla** G. Williamson (Aloe 40(1): 19, 20–23, ills., 2003). **Type:** RSA, Northern Cape (*Wisura* 636 [NBG]). — **Lit:** Bester & al. (2012). **Distr:** RSA (NW to SW Northern Cape: Richtersveld: mouth of the Orange River to Namaqua National Park); sparse open desert vegetation (Namaqualand Strandveld and Namaqualand Coastal Duneveld vegetations), winter-flowering.

Solitary or rarely in clusters of up to 5, ascending from a tangled mass of orange roots; old leaves sheathing, bases forming an oblong to elliptical pseudostem  $\pm$  3–4  $\times$  2 cm; **L**  $\pm$  10, 10 cm  $\times$  4–5 mm, linear, spirally twisted, subacute, flattened, grey-green to dark olive-green, turgid and brittle, forming a tangled twisted mass, epidermis tough; **Inf** peduncle erect, to 10 cm, raceme  $\pm$  3–5 cm, subcapitate, to 22-flowered; **Bra** acute, acuminate, papery, 8  $\times$  3 mm; **Ped** 8–12 mm; **Fl** 1–2 open at a time, densely arranged; **Tep** peach-coloured to greenish-yellow; **OTep** broadly elliptic, 7  $\times$  4 mm; **ITep** ovate, 7  $\times$  5 mm; **Fil** 7 mm, bearded; **Ov** broadly ellipsoid, 2 mm; **Sty** 5 mm; **Fr** globose, 5–7 mm; **Se** 2.5  $\times$  2 mm, black, angular-globose. — [E. Van Jaarsveld]

**B. pendens** G. Williamson & Baijnath (South Afr. J. Bot. 61 (6): 316–319, ills., 1995). **Type:** RSA, Northern Cape (*Williamson* 4738 [NBG]). — **Distr:** RSA (Northern Cape); sheer shady quartzitic sandstone cliff faces, 300–600 m.

Dwarf acaulescent solitary or 2-headed geophytes, pendent from cliff faces; tuber oblong, 3  $\times$  1.5 cm, stellately lobed, lobes tapering into the roots; **L** 1–2, pendent, amplexicaul with basal sheath 1–2 cm, lamina linear, terete, striate, 1.5–1.8  $\times$  0.2–0.5 cm; **Inf** 1, erect, 8–18 cm, up to 4-flowered; peduncle 1 mm  $\varnothing$  at the base,

terete; **Bra** deltoid-acuminate, 3–4  $\times$  1 mm, clasping; **Ped** to 25 mm; **Fl** spreading, stellate,  $\pm$  18 mm  $\varnothing$ , yellow, 10–15 mm apart; **OTep** 8  $\times$  3 mm; **ITep** ovate to ovate-elliptic, 8  $\times$  4 mm, obtuse to subacute; **St** 5 mm; **Ov** globose, 1.5–2 mm  $\varnothing$ ; **Sty** erect, 5 mm; **Fr** not seen; **Se** angled, 2  $\times$  2 mm. — [E. Van Jaarsveld]

**B. pendula** Keighery (Nuytsia 15(2): 241–243, ills., 2004). **Type:** Australia, Western Australia (*Trudgen* 370 [PERTH]). — **Distr:** Australia (Western Australia); red clay soils in tussock grassland vegetation.

Annual succulent herbs without caudex; **R** fibrous; **L** 6–16, linear, softly fleshy, 6–9 cm  $\times$  2–3 mm, green; **Inf** 1–4, axis terete, 12–12 cm; **Ped** 8–35 mm at fruiting time, recurved; **Fl** pendent, somewhat zygomorphic as stamens and style point into opposite directions; **Tep** yellow, 7–8 mm; **St** dissimilar, outer short, glabrous, inner longer, with hairs near the apex; **Anth** yellow-brown; **Ov** with 2 ovules per locule; **Sty** 0.5–1 mm; **Sti** 3-lobed; **Fr** pendent, yellow, globose, 3–4 mm; **Se** unwinged, brown, 4–5 mm, dull, angular.

Similar to *B. semibarbata*, but with pendent flowers and fruits. — [U. Eggli]

**B. praemorsa** (Jacquin) Sprengel (Syst. Veg. 2: 86, 1825). **Type:** not typified. — **Distr:** RSA (Northern Cape, Western Cape, Mpumalanga); rocky sandstone slopes, 155–650 m.

$\equiv$  *Anthericum praemorsum* Jacquin (1793); **incl.** *Anthericum alooides* Thunberg (1794) (*nom. illeg.*, Art. 53.1); **incl.** *Bulbine laxiflora* Baker (1876); **incl.** *Bulbine urgineoides* Baker (1876); **incl.** *Bulbine zeyheri* Baker (1876); **incl.** *Bulbine tetraphylla* Dinter (1931).

Solitary, shortly caulescent, 6–19 cm tall; tuber depressed, sparingly lobed, brownish, to 4 cm  $\varnothing$ , lobes tapering; **R** terete, fleshy, to 3 mm  $\varnothing$ ; stem erect with a ring of bristles at the base surrounding the leaves; **L** 4–6, distichous, unequal, 8.5–19  $\times$  0.4–1.2 cm, ascending, softly succulent, light green, amplexicaul, linear-lanceolate, striate, upper face channelled, lower face convex, apex acute, apiculate; **Inf** 1–2, 27–36 cm, synanthous, densely flowered; peduncle 10–16 cm, biconvex,

to 5 mm  $\emptyset$  at the base; **Fl** stellate, spreading,  $\pm$  20 mm  $\emptyset$ , yellow; **Bra** to 3 mm, ovate-acuminate, clasping; **Ped** 7–8 mm; **Tep** becoming reflexed; **OTep** elliptic, 8  $\times$  2 mm, acute; **ITep** obovate, 8  $\times$  5 mm, obtuse; **St** 5 mm; **Anth** yellow, oblong, 1 mm; **Ov** elliptic-oblong, 2 mm; **Sty** yellow, 5 mm; **Fr** oblong, 10–13  $\times$  4–8 mm; **Se** oblong, 4  $\times$  1.5 mm, grey-black.

According to a preliminary note by Boatwright & al. (2015), this widespread and variable species is not monophyletic in its current circumscription and in need of further study. — [E. Van Jaarsveld]

**B. pusilla** Von Poellnitz (Feddes Repert. Spec. Nov. Regni Veg. 53(1): 46–47, 1944). **Type:** RSA, Western Cape (*Schlechter* 9035 [B]). — **Distr:** RSA (Western Cape); quartzitic sandstone rocks, in crevices; mid-summer-flowering.

Dwarf solitary summer-deciduous geophytes to 2.5 cm tall; tuber globose, 3- to 5-lobed,  $\pm$  1 cm tall, 1.5 cm  $\emptyset$ , with greyish papery tunics, tissue pinkish; **R** grey, fleshy, terete; **L** 2, erectly spreading, grey-green, amplexicaul, linear-lanceolate, 1–3 cm  $\times$  2–4 mm, upper face flat, channelled towards the tip, lower face convex, tip acute; **Inf** 1, 8- to 12-flowered, 5–8 cm; peduncle 1 mm  $\emptyset$  at the base, terete; **Bra** 1.5  $\times$  1 mm, deltoid-acuminate, clasping; **Ped** 7–9 mm; **Fl** spreading and slightly drooping,  $\pm$  8–10 mm  $\emptyset$ ; **Per** stellate, becoming reflexed, pale yellow; **OTep** lanceolate, 7  $\times$  2 mm; **ITep** ovate to ovate-elliptic, 6  $\times$  3.5 mm, obtuse; **St** 6 mm; **Anth** yellow, oblong; **Ov** globose, 1 mm  $\emptyset$ ; **Sty** erect, yellow, 6 mm; **Fr** ovoid, 4  $\times$  3 mm; **Se** 1.5 mm, grey-black. — [E. Van Jaarsveld]

**B. quartzicola** G. Williamson (Haseltonia 4: 19–21, ill. (p. 16), 1996). **Type:** RSA, Northern Cape (*Williamson & Hammer* 5416 [NBG]). — **Distr:** RSA (Northern Cape: Namaqualand); Succulent Karoo, 600 m, flowers late spring and early summer.

Deciduous erect softly succulent herbs to 7 cm tall; tuber deltoid to round, 1.5–2.5 cm  $\emptyset$  and 1.5 cm tall, decurrent into tapering thick and fleshy roots; **L** 3, erect, light green and many-veined, circinate in the upper  $\frac{1}{2}$ , basal part subtended by an elongated papyraceous sheath to

4 cm long, lamina flattened, subterete to terete, 4–8 cm  $\times$  2.5–4 mm, tip acute; **Inf** erect; peduncle slender, to 12 cm; raceme to 6 cm; **Fl** 6–16; **Bra** triangular-acuminate, membranous, to 5 mm; **Ped** to 1.2 mm; **Tep** light yellow, ovate; **OTep** strongly reflexed, 7  $\times$  2.5 mm; **ITep** reflexed at an angle of 45°, 7  $\times$  4 mm; **Fil** slender-bearded; **Ov** oblong, green, 1 mm; **Sty** 6 mm, decurved; **Fr** and **Se** not known. — [E. Van Jaarsveld]

**B. ramosa** Van Jaarsveld (Aloe 40(1): 6–7, ill., 2003). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 14,147 [NBG]). — **Distr:** RSA (Western Cape: Little Karoo); sheer quartzitic sandstone cliff faces in Gamka Thicket vegetation.

Plants rosulate, dividing to form dense groups; **R** fleshy, terete; stem short, 2.5 cm  $\emptyset$ ; **L** 6–8, green, obscurely striate, soft, ascending to slightly falcate, older leaves spreading, lamina linear to triangular-lanceolate, 8–11  $\times$  1.5–2.3 cm, upper face flat, lower face convex, apex acute; **Inf** 1–2, 3–4.7 cm, laxly 20- to 35-flowered in the upper  $\frac{1}{3}$ , slightly drooping; peduncle flattened, 3–4 mm wide at the base, terete upwards and tapering to 2 mm  $\emptyset$ ; **Bra** membranous, withering, the lower triangular-acuminate, 2–3  $\times$  1 mm; **Ped** 11–15 mm, terete; **Fl** spreading, stellate,  $\pm$  18 mm  $\emptyset$ , yellow; **OTep** elliptic, 9  $\times$  3 mm, obtuse; **ITep** 9  $\times$  6 mm, obtuse; **St** 6 mm; **Anth** yellow, 1 mm, oblong; **Ov** globose, 1.5 mm  $\emptyset$ ; **Sty** erect, terete, yellow, 6.5 mm; **Fr** rounded, 4  $\times$  3 mm; **Se** 1.5 mm, oblong-elliptic, grey-black. — [E. Van Jaarsveld]

**B. retinens** Van Jaarsveld & S. A. Hammer (Aloe 42 (1–2): 14–15, ill., 2005). **Type:** RSA, Eastern Cape (*Van Jaarsveld & Welsh* 15747 [NBG]). — **Distr:** RSA (Eastern Cape); quartzitic sandstone cliffs in Gamtoos Thicket vegetation.

Ascending, branched, cluster-forming, to 9  $\times$  9 cm (excl. inflorescence), with 3–9 rosettes; tubers ovoid, 1.2–2  $\times$  1–1.5 cm, covered with dry remains of the sheathing leaf bases that weather to form a fibrous network, flesh yellow; **R** grey, fleshy, terete, 1.5 mm  $\emptyset$ ; **L** 5–7 in an apical rosette, forming a short neck to 7 mm at the base, erect, soft-textured, linear and subterete, 5–8

× 0.5–0.7 cm, surface smooth, grey-green due to a dense powdery bloom, obscurely striate, apex acute, apiculate; **Inf** 35–49 cm, raceme 23–31 cm, 17- to 35-flowered; **Bra** deltoid, acuminate, 2 × 1 mm, clasping; **Ped** 14–17 mm; **Fl** drooping, 15–20 mm Ø; **Tep** stellately spreading, becoming reflexed, pale orange-yellow; **OTep** elliptic, 11 × 3 mm; **ITep** ovate to ovate-elliptic, 12 × 5 mm, obtuse; **St** 8 mm; **Ov** globose, 1.5 mm; **Sty** erect, to 6 mm; **Fr** obovoid, 6 × 2.5 mm; **Se** 2.2 × 1.2 mm, black. — [E. Van Jaarsveld]

**B. rhopalophylla** Dinter (Repert. Spec. Nov. Regni Veg. 29 (11–20): 271–272, 1931). **Type:** Namibia (*Dinter* 6494 [LUS]). — **Distr:** S Namibia, RSA (Northern Cape: Richtersveld); Succulent Karoo, 30–600 m, flowers in mid-winter.

Dwarf rosulate succulent geophytes to 5 cm tall; tuber depressed-globose, 1.5–2 cm tall and wide; **R** terete; **L** 2–4, erect, green, club-shaped, 2–3 × 0.4–1 cm, apex obtuse, mucronate; **Inf** 4–4.5 cm, laxly flowered; peduncle terete, 0.75 mm Ø; **Bra** triangular-lanceolate, 2 × 0.75 mm; **Ped** terete, 2–5 mm; **Fl** spreading, stellate, 12 mm Ø, yellow; **OTep** oblong-ovate, 6 × 1.5 mm; **ITep** 5 × 2 mm, obtuse; **St** 3 mm; **Ov** 2 × 1 mm, oblong; **Sty** erect, terete, 4 mm; **Fr** not seen; **Se** angled, 5 × 3 mm, angles almost winged. — [E. Van Jaarsveld]

**B. rupicola** G. Williamson (*Bradleya* 18: 35–36, ills., 2000). **Type:** RSA, Eastern Cape (*Williamson* 5927 [NBG]). — **Distr:** RSA (Eastern Cape); crevices in rocky kloofs, 600–800 m, flowers mid-summer.

Dwarf geophytes, proliferating to form chains of ovoid tubers, tubers 0.8–1.2 × 1–1.2 cm, with up to 7 horizontal incremental growth lines; **R** 6, spreading, to 40 × 1.2 mm; **L** 3–4, rosulate, erect, arising from papery sheathing remains of old leaves, lanceolate, terete to subterete, acute, 3–6 × 0.3–0.7 cm, transparently green, margins finely toothed towards the base; **Inf** solitary, erect, to 22 cm, to 8-flowered; peduncle to 1.5 mm Ø at the base, terete; **Bra** deltoid-acuminate, 3 × 2 mm; **Ped** 10 mm; **Tep** recurved, light yellow; **OTep** ovate with narrow obtuse tip, 7 × 2 mm; **ITep** broadly ovate, 7 × 3 mm, tip emarginate; **St**

projecting forwards in a tight bunch; **Ov** ovoid, 1.3 mm; **Sty** erect, 5.5 mm; **Sti** minute, rugulose; **Fr** and **Se** not seen. — [E. Van Jaarsveld]

**B. sedifolia** Schlechter *ex* Von Poellnitz (Feddes Repert. Spec. Nov. Regni Veg. 53(1): 47–48, 1944). **Type:** RSA, Western Cape (*Schlechter* 11003 [B]). — **Distr:** RSA (Northern Cape, Western Cape); Fynbos on quartzitic sandstone, in rock crevices, 615–925 m.

Rosulate evergreen solitary succulents 2.5–4 cm tall; tuber depressed-globose, 1–1.2 cm wide and tall; **R** terete; **L** 6–10, linear-lanceolate, acuminate, 1.6–3 cm × 3–4 mm, upper face flat, lower face convex, tip acute; **Inf** 5–17 cm, laxly flowered in the upper ½; peduncle terete, 1 mm Ø at the base; **Bra** triangular-lanceolate, 2 × 1 mm; **Ped** terete, 7 mm; **Fl** spreading, stellate, 12–15 mm Ø, yellow; **OTep** oblong-ovate, 7 × 2 mm; **ITep** ovate, 6 × 4 mm, obtuse; **St** 4 mm; **Ov** ovate to ellipsoid, 1–1.5 mm; **Sty** erect, 5 mm, terete; **Fr** ellipsoid, 3–4 mm; **Se** angular, 1 mm Ø. — [E. Van Jaarsveld]

**B. semenaliundata** G. Williamson (*Aloe* 40 (1): 8, 2003). **Type:** RSA, Western Cape (*Williamson* 5931 [NBG]). — **Lit:** Williamson (2000: 32–34). **Distr:** RSA (Western Cape: Cederberg); shallow pockets of bedrock, Fynbos vegetation, flowering in late spring.

≡ *Bulbine undulata* G. Williamson (2000) (*nom. illeg.*, Art. 53.1).

Ascending from dome-shaped tubers, tubers 1.3–1.5 × 0.8–0.9 cm, truncate at the base and with radiating tapering roots; **L** 4, hysteranthous, erect, linear, terete, translucent shiny green, 8 × 0.3 cm, with a broad sheathing base, shorter leaves ± 4 × 0.12 cm, after withering of the leaves basal sheaths tightening into a narrow cylinder ± 3.5 × 0.2 cm, clasping the developing inflorescence; **Inf** 14.5 cm; **Fl** 6–20 in a lax raceme; **Bra** 1.2 × 1 mm, triangular-acuminate; **Ped** ± 7 mm; **Tep** light pale yellow; **OTep** reflexed, lanceolate, obtuse, 7 × 2 mm; **ITep** narrowly ovate, obtuse, 7 × 4 mm; **Fil** 6 mm, bearded; **Ov** globose, 1 mm; **Sty** and **Sti** 6 mm; **Fr** ovoid, 2 × 1.8 mm; **Se** 1 × 0.8 mm, narrowly



pyramidal, surface black, rough. — [E. Van Jaarsveld]

**B. semibarbata** (R. Brown) Haworth (Revis. Pl. Succ., 33, 1821). **Type:** Australia, South Australia (*Brown* s.n. [BM]). — **Distr:** Australia (widespread throughout); granite outcrops and salt lake margins; neophyte in England. **I:** Cunningham & al. (1981: 183).

≡ *Anthericum semibarbatum* R. Brown (1810) ≡ *Phalangium semibarbatum* (R. Brown) Kuntze (1891) ≡ *Bulbinopsis semibarbata* (R. Brown) Borzi (1897); **incl.** *Bulbine floribunda* Schrader ex Bentham (1878); **incl.** *Bulbine semibarbata* f. *gracilescens* Domin (1912).

Annual succulent herbs without caudex; **R** fibrous; **L** 6–16, linear to subulate, channelled, 1.5–27 × to 0.5 cm wide, green, rarely glaucous; **Inf** erect, 1 to many, axis terete; **Ped** 8–25 mm at fruiting time, erect to recurved; **Tep** 3–7 mm, yellow; **St** 3 short, 3 long, closely bunched; **Anth** reddish, orange or yellow-brown, erect to horizontal after dehiscence; **Ov** with 2 ovules per locule; **Sty** straight, 0.5–1.5 mm; **Fr** globose, 2–4.5 mm; **Se** smooth.

Reported as alien invasive in England by Shaw (2002). — [U. Egli]

**B. spongiosa** Van Jaarsveld (*Bradleya* 33: 158–160, ills. (pp. 157–160), 2015). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 23410 [NBG]). — **Distr:** RSA (Western Cape: Badspoort area); quartzitic sandstone cliff faces, Succulent Karoo, spring-flowering.

Geophytes, first solitary but tubers proliferating from the side filling crevices; tubers dark brown, conical, 1.6–2.2 × 1.5–1.8 cm wide at the truncate base; **R** grey-brown from the perimeter of the tuber, to 5 mm Ø at the base and 5–10 cm long, tapering; **L** erect, 2–3, 9–20 × 0.5–0.8 cm, ascending, linear-lanceolate, soft-textured and faintly translucent, pale grey-green, obscurely striate, tapering into the acute apex, smooth but wrinkled when withering, margin entire, inner tissue (mesophyll) distinctly spongy, leaf bases amplexicaul, persistent and forming a tight neck to 2 cm long, weathering leaving a few dry fibres; **Inf** 13.5–22 cm, raceme 4.5–7 cm

making up the upper ¼, sparsely 6- to 20-flowered; peduncle to 3 mm Ø at the base, biconvex, grey-green; **Bra** deltoid, to 3 × 0.75 mm, acuminate, clasping; **Ped** 10–15 mm; **Per** stellate, ± 16–20 mm Ø; **Tep** pale yellow with greenish-yellow midstripes, apices obtuse; **OTep** narrowly oblanceolate, to 10 × 4 mm; **ITep** elliptic to elliptic-oblanceolate, to 10 × 4.5 mm; **St** to 5 mm, bearded in the central part with hairs 1–2 mm long; **Ov** obovoid, to 1.5 mm Ø; **Sty** erect, to 6 mm; **Fr** obovoid, to 5–7 × 3–4 mm, ascending; **Se** 1.5–2 × 1.5 mm, grey-brown, angular.

The spongy leaf tissue appears unique in the genus. — [E. Van Jaarsveld]

**B. stolonifera** Baijnath ex G. Williamson (*Aloe* 43(4): 93–94, ills., 2007). **Type:** RSA, Northern Cape (*Williamson* 5967 [NBG]). — **Distr:** RSA (Northern Cape); Succulent Karoo, sandy loam, winter-flowering.

To 30 cm tall (excl. inflorescence); tuber subglobose, 4.5–5.2 cm Ø; **R** 3–11 cm long, spreading, elongate-clavate and with scattered swellings, producing stoloniferous growths; **L** up to 5, arising from a pseudo-stem, distichous, 10–16 × 1 cm, with an adaxial channel in the lower ⅓ and a triangular base ± 1.5 cm broad; **Inf** ± 32 cm, raceme subdense with up to 60 flowers; **Ped** 28 mm; **Bra** triangular, 5 × 2 mm; **Fl** acrid-scented; **Tep** reflexed; **OTep** 11 × 3–3.6 mm, light greenish-yellow; **ITep** 11 × 5 mm, light yellow; **St** 9 mm with glandular clavate hairs; **Ov** 3 × 1.8 mm; **Sty** 7.5 mm; **Fr** 15 × 7 mm; **Se** 6 × 2–2.5 mm, blackish-brown, narrowly oblong. — [E. Van Jaarsveld]

**B. striata** Van Jaarsveld & Baijnath (*South Afr. J. Bot.* 53(6): 424–426, ills., 1987). **Type:** RSA, Northern Cape (*Van Jaarsveld & Patterson* 6640 [NBG]). — **Distr:** RSA (Northern Cape); Succulent Karoo, quartz rocks, 900–1000 m, spring-flowering.

Solitary geophytes; tuber oblong, ± 2.5 × 1.8 cm, rounded at the top with dark brown tunics overtopped with a ring of bristles; **R** in appressed bundles; **L** 4–6, rosulate, spreading, ovate-lanceolate, 5–15 × 2.5–4 cm, upper face striate,

translucent; **Inf** 1, erect, to 57 cm; peduncle 3.5 mm  $\varnothing$ , terete; **Bra** membranous, deltoid-acuminate, 2  $\times$  1 mm; **Ped** 10–20 mm, ascending; **Fl** stellate, 14–16 mm  $\varnothing$ ; **Tep** pale yellow, reflexed when fully open; **OTep** ovate-elliptic, 8  $\times$  1.5 mm; **ITep** 8  $\times$  2.5 mm; **St** 4–5 mm; **Ov** globose; **Sty** 5 mm; **Fr** not seen; **Se** black, oblong-angular, 3  $\times$  1 mm. — [E. Van Jaarsveld].

**B. succulenta** Compton (Trans. Roy. Soc. South Africa 14: 275, 1931). **Type:** RSA, Western Cape (*Compton* 2910 [NBG]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo, 615–925 m, spring-flowering.

**Incl.** *Bulbine hantamensis* Von Poellnitz (1944).

Acaulescent, rosulate, up to 13 cm tall, solitary; tuber oblong-ovoid, 3  $\times$  1.5 cm with black tunics and a ring of bristles surrounding the leaves; **R** brownish, tips yellow, terete; **L** 8–10, amplexicaul, glaucous-green, variable, ascending, linear-clavate, 2–13  $\times$  0.3–1 cm, widening towards the tip, lamina obscurely striate, upper face flat, lower face convex, tip obtuse to acute, mucronate; **Inf** 1, 10–20 cm, ascending to spreading, laxly flowered in the upper  $\frac{1}{6}$ , flowers 3–7 mm apart; peduncle 1.5–4 mm  $\varnothing$  at the base, biconvex, terete upwards; **Bra** 4  $\times$  1 mm, membranous, deltoid-acuminate, clasping; **Ped** 8–10 mm; **Per** stellate, 15–20 mm  $\varnothing$ , yellow; **Tep** becoming reflexed; **OTep** elliptic-lanceolate, 7–10  $\times$  2 mm; **ITep** broadly ovate, 7–9  $\times$  3–4 mm, obtuse; **St** 5–6 mm; **Anth** yellow, oblong; **Ov** globose, 2 mm  $\varnothing$ ; **Sty** erect, yellow, 5 mm; **Fr** ovoid, 10  $\times$  5 mm; **Se** grey-black, 2  $\times$  4 mm. — [E. Van Jaarsveld]

**B. suurbergensis** Van Jaarsveld & A. E. van Wyk (Aloe 42(3): 48–50, ill., 2005). **Type:** RSA, Eastern Cape (*van Jaarsveld & Burring* 19228 [NBG]). — **Distr:** RSA (Eastern Cape: Suurberg, Witterivier); sheer quartzitic sandstone rock faces, spring-flowering.

Plants first solitary, then dividing to form pendent shrubs, without tuber; stems pendent, to 70  $\times$  1.5 cm, covered with persistent leaf bases weathering to form a fibrous network, basal stem part often becoming glabrous, grey-brown,

smooth, with aerial roots; **R** grey-brown, fleshy, terete,  $\pm$  1.5–2 mm  $\varnothing$ ; **Ros**  $\pm$  15 cm  $\varnothing$ , curving upwards at the stem tips; **L** 6–10 per rosette, linear-lanceolate, 7–17  $\times$  1.2–1.8 cm, upper face flat, lower face convex to rounded, becoming channelled during drought, soft-textured, pale green, smooth, obscurely striate, margin entire, apex acute, mucronate; **Inf** 11–35 cm, raceme 10–15.3 cm, sparsely flowered with 20–30 flowers; **Bra** deltoid, 3  $\times$  0.5 mm, acuminate, clasping; **Ped** 8–10 mm; **Per** stellate,  $\pm$  13 mm  $\varnothing$ ; **Tep** bright yellow, apices obtuse to emarginate; **OTep** narrowly oblanceolate, 7–9  $\times$  1.5–2 mm; **ITep** elliptic to elliptic-oblanceolate, 7–8  $\times$  2.5–3 mm; **St** to 7 mm, bearded in the central part with hairs 1–2 mm long; **Ov** obovoid, 1 mm  $\varnothing$ ; **Sty** 4.5 mm; **Fr** obovoid, to 3  $\varnothing$  2.5 mm, ascending; **Se** 3  $\times$  1.5 mm, black. — [E. Van Jaarsveld]

**B. tecta** G. Williamson (Aloe 51(1): 16–17, ill., 2014). **Type:** RSA, Northern Cape (*du Toit* s.n. in *Williamson* 6045 [BOL]). — **Distr:** RSA (Northern Cape); Succulent Karoo vegetation, spring-flowering.

Plants solitary; tuber napiform, to 1.7  $\times$  1.2 cm, with numerous spreading fusiform **R** from a flat base; **L** 4, alternate, to 4.5  $\times$  0.9 cm, ascending, broadly lanceolate to narrowly elliptic, apex obtuse to broadly acute, each with 3 broad, prominent, rounded, longitudinal ridges, base narrow to form a tubular sheath to 2  $\times$  0.8 cm, surrounded by tight white sheaths; **Inf** erect, 2, to 13 cm, peduncle terete, to 1.8  $\varnothing$  mm, reddish-brown, lax to subdense, to 10-flowered; **Bra** 2  $\times$  1.5 mm; **Ped** 10 mm; **Fl** 16 mm  $\varnothing$ , nodding at 45° or porrect; **Tep** strongly reflexed, canary-yellow; **OTep** narrowly elliptic, to 8  $\times$  2 mm; **ITep** ovate, to 8  $\times$  4 mm; **St** dimorphic, 7 mm, bearded with a cluster of glandular hairs, outer with a single cluster; **Ov** dark olive-green, 2  $\times$  1.2 mm, subglobose, minutely pitted; **Sty** 4 mm; **Fr** narrowly ovoid, 4  $\times$  3 mm; **Se** pyramidal, 2  $\times$  2 mm, dark brownish, granulate. — [E. Van Jaarsveld]

**B. tecta** ssp. **parvifolia** G. Williamson (Aloe 51(1): 16–18, ill., 2014). **Type:** RSA, Northern

Cape (*du Toit* s.n. in *Williamson* 6046 [BOL]). — **Distr:** RSA (Northern Cape); sandy pans among sandstone outcrops.

**L** broadly ovate, subacute,  $1.5 \times 0.7$  cm, becoming distinctly truncate when dying off; **Inf** laxly 6-flowered; **Fl** porrect; **OTep**  $7 \times 2$  mm, strongly reflexed; **ITep**  $7 \times 4$  mm. — [E. Van Jaarsveld]

**B. tecta** ssp. *tecta* — **Distr:** RSA (Northern Cape); granite domes.

**L** to  $4.5 \times 0.9$  cm, not becoming truncate when dying off; **Inf** > 6-flowered; **Fl** nodding at  $45^\circ$ ; **OTep** narrowly elliptic,  $8 \times 2$  mm; **ITep** ovate,  $8 \times 4$  mm. — [E. Van Jaarsveld]

**B. thomasiae** Van Jaarsveld (*Aloe* 40(1): 5, ills. (p. 6), 2003). **Type:** RSA, Eastern Cape (*Van Jaarsveld & Ems* 16631 [NBG]). — **Distr:** RSA (Eastern Cape: Lower Bashee River); S-facing cliffs in Valley Bushveld vegetation, spring-flowering.

Plants short-stemmed, with pendent dividing **Ros** forming clusters of up to 8 heads; tuber ovoid,  $2 \times 1.8$  cm, tapering slightly towards the neck, sparsely covered with few soft fibres; **R** terete, to 2 mm  $\varnothing$ ; **Ros** 15 cm  $\varnothing$ ; **L** very soft, up to 7, drawn together, pendent or curving downwards, linear-lanceolate to triangular-lanceolate,  $8\text{--}17 \times 1.4\text{--}3$  cm, base clasping, upper face of lamina channelled to flattened, lower face rounded, glaucous, becoming reddish-pink during dry winters, faintly translucent and striate, covered with short pointed papillae, apex acute, mucronate, margins acute, translucent, minutely ciliate; **Inf** 25–29 cm, raceme subcapitate, 4–8 cm, pointed, densely flowered, flowers secundly arranged; **Bra** deltoid-ovate, cymbiform,  $4\text{--}5 \times 3$  mm, apex acuminate, keel and margins minutely ciliate, clasping; **Ped** 15–20 mm; **Per** stellate,  $\pm 15$  mm  $\varnothing$  when fully expanded; **Tep** spreading becoming reflexed, orange-yellow, slightly channelled and incurved at the tips; **OTep** oblong-obovate,  $8 \times 3$  mm; **ITep** ovate-lanceolate,  $7.5 \times 2$  mm, obtuse; **St** to 6 mm, bearded in the distal  $\frac{1}{4}$ ; **Ov** globose, 1.5 mm; **Fr** obovoid,  $5 \times 4$  mm, pendent; **Se** to 2 mm  $\varnothing$ , angular, black. — [E. Van Jaarsveld]

**B. torsiva** G. Williamson (*Haseltonia* 4: 21, ills. (pp. 17, 20), 1996). **Type:** RSA, Northern Cape (*Williamson & Hammer* 5420 [NBG]). — **Distr:** RSA (Northern Cape: Richtersveld); Succulent Karoo, 400–800 m, flowers late spring to mid-summer.

Deciduous erect softly succulent herbs to 11 cm tall; tuber depressed-pyramidal, 2–3 cm  $\varnothing$  and 1.5 cm tall, tapering into fleshy decurrent roots; **L** 3, erect, light green, multiveined, basal part subtended by an elongated papyraceous sheath 4–15 mm long, lamina subterete, forming tight spirals,  $5\text{--}8 \times 1.5\text{--}2$  mm, tip acute; **Inf** erect; peduncle slender, 5–15 cm; raceme 2.5–6 cm with 6–12 flowers; **Bra** narrowly triangular-acuminate, membranous, to 1 mm; **Ped** to 8 mm; **Tep** strongly reflexed, light yellow; **OTep** subacute,  $5\text{--}7 \times 1.3\text{--}2.5$  mm; **ITep** elliptic,  $7 \times 4$  mm; **Fil** stout, bearded; **Ov** oblong to globose, dark green, 1 mm; **Sty** 4 mm, yellow; **Fr** subglobose to oblong,  $\pm 2$  mm; **Se** black, pyramidal, with undulate ridges, 1–1.5 mm  $\varnothing$ . — [E. Van Jaarsveld]

**B. torta** N. E. Brown (*Bull. Misc. Inform. Kew* 1908: 409, 1908). **Type:** RSA, Western Cape (*Wiers* s.n. [K]). — **Distr:** RSA (Northern Cape, Western Cape); dry Fynbos, 230–1000 m, spring-flowering.

**Incl.** *Bulbine circinata* Schlechter ex Von Poellnitz (1944); **incl.** *Bulbine circinata* var. *minor* Von Poellnitz (1944); **incl.** *Bulbine mallyana* Schlechter ex Von Poellnitz (1944).

Small rosulate geophytes to 5–12 cm tall; tuber depressed, 2 cm  $\varnothing$ , 1 cm tall; **R** terete; **L** numerous, 3.5–12 cm  $\times$  1 mm, tortuose, filiform; **Inf** 8–10 cm, laxly flowered; peduncle 1 mm  $\varnothing$  at the base; **Bra** triangular-lanceolate,  $3 \times 1$  mm; **Ped** terete, 8–10 mm; **Fl** spreading, stellate, 13–14 mm  $\varnothing$ , yellow; **OTep** oblong-ovate,  $7 \times 1.5$  mm; **ITep**  $6 \times 4$  mm, obtuse; **St** 5 mm; **Anth** 0.5 mm, oblong; **Ov** globose, 1.5 mm; **Sty** erect, terete, 3 mm; **Fr** globose; **Se** 2 mm. — [E. Van Jaarsveld]

**B. truncata** G. Williamson (*Haseltonia* 4: 19, ills. (pp. 15, 20), 1996). **Type:** RSA, Northern Cape (*Williamson & Hammer* 5415 [NBG]). —

**Distr:** RSA (Northern Cape: Namaqualand); Succulent Karoo, 400–600 m, flowers in mid-summer.

Deciduous erect soft acaulescent herbs to 3.5 cm tall; tuber dome-shaped, to 1.1 cm wide with up to 6 thick and fleshy **R** spreading downwards and decurrent and tapering from the tuber; **L** up to 3, erect, dull green, surface minutely asperulous with 3 longitudinal veins, outer 2 leaves slightly falcate, 3 cm × 4 mm, distinctly truncate, inner leaf smaller and acute, all leaves subtended by an elongated papyraceous sheath to 4 mm long; **Inf** erect; peduncle purple, slender, to 5 cm; raceme to 2.5 cm; **Fl** 6–8; **Bra** triangular-acuminate, membranous, to 1.5 mm; **Ped** to 7 mm; **Tep** brownish-orange with darker midvein, reflexed; **OTep** elliptic-acuminate, obtuse, 7 × 1.8 mm; **ITep** obovate, 7 × 4 mm; **Fil** slender, 6.5 mm; **Ov** ellipsoid, green, 2 mm; **Sty** 5 mm; **Se** up to 3 per fruit, deltoid, runcate, to 2 mm wide. — [E. Van Jaarsveld]

**B. vagans** E. M. Watson (in George, A. S. (ed.), *Fl. Austral.* 45: 470, ill., 1987). **Type:** Australia, Queensland (*Watson* 152 [CBG, AD, BRI, K]). — **Distr:** Australia (SE Queensland, NE New South Wales); usually in rock crevices. **I:** Forster (1993); Kapitany (2007: 30–31).

Perennial succulent herbs without caudex; **R** succulent; **L** many, linear to subulate, channelled, 20–60 cm, 2–8 mm wide, somewhat flaccid, green, not glaucous; **Inf** 1 to many, straggling, axis angular; **Ped** 18–24 mm at fruiting time, often twisting and drooping at the tip; **Fl** slightly zygomorphic due to the asymmetrical placement of stamens and style; **Tep** 8–13 mm, yellow; **St** 3 short, 3 long, closely bunched and deflexed to one side; **Anth** yellow, ± basifixed, inclining over the style after dehiscence; **Ov** with 2–4 ovules per locule; **Sty** erect or down-curved, 2–3 mm; **Fr** 3-lobed, 3–5 mm; **Se** heavily ridged.

Vaughton & al. (2008) found that the plants are self-fertile, and that spontaneous self-pollination occurs in wilting flowers, ensuring reproductive success (contrary to the situation for *B. bulbosa*), although selfing results in inbreeding depression. — [U. Egli]

**B. vitrea** G. Williamson & Baijnath (South Afr. J. Bot. 61(6): 314–316, ills., 1995). **Type:** RSA, Northern Cape (*Williamson* 4471 [NBG]). — **Distr:** RSA (Northern Cape: Richtersveld); Succulent Karoo, 200–380 m, flowers in mid-summer. **I:** Smale (2002).

Dwarf solitary summer-deciduous geophytes to 1 cm tall; tuber globose, 3- to 5-lobed, ± 1–1.5 cm Ø, 1 cm tall, with greyish papery tunics, flesh pinkish where exposed; **R** grey, succulent, terete; **L** 1–4, ascending, linear-lanceolate, 0.5–1 × 0.2–0.4 cm, tessellate, grey-green tinged pink, amplexicaul, surface undulating, older leaves becoming truncate, upper face flat, lower face convex, apex acute; **Inf** 1–3, 2.5–6 cm, 3- to 7-flowered in the upper 1/3, ascending; peduncle 1 mm Ø at the base, terete; **Bra** 3 × 1 mm, membranous, deltoid-acuminate, amplexicaul; **Ped** 4 mm; **Fl** 2–6 mm apart; **Per** stellate, becoming reflexed, ± 10–14 mm Ø, yellow; **OTep** ovate-lanceolate, 5 × 1.5–2 mm; **ITep** ovate to ovate-elliptic, 5 × 3 mm, obtuse; **St** 4.5 mm; **Anth** yellow, oblong, 1 mm; **Ov** globose, 1 mm Ø, yellowish-green, grooved; **Sty** erect, 5 mm; **Fr** ovoid, 2 mm long; **Se** 1 mm. — [E. Van Jaarsveld]

**B. vittatifolia** G. Williamson (Haseltonia 4: 21–22, ills. (pp. 18, 20), 1996). **Type:** RSA, Northern Cape (*Williamson* 5527 [NBG]). — **Distr:** RSA (Northern Cape: Namaqualand); Succulent Karoo, 800–1000 m, flowers in mid-summer. **I:** Smale (2002).

Small rosulate deciduous geophytes to 8 cm tall; tuber depressed-ovoid, 3–4.5 × 3–4 cm Ø; **L** 15–20 per plant, 2–3.5 × 0.2–0.3 cm, erect, upper 1/2 curved horizontally towards the light, softly succulent with translucent greenish-white base below ground-level, upper face flat to slightly convex, translucent and with 3 darker green striations, lower face convex, not translucent, tip acute, mucronate; **Inf** 1–4, to 12–19 cm with 25–45 spreading flowers, 1–1.5 mm Ø at the base; **Bra** triangular-acuminate, 1.5 × 1 mm; **Ped** terete, 4–8 mm; **Per** stellately spreading, yellow, 12 mm Ø; **OTep** oblong-lanceolate, 7 × 1.5 mm, tips acute; **ITep** 6 × 2 mm, tips obtuse; **St** 5–6 mm; **Fil** bearded in the upper 1/3; **Ov** globose, 1 mm; **Sty** erect, terete, 4.5 mm; **Sti** capitate; **Fr**

globose, 7 mm  $\varnothing$ ; **Se** 3  $\times$  4 mm, broadly ellipsoid, angled, shiny, black. — [E. Van Jaarsveld]

**B. wiesei** L. I. Hall (South Afr. J. Bot. 3(6): 357, 1984). **Type:** RSA, Western Cape (*Wiese* s.n. [NBG 126754, K, PRE]). — **Distr:** RSA (Western Cape); Succulent Karoo, quartz flats,  $\pm$  200 m, flowers from late spring to early summer. **I:** Smale (2002).

Dwarf deciduous acaulescent rosulate solitary geophytes; tuber depressed, globose above, flat below, 1 cm tall and 1.5 cm wide, with a ring of bristles surrounding the rosettes; tunics brown; **R** fleshy, terete; **L** to 20, crowded, oblong-acute, ascending, 3.5–4  $\times$  0.5 cm, upper face flat to slightly convex, lower face convex, dull silvery-green, apex acute; **Inf** 1, to 10 cm, 20-flowered; peduncle wiry, terete, 1 mm  $\varnothing$  at the base; **Bra** 3 mm, deltoid-cuspidate; **Ped** 8–12 mm; **Per** stellate, becoming reflexed, to 16 mm  $\varnothing$ , yellow; **OTep** lanceolate, 8  $\times$  3 mm; **ITep** 8  $\times$  6 mm, obtuse; **St** 6 mm; **Ov** oblong, 1.5 mm; **Sty** oblique, terete, yellow, 7 mm; **Fr** pyriform, 4  $\times$  3 mm; **Se** black, oblong, 2  $\times$  1 mm. — [E. Van Jaarsveld]

## References

- Baijnath, H. (1977) Taxonomic studies in the genus *Bulbine* Wolf, sensu lat. Reading (GB): Reading University, unpublished Ph.D. thesis.
- Bester, S. P. [et al. 2012], Herman, P. P. J. & Klopper, R. R. (2012) National Herbarium plant collecting programme reveals new country and provincial distribution records from South African National Parks (*Apocynaceae*, *Asteraceae* & *Xanthorrhoeaceae*: *Asphodeloideae*). *Phytotaxa* 62: 44–56, maps., ills. <https://doi.org/10.11646/phytotaxa.62.1.9>
- Boatwright, J. S. & Manning, J. C. (2010) Notes on African plants. *Asphodelaceae*. Inclusion of the genus *Jodrellia* in *Bulbine* (*Asphodeloideae*). *Bothalia* 40(1): 59. <https://doi.org/10.4102/abc.v40i1.183>
- Boatwright, J. S. [et al. 2015], Manning, J. C., Ramdhani, S., Bank, M. van der & Forest, F. (2015) Towards a revision of *Bulbine* (*Asphodeloideae*, *Asphodelaceae*): Phylogeny and problem species. *South Afr. J. Bot.* 82: 172. <https://doi.org/10.1016/j.sajb.2015.03.021>
- Coopeosamy, R. M. (2011) Traditional information and antibacterial activity of four *Bulbine* species (Wolf). *Afr. J. Biotechnol.* 10(2): 220–224. <https://doi.org/10.5897/AJB10.1435>
- Craib, C. (2002) *Bulbine flavosa* [sic!]. An interesting tuberous species from western Gauteng and Mpumalanga. *Veld Fl.* (1975+) 88(1): 20–21, ills.
- Cunningham, G. M. [et al. 1981], Mulham, W. E., Milthorpe, P. L. & Leigh, J. H. (1981) *Plants of Western New South Wales*. Sydney (AU): New South Wales Government Printer.
- Devey, D. S. [et al. 2006], Leitch, I., Rudall, P. J., Pires, J. C., Pillon, Y. & Chase, M. W. (2006) Systematics of *Xanthorrhoeaceae* sensu lato, with an emphasis on *Bulbine*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 245–351. <https://doi.org/10.5642/aliso.20062201.28>
- Duffy, K. J. & Johnson, S. D. (2015) Staminal hairs enhance fecundity in the pollen-rewarding self-incompatible lily *Bulbine abyssinica*. *Bot. J. Linn. Soc.* 177 (3): 481–490, ills. <https://doi.org/10.1111/boj.12252>
- Forster, P. I. (1993) *Bulbine vagans* E. M. Watson (*Asphodelaceae*), a restricted Australian endemic. *Aloe* 30(1): 23–24, ills.
- Helme, N. (2013) The arid limestones of the Knersvlakte. *Veld Fl.* (1975+) 99(3): 138–141, ills.
- Jaarsveld, E. J. van & Wyk, A. E. (B.) van (2005) A new cliff-dwelling *Bulbine* species (*Asphodelaceae*) from the Eastern Cape. *Aloe* 42(3): 48–51, ills., map, key.
- Kapitany, A. (2007) Australian succulent plants. An introduction. Boronia (AU): Published by the author.
- Kativu, S. (1996) *Asphodelaceae* of the Flora Zambesiaca area. *Kirkia* 16: 27–53.
- Kativu, S. (2001) *Asphodelaceae*. In: Pope, G. V. (ed.): *Flora Zambesiaca*; 12(3): 25–48, keys. Richmond (GB): Royal Botanic Gardens Kew.
- Moore, I. S. F. [et al. 2016], Brown, E. A., Telford, I. R. H. & Bruhl, J. J. (2016) Chromosome evolution in *Bulbine glauca* (*Asphodelaceae* or *Xanthorrhoeaceae* subfam. *Asphodeloideae*) indicates six species, not one. *Austral. J. Bot.* 64(3): 206–218. <https://doi.org/10.1071/BT15242>
- Naidoo, Y. [et al. 2011], Heneidak, S., Kasim, N. & Baijnath, H. (2011) Morphology, developmental ultrastructure and ultracytochemistry of staminal hairs in *Bulbine inflata* (*Asphodelaceae*) in relation to function. *Flora (Jena)* 206 (12): 1069–1075, ills. <https://doi.org/10.1016/j.flora.2011.04.011>
- Newton, L. E. (2011) *Uses of succulent plants in East Africa*. Nairobi (KE): Succulenta East Africa/Nature Kenya.
- Pather, N. [et al. 2011], Viljoen, A. M. & Kramer, B. (2011) A biochemical comparison of the *in vivo* effects of *Bulbine frutescens* and *Bulbine natalensis* on cutaneous wound healing. *J. Ethnopharmacol.* 133(2): 364–370. <https://doi.org/10.1016/j.jep.2010.10.007>
- Sebsebe Demissew & Nordal, I. (2010) *Aloes and lilies of Ethiopia and Eritrea*. Ed. 2. Addis Ababa (ET): Shama Books.
- Shaw, J. M. H. (2002) *Bulbine semibarbata* (R. Br.) Haw., the Leek Lily as a new British alien. *BSBI [Bot. Soc. Brit. Isles] News* 91: 45–46.



- Smale, T. (2002) *Bulbine* — a neglected genus. *Brit. Cact. Succ. J.* 20(4): 207–214, ills.
- Vaughton, G. & Ramsey, M. (2010) Floral emasculation reveals pollen quality limitation of seed output in *Bulbine bulbosa* (*Asphodelaceae*). *Amer. J. Bot.* 97 (1): 174–178. <https://doi.org/10.3732/ajb.0900183>
- Vaughton, G. [ & al. 2008], Ramsey, M. & Simpson, I. (2008) Does selfing provide reproductive assurance in the perennial herb *Bulbine vagans* (*Asphodelaceae*)? *Oikos* 117: 390–398. <https://doi.org/10.1111/j.2007.0030-1299.16365.x>
- Watson, E. M. (1986a) Cytoevolutionary studies in the genus *Bulbine* Wolf (*Liliaceae*). I. The Australian perennial taxa (*B. bulbosa* s.l.). *Austral. J. Bot.* 34: 481–504. <https://doi.org/10.1071/BT9860481>
- Watson, E. M. (1986b) Cytoevolutionary studies in the genus *Bulbine* Wolf (*Liliaceae*). II. The Australian annual taxa (*B. semibarbata* s.l.). *Austral. J. Bot.* 34: 505–522. <https://doi.org/10.1071/BT9860505>
- Watson, E. M. (1987) *Bulbine*. In: George, A. S. (ed.): *Flora of Australia*, 45: 236–241. Canberra (AU): Australian Government Publishing Service.
- Whitehouse, C. M. (2002) *Asphodelaceae*. In: Beentje, H. J. (ed.): *Flora of Tropical East Africa*. Rotterdam (NL) / Brookfield (US): A. A. Balkema.
- Williamson, G. (2000) Four new, succulent *Bulbine* species (*Asphodelaceae*) from the Western and Eastern Cape Provinces of the Republic of South Africa. *Bradleya* 18: 31–40, ills. <https://doi.org/10.25223/brad.n18.2000.a3>
- Williamson, G. (2004) The typification of *Bulbine mesembryanthoides* Haw. *Aloe* 42(2–3): 55.
- Williamson, G. (2016) An account of the interesting biodiversity in a selected number of species in the genus *Bulbine* Wolf, *Asphodelaceae*. *Cact. Succ. J. (US)* 88(1): 4–22, ills. <https://doi.org/10.2985/015.088.0101>
- Wyk, B-E. van [ & al. 1997], Oudtshoorn, B. van & Gericke, N. (1997) *Medicinal plants of South Africa*. Pretoria (ZA): Briza Publications.
- Zukulu, S. [ & al. 2012], Dold, T., Abbott, T. & Raimondo, D. (2012) *Medicinal and charm plants of Pondoland*. Pretoria (ZA): South African National Biodiversity Institute SANBI.





## Bulbinella ASPHODELACEAE

E. Van Jaarsveld

**Bulbinella** Kunth (Enum. Pl. 4: 569, 1843). **Type:** *Anthericum triquetrum* Linné *fil.* [type according to E. Phillips, Gen. South Afr. Fl. Pl., ed. 2, 183, 1951]. — *Asphodeloideae* — **Lit:** Perry (1999: synopsis South Africa). **Distr:** RSA, New Zealand. **Etym:** Lat. diminutive of the name *Bulbine*, for the overall similarity but sometimes smaller stature of the species.

Deciduous perennial geophytes, caulescent or acaulescent; rhizome compact, subterranean, annually replaced; stems surrounded by membranous cataphylls that often leave fibrous remains; **R** fascicled, numerous, swollen, fusiform or with swollen tubers at the ends; **L** variable, crowded at the upper part of the stem, filiform to linear, tapering, herbaceous to somewhat fleshy, triquetrous to subterete or canaliculate, veins prominent or masked, margin entire, denticulate to ciliate, apex acuminate; **Inf** simple, many-flowered racemes, cylindrical, conical to subcorymbose, scape unbranched, naked, terete, with a **Bra** below each flower; **Fl** actinomorphic; **Per** stellate, yellow, orange, white or cream, 6–12 mm Ø; **Tep** 6, equal to subequal, free, rarely connate at the extreme base, oblong, persistent; **St** 6, adnate to the base of the tepals; **Fil** subulate to filiform,

apiculate, glabrous; **Anth** subglobose, dorsifixed, versatile; **Ov** superior, subglobose to ovoid, 3-locular, ovules 2 per locule; **Sty** terete; **Sti** minute, apical; **Fr** capsules, subglobose to ovoid, dehiscent, loculicidally 3-valved, sessile or stipitate, apex with the persistent style; **Se** 1–2 per locule, narrowly or broadly triangular, black, narrowly to distinctly winged.

A genus with a disjunct distribution – 18 species in RSA, and 6 species in New Zealand (both islands as well as Auckland and Campbell Islands). The greatest diversity is in the winter rainfall regions of RSA (mainly Western Cape). *Bulbine* (all species ± to distinctly succulent) is related, but at once distinguished by the bearded filaments. Most species of *Bulbinella* are geophytes in seasonally moist depressions, but with the exception of the taxon covered below are not succulent.

The following names are of unresolved application but are referred to this genus: *Phalangium tenuifolium* Kuntze (1898) ≡ *Bulbine tenuifolia* (Kuntze) Baker *ex* Dyer (1903).

**B. calcicola** J. C. Manning & Goldblatt (Bothalia 40(2): 197–199, ill., 2010). **Type:** RSA, Western Cape (*Claassens & Claassens* 11 [NBG, K, MO]). — **Distr:** RSA (Western Cape); Saldanha Limestone Strandveld vegetation on semi-arid summer-dry coastal limestone flats, flowers in early summer.

Plants solitary, 30–80 cm tall; **R** fascicled, numerous, to 18 cm, some uniformly swollen,

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others often with wiry basal portion and a succulent fusiform distal portion; **L** numerous (20–50), subequal, succulent, the younger shorter, lamina linear, 63 cm × 1.5–2 mm, slightly coiled or twisted distally, triquetrous (triquetrous-cannaliculate when dry), bright green, glabrous, margin ciliolate-denticulate, basal leaf parts expanded to form a white membranous sheath, outer sheaths encircling inner leaves and the scape, sheathing neck 2–3 cm long, with coarse straight loose bristle-like fibres; **Inf** raceme cylindrical or narrowly conical, 50- to 150-flowered, 5 × 1 cm at flowering time, elongating to 20 cm at fruiting time, scape erect, 1–2 mm Ø, reddish; **Bra** membranous, triangular-acuminate, 2–3 × 1.5–2 mm; **Ped** suberect, 3–4 mm;

**Fl** stellate, 6–7 mm Ø, slightly scented; **Tep** bright yellow with greenish midrib, connate basally, elliptic-oblong, inner broader, 3–4 × 1.5–2 mm; **Fil** filiform, suberect, 2.5–3 mm; **Ov** ovoid, 1 mm, 3-lobed; **Sty** filiform, 1.5–1.8 mm; **Fr** ovoid, 3–3.5 × 2–2.5 mm, reddish-brown; **Se** shield-shaped, slightly convex, 3.1–3.5 × 1.8 mm, dull black with a glossy spot on the basal face.

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## References

- Perry, P. (1999) *Bulbinella* in South Africa. Pretoria (ZA): National Botanical Institute (= *Strelitzia* No. 8).



## × *Cummingara* ASPHODELACEAE

U. Eggli

× **Cummingara** G. D. Rowley (Haworthiad 13 (3): 115, 1999). — **Aloioideae** — **Lit:** Cumming (1999). **Etym:** For David Morton Cumming (\*1942), Scottish medical laboratory technician, amateur botanist and plant breeder, lived in Australia from 1962 and established Silky Oaks nursery, moved to RSA in 1994; plus the suffix ‘-ara’, indicating plurigeneric hybrids.

**Incl.** × *Smithara* D. M. Cumming (1999) (*nom. illeg.*, Art. 53.1).

= *Gasteria* × *Haworthia* × *Poellnitzia*. The two known combinations have not been named formally.

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### References

Cumming, D. M. (1999) New nothogenera proposed for four trigenic hybrids within *Aloaceae*. *Haworthiad* 13 (1): 20–21.

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## × *Gasteraloe* ASPHODELACEAE

L. E. Newton

× **Gasteraloe** Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931). — **Alooidae** — **Lit:** Walther (1930: as *Gastrolea*); Newton (1998); Mays (2009: cultivar synopsis).

**Incl.** × *Gastrolea* E. Walther (1930) (*nom. inval.*, Art. H6.2).

**Incl.** × *Lomateria* Guillaumin (1931).

**Incl.** × *Gastrolirion* E. Walther (1933) (*nom. inval.*, Art. H6.2).

**Incl.** × *Chamaeteria* D. M. Cumming (1974).

**Incl.** × *Gaslauminia* P. V. Heath (1994).

**Incl.** × *Gasterlirion* Mays & G. D. Rowley (2006).

**Incl.** × *Gastulista* G. D. Rowley (2014).

**Incl.** × *Gastonialoe* C. C. Walker (2017).

= *Aloe* × *Gasteria*. Mostly acaulescent or almost so, mostly caespitose; **L** rosulate, variously spotted or tuberculate, margins with teeth; **Inf** lateral, simple or branched; racemes lax; **Fl** bracteate, pedicellate, nutant or spreading, zygomorphic; **Per** tube sometimes inflated at the base, often curved above the ovary, usually reddish at the base, greenish towards the tip, lobes often longer than the tube; **St** and **Sty** scarcely exerted. — **Cytology:** Most of the taxa for which chromosomes have been counted have a somatic number

of  $2n = 14$ , but one count of  $2n = 28$  and two aneuploids have also been reported. These are summarized by Riley & Majumdar (1979).

Rowley (1982) included × *Poellneria* (= *Poellnitzia* × *Gasteria*) as a synonym here, but *Poellnitzia* is an accepted genus distinct from *Aloe*.

In addition to the nothotaxa reported below, numerous other crosses are listed in the literature (see Mays (2009) for an illustrated synopsis).

× **G. bedinghausii** (Radl) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931).

≡ *Aloe* × *bedinghausii* Radl (1896) ≡ × *Gastrolea bedinghausii* (Radl) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe aristata* × *Gasteria disticha*. Habit approaching *A. aristata*; **L** 6 × 2 cm, shape and ornamentation approaching *G. disticha*. — **Cytology:**  $2n = 14$  (Resende 1937: as *Aloe*).

× **G. beguinii** (hort. ex Radl) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931).

≡ *Aloe* × *beguinii* hort. ex Radl (1896) ≡ × *Gastrolea beguinii* (hort. ex Radl) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe aristata* × *Gasteria carinata* var. *verrucosa*.

× **G. beguinii** nvar. **beguinii**.

= *Aloe aristata* (as *A. longiaristata*) × *Gasteria carinata* var. *verrucosa* (as *G. verrucosa*). Larger and coarser than *A. aristata*, usually simple; **L**

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10 × 2.5 cm, dark green, with prominent scattered white pearly tubercles; **Inf** to 60 cm; raceme lax; **Fl** pink at the base, primrose-yellow with green mid-stripe above, 38 mm, tube slightly inflated at the base, straight. — **Cytology**: 2n = 14 (Resende 1937: as *Aloe*).

×**G. beguinii** nvar. **chludowii** (Radl) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982).

≡ *Aloe* × *chludowii* Radl (1896) ≡ × *Gastrolea chludowii* (Radl) E. Walther (1930) (*nom. inval.*, Art. 43.1) ≡ × *Gasteraloe chludowii* (Radl) Guillaumin (1931) ≡ × *Gastrolea beguinii* nvar. *chludowii* (Radl) G. D. Rowley (1973) (*nom. inval.*, Art. 43.1).

= *Aloe aristata* × *Gasteria carinata* var. *verrucosa* (as *G. verrucosa* var. *asperrima*). Differs from nvar. *beguinii*: **L** 12–16 cm.

×**G. beguinii** nvar. **perfectior** (Radl) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931).

≡ *Aloe* × *beguinii* var. *perfectior* Radl (1896) ≡ *Aloe* × *perfectior* (Radl) A. Berger (1908) ≡ × *Gastrolea perfectior* (Radl) E. Walther (1930) (*nom. inval.*, Art. 43.1) ≡ × *Gastrolea beguinii* var. *perfectior* (Radl) G. D. Rowley (1955) (*nom. inval.*, Art. 43.1).

= *Aloe aristata* × *Gasteria carinata* var. *verrucosa* (as *G. verrucosa*). Differs from nvar. *beguinii*: To 20 cm tall; **L** longer and brighter green.

×**G. derbetzei** (hort. ex A. Berger) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931).

≡ *Aloe* × *derbetzei* hort. ex A. Berger (1908) ≡ × *Gastrolea derbetzei* (hort. ex A. Berger) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe striata* × *Gasteria acinacifolia*.

×**G. gloriosa** (Radl) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982).

≡ *Aloe hybrida* var. *gloriosa* Radl (1896) ≡ × *Lomateria gloriosa* (Radl) Guillaumin (1931).

= *Aloe purpurea* (as *Lomatophyllum purpureum*) × *Gasteria bicolor* var. *bicolor* (as *G. maculata*). **L** 40 × 3 cm, dark green with large whitish spots, margin scarcely toothed.

×**G. lapaixii** (Radl) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931). — **Lit**: Rowley (1968).

≡ *Aloe* × *lapaixii* Radl (1896) ≡ × *Gastrolea lapaixii* (Radl) H. Jacobsen (1954) (*nom. inval.*, Art. 43.1).

×**G. lapaixii** nvar. **lapaixii**.

= *Aloe aristata* (as *A. longiaristata*) × *Gasteria bicolor* var. *bicolor* (as *G. maculata*). Larger and coarser than *A. aristata*, usually simple; **L** rosulate, deltoid-lanceolate, 10 × 2 cm, dark green with a few large whitish spots in irregular transverse bands, margin with blunt white teeth; **Inf** to 1.2 m, simple or with 1 to 3 branches; racemes 20–25 cm, lax; **Fl** pink with green longitudinal stripes, 25–27 mm, base attenuate; **St** not exerted. — **Cytology**: 2n = 14 (Resende 1937: as *Aloe*).

×**G. lapaixii** nvar. **latifolia** (Radl) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931).

≡ *Aloe* × *lapaixii* var. *latifolia* Radl (1896).

Differs from nvar. *lapaixii*: **L** broader, slightly acute, margin strongly toothed.

×**G. lynchii** (Baker) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982).

≡ *Aloe* × *lynchii* Baker (1881) ≡ × *Gastrolea lynchii* (Baker) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe striata* × *Gasteria carinata* var. *verrucosa*.

×**G. mortolensis** (A. Berger) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931).

≡ *Aloe* × *mortolensis* A. Berger (1908) ≡ × *Gastrolea mortolensis* (A. Berger) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe ?variegata* × *Gasteria acinacifolia*. Caulescent; stem procumbent, 40–60 cm, suckering at the base; **L** rosulate, deltoid-lanceolate, 25 × 9 cm, glossy green, with rounded white spots in irregular transverse bands, more numerous on the lower face, margins with teeth 2 mm, 10–18 mm apart; **Inf** simple or with up to 3 branches; racemes 30 cm, lax; **Bra**

cuspidate, 25 mm; **Ped** 30–35 mm; **Fl** 58–60 mm, base orange, pale brownish-green or grey towards the tip, base not inflated; **St** not exerted.

×**G. nowotnyi** (Radl) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982).

≡ *Aloe* ×*nowotnyi* Radl (1896) ≡ ×*Gastrolea nowotnyi* (Radl) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe aristata* (as *A. longiaristata*) × *Gasteria* sp. **L** rosulate, deltoid, 3.5 × 2–2.5 cm, bright green with spots, fewer on the upper face. — **Cytology**: 2n = 20 (Brandham 1969).

×**G. peacockii** (Baker) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982). **Type**: not preserved.

≡ *Gasteria* ×*peacockii* Baker (1880) ≡ ×*Gastrolea peacockii* (Baker) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe* sp. (as *A. heteracantha*) × *Gasteria acinacifolia* (as *G. acinacifolia* var. *ensifolia*).

×**G. pethamensis** (Baker) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982). **Type**: not preserved. — **I**: Walther (1930: as *Gastrolea*).

≡ *Gasteria* ×*pethamensis* Baker (1880) ≡ ×*Gastrolea pethamensis* (Baker) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe variegata* × *Gasteria carinata* var. *verrucosa*.

×**G. pfrimmeri** Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339–340, 1931).

≡ ×*Gastrolea pfrimmeri* (Guillaumin) E. Walther (1933) (*nom. inval.*, Art. 43.1).

= *Aloe variegata* × *Gasteria* sp. **L** 10 in dense **Ros** 18 cm Ø × 7 cm high, deltoid, upper face concave, lower face obliquely keeled, tip acute, to 10 × 4 cm, green with numerous irregularly confluent white spots, denser on the upper face; **Inf** to 30 cm, branching; racemes 8 cm, dense; **Bra** 5 mm; **Fl** red with green markings on the lobes, 30 mm; **St** not exerted.

×**G. prorumpens** (A. Berger) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982).

≡ *Aloe* ×*prorumpens* A. Berger (1908) ≡ ×*Gastrolea prorumpens* (A. Berger) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe* sp. × *Gasteria* sp.

×**G. quehlii** (Radl) G. D. Rowley (Nation. Cact. Succ. J. 37(2): 49, 1982).

≡ *Aloe* ×*quehlii* Radl (1896) ≡ ×*Gastrolea quehlii* (Radl) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe* sp. × *Gasteria bicolor* var. *bicolor* (as *G. maculata* or *G. picta* var. *formosa*). **L** deltoid, 4 cm wide, with a few spots; **Inf** 60–70 cm, branching; racemes 30–40 cm; **Fl** 25 mm.

×**G. radlii** L. E. Newton (Brit. Cact. Succ. J. 15(1): 34, 1997).

**Incl.** *Aloe* ×*imbricata* hort. ex A. Berger (1908) (*nom. illeg.*, Art. 53.1) ≡ ×*Gastrolea imbricata* (hort. ex A. Berger) E. Walther (1930) (*nom. inval.*, Art. 43.1) ≡ ×*Gasteraloe imbricata* (hort. ex A. Berger) G. D. Rowley (1982).

= *Aloe variegata* or *A. serrulata* × *Gasteria* sp. **L** rosulate, in 5 rows, lanceolate-deltoid with shortly mucronate tip, 6 × 2 cm, green, margin cartilaginous, warty.

×**G. rebutii** (hort. ex A. Berger) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 340, 1931).

≡ *Aloe rebutii* hort. ex A. Berger (1908) ≡ ×*Gastrolea rebutii* (hort. ex A. Berger) E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe variegata* × *Gasteria* sp. **L** spiral in 5 rows, 13–14 × 2.5–3.5 cm, green with numerous spots in irregular transverse bands, margin with minute teeth; **Inf** with raceme 35 cm; **Fl** subsecund, 33–35 mm, base slightly inflated to 9 mm Ø; **St** not exerted. — **Cytology**: 2n = 14 (Brandham 1969: as *Gasteria*).

×**G. sculptilis** G. D. Rowley ex L. E. Newton (Haseltonia 5: 94, 1998). **Type**: [icono]: Cact. Succ. J. (US) 7(9): 136, 1936. — **I**: Poindexter (1936).

**Incl.** ×*Gastrolea sculptilis* Poindexter (1936) (*nom. inval.*, Art. 36.1, 43.1).

= *Aloe variegata* × *Gasteria* × *cheilophylla*. Acaulescent or shortly caulescent, suckering sparsely; **L** with a groove on the upper face, with keel on the lower face, ±18 × 8.5 cm, olive-green with numerous whitish spots, mostly in irregular transverse bands, margin white, denticulate; **Inf** ±50 cm, branched; **Fl** pale red with yellowish tip, 30 mm. — **Cytology**: 2n = 14 (Cutler & Brandham 1977).

The plant was described as sterile by Poindexter (1936).

× **G. simoniana** (Deleuil ex Rebut) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 340, 1931).

≡ *Aloe* × *simoniana* Deleuil ex Rebut (1893)  
 ≡ × *Gastrolea simoniana* (Deleuil ex Rebut)  
 H. Jacobsen (1954) (*nom. inval.*, Art. 43.1).

= *Aloe aristata* × *Gasteria disticha*. Plants to 40 cm tall; **L** 15–20 × 5–6 cm, green with numerous spots.

× **G. smaragdina** (hort. ex A. Berger) Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 340, 1931).

≡ *Aloe* × *smaragdina* hort. ex A. Berger (1908)  
 ≡ × *Gastrolea smaragdina* (hort. ex A. Berger)  
 E. Walther (1930) (*nom. inval.*, Art. 43.1).

= *Aloe variegata* × *Gasteria acinacifolia* (as *G. ?candicans*). Suckering freely at the base; **L** ±15, rosulate, lanceolate-deltoid, 20 × 7 cm, pale green, glossy, with whitish-green spots in irregular transverse bands, margin with minute teeth; **Inf** simple or with few **Br**; raceme

20–30 cm, lax; **Bra** deltoid, cuspidate; **Ped** ±12 mm; **Fl** bright red, 40 mm, base not inflated; **St** not exerted. — **Cytology**: 2n = 14 (Brandham 1969).

## References

- Brandham, P. E. (1969) Chromosome behaviour in the *Aloineae*. I. The nature and significance of E-type bridges. *Chromosoma* 27: 201–215. <https://doi.org/10.1007/BF00326145>.
- Cutler, D. F. & Brandham, P. E. (1977) Experimental evidence for the genetic control of leaf surface characters in hybrid *Aloineae* (*Liliaceae*). *Kew Bull.* 32(1): 23–32, ill., chrom.nos. <https://doi.org/10.2307/4117256>.
- Mays, H. (2009) Hybrids & cultivars of the succulent *Asphodelaceae*. Volume 1. *Aloe, Astroloba, Bulbine, Gasteria* & nothogenera. St. Michaels on Wyre (GB): Harry Mays.
- Newton, L. E. (1998) Unnamed hybrids of × *Gasteraloe* alliance. *Bradleya* 16: 115–118, ill. <https://doi.org/10.25223/brad.n16.1998.a10>
- Poindexter, R. W. (1936) New garden species. VII. *Gastrolea sculptilis*. *Cact. Succ. J. (US)* 7(9): 136, ill.
- Resende, F. (1937) Über die Ubiquität der SAT-Chromosomen bei den Blütenpflanzen. *Planta* 26(5): 757–807. <https://doi.org/10.1007/BF01915460>.
- Riley, H. P. & Majumdar, S. K. (1979) *The Aloineae*. A biosystematic survey. Lexington (US): University Press of Kentucky.
- Rowley, G. D. (1968) Rowley Reporting. *Gastroleas*. *Nation. Cact. Succ. J.* 23(3): 57.
- Rowley, G. D. (1982) Intergeneric hybrids in succulents. *Nation. Cact. Succ. J.* 37(1): 2–6, (2): 45–49, (3): 76–80, (4): 119, ill.
- Walther, E. (1930) *Gastrolea*. *Cact. Succ. J. (US)* 2(3): 303–307, ill.



## × *Gasterhaworthia* ASPHODELACEAE

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× ***Gasterhaworthia*** Guillaumin (Bull. Mus. Nation. Hist. Nat., Sér. 2, 3: 339, 1931). — *Alooidae* — **Lit:** Cumming (1999); Mays (2009: ill. synopsis).

**Incl.** × *Haworthio-gasteria* Kondo & Megata *ex* Megata (1943) (*nom. inval.*, Art. H6.2).

**Incl.** × *Gasworthia* Gates (1955) (*nom. illeg.*, Art. 52.1).

**Incl.** × *Gasworthiopsis* G. D. Rowley (2014).

= *Gasteria* × *Haworthia*. Rowley (1982: 76) lists 5 known combinations (1 cultivar, 4 formally named), and Mays (2009) presents short

descriptions and illustrations of c. 30 more recently published cultivars.

### References

Cumming, D. M. (1999) New nothogenera proposed for four trigeneric hybrids within *Aloaceae*. *Haworthiad* 13 (1): 20–21.

Mays, H. (2009) Hybrids & cultivars of the succulent *Asphodelaceae*. Volume 1. *Aloe*, *Astroloba*, *Bulbine*, *Gasteria* & nothogenera. St. Michaels on Wyre (GB): Harry Mays.

Rowley, G. D. (1982) Intergeneric hybrids in succulents. *Nation. Cact. Succ. J.* 37(1): 2–6, (2): 45–49, (3): 76–80, (4): 119, ills.

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## Gasteria ASPHODELACEAE

E. Van Jaarsveld

**Gasteria** Duval (Pl. Succ. Horto Alencon., 6, 1809). **Type:** *Aloe angustifolia* Aiton [lectotype, selected by Maire, Fl. Afr. Nord. 5: 71, 1958]. — **Alooiideae** — **Lit:** Jaarsveld (1992: synopsis); Jaarsveld & Ward-Hilhorst (1994: monograph); Jaarsveld (2008: updated synopsis); Mays (2009: ill. synopsis of cultivars). **Distr:** S Namibia, RSA (mostly below the escarpment, mainly in the Eastern Cape); mainly in Albany thicket vegetation. **Etym:** Gr. “gaster,” stomach; for the stomach-shaped basally inflated perianth.

**Incl.** *Papilista* Rafinesque (1840). **Type:** *Aloe verrucosa* Miller.

Slow-growing perennial glabrous leaf succulents; **R** mostly terete, slightly succulent to somewhat clavate; plants acaulescent or **Br** short, rarely pendent and long-stemmed, solitary or proliferating from the base to form dense groups; **L** ± brittle, mottled, often with dense white spots in transverse bands, dimorphic, distichous in the juvenile phase becoming rosulate or sometimes remaining distichous; juvenile **L** lorate, flat above, convex below, adult **L** linear to lorate-lanceolate to triangular, margin acute, rounded, wavy or rugulose, sometimes tuberculate-crenulate with white

tubercles ± merging towards the apex, forming a continuous margin which may be entire, serrulate, crenulate or rarely denticulate, epidermis asperulous, tuberculate, rugulose or smooth, **L** tip truncate, obtuse, acute or acuminate, rarely retuse, mucronate; **Inf** terminal but pushed aside by the **L** and thus appearing lateral, 1–5 per plant, racemose or paniculate, ± secund; **Fl** 6-merous, pendent, laxly arranged in the upper ½ of the inflorescence; **Per** pink to reddish (rarely nearly white), apically white with green striae; **Tep** fused for the greater part of their length forming a curved basally asymmetrically gasteriform tube, gasteriform part variously shaped, extending for up to ⅔ of the perianth length; **St** 6, included or rarely exserted; **Fil** becoming contracted after anthesis; **Ov** oblong-ovoid, 3-locular, with 6 grooves on the outside; **Sty** becoming shortly exserted after anthesis; **Sty** apical, minute, 3-lobed; **Fr** erect oblong 3-angled woody capsules, dehiscent longitudinally; **Se** black, compressed, irregularly angled and obscurely oblong in outline, 2–8 mm.

*Gasteria* is a monophyletic genus of 25 species. Some taxa are extremely variable with many local forms. DNA analyses confirm the circumscription of *Gasteria*, as well as its close affinity with *Aloe*, *Haworthia* and *Astroloba* (Grace & Rønsted 2013), and Daru & al. (2013) and Manning & al. (2014) place *Gasteria* as sister to *Haworthia* subgen. *Hexangulares*.

A recent study (Zonneveld & Jaarsveld 2005) of total nuclear DNA content using flow cytometry suggested the centre of origin in the

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SE Cape, which is also the centre of diversity of *Gasteria*, with the derived species occurring in the north-east. This work also revealed *G. rawlinsonii*, an obligatory cliff-dwelling species, as the most basal species in the genus. Other early-diverging species include *G. armstrongii*, *G. ellaphieae*, *G. glauca*, *G. glomerata*, *G. nitida*, *G. polita*, *G. pulchra* and *G. vlokii*. This differs from the results of a detailed study of the whole *Aloodeae* by Daru & al. (2013), where *G. pillansii* is recovered as ancestral sister to the rest of the genus.

The genus was monographed by Jaarsveld & Ward-Hilhorst (1994) and updated by Jaarsveld (2008). The division into two sections with two series each of Jaarsveld & Ward-Hilhorst (1994) was shown to be artificial in the molecular analysis of Zonneveld & Jaarsveld (2005), but these infrageneric taxa are morphologically clearly circumscribed and are here maintained for practical reasons:

- Sect. *Gasteria*: **L** lorate, smooth or asperulous (rarely tuberculate), distichous or spirally distichous; **Per** 12–50 mm, gasteriform portion globose or globose-ellipsoid (rarely narrowly ellipsoid):
  - [1] Ser. *Gasteria*: **Per** 12–22 (–25) mm, gasteriform part  $> \frac{1}{2}$  of the **Per** length. — 8 species from the Lower Karoo regions and the Eastern Cape.
  - [2] Ser. *Namaquana* Van Jaarsveld 1992: **Per** 25–45 (–50) mm, gasteriform part  $\leq \frac{1}{3}$  of the **Per** length, globose but often  $\pm$  indistinct from the upper part of the **Per** and of  $\pm$  the same  $\emptyset$ . — Only *G. pillansii* from the Namaqualand.
- Sect. *Longiflorae* Haworth 1827: **L** tapering, smooth or tuberculate (rarely asperulous), rosulate; **Per** 18–45 (–50) mm, gasteriform portion narrowly ellipsoid.
  - [3] Ser. *Longifoliae* (Haworth) Van Jaarsveld 1992: **Per** 35–50 mm, hardly gasteriform. — 3 species from the Eastern Cape, Mpumalanga, as well as Swaziland.
  - [4] Ser. *Multifariae* (Haworth) Van Jaarsveld 1992: **Per** 18–33 mm, gasteriform part  $\pm$  well defined. — 14 species from the Western Cape and Eastern Cape.

**Conservation:** Jaarsveld and Raimondo have included 18 *Gasteria* species in the Red List of South African Plants (Raimondo & al. 2009). Their status ranges from “near threatened” (*G. batesiana*), “rare” (*G. baylissiana*, *G. bicolor* var. *liliputana*, *G. retusa*, *G. thunbergii*, *G. ellaphieae*, *G. rawlinsonii*, *G. tukhelensis*, *G. vlokii*), “vulnerable” (*G. croucheri*, *G. pillansii* var. *hallii*) to “critically rare” (*G. batesiana* var. *dolomitica*, *G. disticha*, *G. doreeniae*, *G. glauca*, *G. glomerata*, *G. armstrongii*, *G. polita*). Most, although rare, are secure due to habitat inaccessibility. However, the biggest threat, apart from unsustainable harvesting for the traditional medicinal market (Crouch & al. 2000), remain urban and agricultural expansion.

**Horticulture:** *Gasteria* are popular indoor horticultural subjects. Most require some form of shading. They are easily propagated by off-shoots, leaf cuttings or seed which should be sown when fresh. They hybridize readily, and some cultivars have been developed (see, e.g., Jaarsveld 2009).

The following names are of unresolved application but are referred to this genus:

*Aloe angulata* var. *striata* Willdenow (1811); *Aloe guttata* Salm-Dyck (1834)  $\equiv$  *Gasteria nigricans* var. *guttata* (Salm-Dyck) Baker (1880); *Aloe linguaefolia* Willdenow (1809); *Aloe linguaefolia* var. *angustifolia* Willdenow (1809); *Aloe linguaefolia* var. *latifolia* Willdenow (1809); *Aloe linguiformis* De Candolle (1800); *Aloe macchiata* Da Pare (1835); *Aloe nigricans* var. *crassifolia* Salm-Dyck (1817); *Aloe nigricans* var. *fasciata* Salm-Dyck (1821)  $\equiv$  *Gasteria nigricans* var. *fasciata* (Salm-Dyck) Haworth (1821)  $\equiv$  *Gasteria fasciata* (Salm-Dyck) Haworth (1827); *Aloe nigricans* var. *latifolia* Salm-Dyck (1821) (*nom. illeg.*, Art. 52.1?); *Aloe nitida* var. *brevifolia* Salm-Dyck (1816) (*nom. inval.*, Art. 43.1); *Aloe pseudonigricans* Salm-Dyck (1817)  $\equiv$  *Gasteria pseudonigricans* (Salm-Dyck) Haworth (1821); *Aloe quadrangularis* Da Pare (1835); *Aloe subcarinata* var. *striata* Salm-Dyck (1821) (*nom. illeg.*, Art. 52.1); *Aloe subnigricans* var. *canaliculata* Salm-Dyck (1834)  $\equiv$  *Gasteria subnigricans* var. *canaliculata* (Salm-Dyck) A. Berger (1908)

(*incorrect name*, Art. 11.4)  $\equiv$  *Gasteria pseudo-nigricans* var. *canaliculata* (Salm-Dyck) H. Jacobsen (1955); *Aloe trigona* Salm-Dyck (1821)  $\equiv$  *Gasteria trigona* (Salm-Dyck) Haworth (1827); *Aloe trigona* var. *elongata* Salm-Dyck (1821) (*nom. illeg.*, Art. 52.1); *Gasteria acinacifolia* var. *spathulata* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1?); *Gasteria angulata* var. *truncata* (Willdenow) A. Berger (1908); *Gasteria brevifolia* Haworth (1812); *Gasteria brevifolia* var. *laetevirens* Haworth (1827); *Gasteria brevifolia* var. *perviridis* Haworth (1827); *Gasteria crassifolia* Haworth (1827); *Gasteria dicta* N. E. Brown (1876); *Gasteria elongata* Baker (1896); *Gasteria fasciata* var. *laxa* Haworth (1827); *Gasteria formosa* Haworth (1827)  $\equiv$  *Gasteria picta* var. *formosa* (Haworth) Baker (1880); *Gasteria gracilis* Hort. Saunders *ex* Baker (1880); *Gasteria laevis* Haworth (1827); *Gasteria linita* Haworth (1827); *Gasteria nigricans* var. *polypspila* Baker (1880)  $\equiv$  *Gasteria fasciata* var. *polypspila* (Baker) A. Berger (1908); *Gasteria prolifera* Lemaire (1869); *Gasteria subnigricans* Haworth (1827) (*nom. illeg.*, Art. 52.1)  $\equiv$  *Aloe subnigricans* (Haworth) Sprengel (1828)  $\equiv$  *Gasteria nigricans* var. *subnigricans* (Haworth) Baker (1880); *Gasteria subnigricans* var. *glabrior* Haworth (1827) (*incorrect name*, Art. 11.4)  $\equiv$  *Gasteria pseudonigricans* var. *glabrior* (Haworth) H. Jacobsen (1955); *Gasteria transvaalensis* Hort. De Smet *ex* Baker (1889).

**G. acinacifolia** (Jacquin) Haworth (Suppl. Pl. Succ., 49, 1819). **Type:** [lecto — icono]: Jacquin, Eclog. Pl. Rar. 49, t. 31, 1811–1816. — **Distr:** RSA (Eastern Cape); Alagoa and Albany Dune Strandveld vegetations, flowers spring to mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 40–41); Retief (2015).

$\equiv$  *Aloe acinacifolia* Jacquin (1811); **incl.** *Gasteria acinacifolia* var. *acinacifolia*; **incl.** *Aloe acinacifolia* var. *angustifolia* Salm-Dyck (1817); **incl.** *Aloe acinacifolia* var. *laetevirens* Salm-Dyck (1817); **incl.** *Gasteria nitens* Haworth (1819)  $\equiv$  *Aloe nitens* (Haworth) Roemer & Schultes (1829)  $\equiv$  *Gasteria acinacifolia* var. *nitens* (Haworth) Baker (1880); **incl.** *Gasteria candicans* Haworth (1821)  $\equiv$  *Aloe candicans* (Haworth) Roemer &

Schultes (1829); **incl.** *Gasteria ensifolia* Haworth (1825)  $\equiv$  *Aloe ensifolia* (Haworth) Roemer & Schultes (1829)  $\equiv$  *Gasteria acinacifolia* var. *ensifolia* (Haworth) Baker (1880); **incl.** *Gasteria pluripuncta* Haworth (1827)  $\equiv$  *Aloe pluripuncta* (Haworth) Roemer & Schultes (1829)  $\equiv$  *Gasteria acinacifolia* var. *pluripuncta* (Haworth) Baker (1896); **incl.** *Gasteria venusta* Haworth (1827)  $\equiv$  *Aloe venusta* (Haworth) Roemer & Schultes (1829)  $\equiv$  *Gasteria acinacifolia* var. *venusta* (Haworth) Baker (1896); **incl.** *Gasteria inexpectata* Von Poellnitz (1938).

[4] Acaulescent, decumbent to erect, 25–75  $\times$  65 cm, solitary or proliferating to form small groups; **L** rosulate, 22–60  $\times$  4.5–10 cm, linear-lanceolate to lorate, erectly spreading and sometimes falcate, keeled, both surfaces dark green, with dense white spots arranged in transverse bands, epidermis smooth, rarely slightly tuberculate, margin cartilaginous, serrulate, rarely entire, tip acute, rarely obtuse, mucronate; juvenile **L** distichous, lorate, patent to erectly spreading, tuberculate, rarely smooth; **Inf** variable racemose panicles, usually flat-topped, to 1 m, branched, branches horizontal to erectly spreading; **Per** 35–45 (–50) mm, gasteriform part narrowly ellipsoid,  $\frac{1}{2}$  of the perianth length, 5–9 mm  $\varnothing$ , pink, often not constricted and indistinct, upper  $\frac{1}{2}$  white with green striations; **Sty** included or exerted for up to 5 mm; **Fr** 35–43 mm, truncate or obtuse; **Se** 6–8  $\times$  5–6 mm.

One of the largest species of the genus, confined to the SE coast of RSA.

**G. armstrongii** Schönland (Rec. Albany Mus. 2(4): 258, 1912). **Type:** RSA, Eastern Cape (*Anonymus* s.n. [K]). — **Distr:** RSA (Eastern Cape): Humansdorp Shale Renosterveld vegetation, well camouflaged on the pebble background, flowers in mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 49, as *G. nitida* var.).

$\equiv$  *Gasteria nitida* var. *armstrongii* (Schönland) Van Jaarsveld (1992).

[4] Plants solitary or proliferating to form small clusters; **L** remaining distichous, to 5  $\times$  3 cm, patent, lorate, surface tuberculate, rarely smooth, tip somewhat retuse, obtuse or truncate, mucronate; **Inf** racemose, 40–50 cm; **Per** 20 mm, bright reddish-pink, stipitate for 2–3 mm, gasteriform for



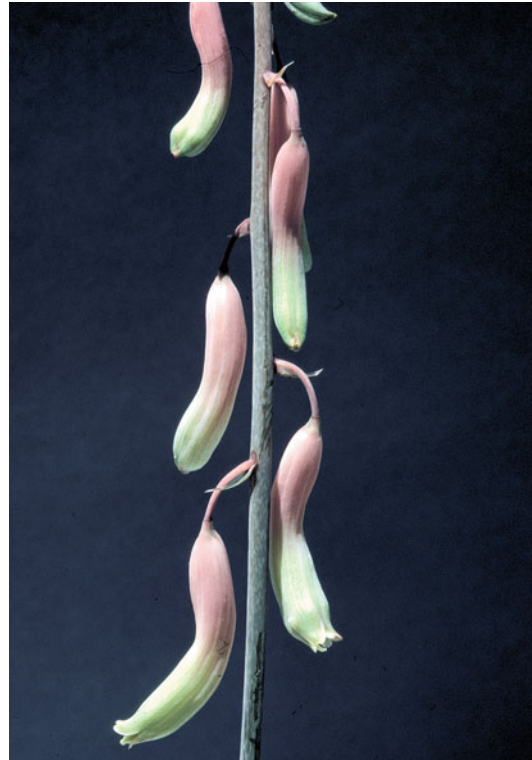
slightly  $> \frac{1}{2}$  of the length, 5–8 mm  $\varnothing$ , narrowly ellipsoid, constricted above into a tube 4–5 mm  $\varnothing$ , lobes erectly spreading, obtuse, yellowish; **Sty** included; **Fr** oblong, 24–30  $\times$  8 mm; **Se** 3–4  $\times$  2 mm.

Treated at species rank on the base of the DNA analyses of Zonneveld & Jaarsveld (2005). This is a very rare species, and its coastal habitat is threatened by agriculture and urban expansion.

**G. barbae** Van Jaarsveld (CactusWorld 32(4): 257, ill. (pp. 257–260), 2015). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 25246 [NBG]). — **Distr:** RSA (Western Cape); sheer coastal cliffs, South Outeniqua Sandstone Fynbos vegetation, flowers late spring.

[3] Acaulescent, decumbent, 8–12  $\times$  8–24 cm, solitary or proliferating from the base forming clusters of 3–5 heads; **L** 8–12 per rosette, rosulate (but distichous in juvenile plants), linear-lanceolate, linear or deltoid-lanceolate to (4-) 12–17  $\times$  2.2–3.8 cm, (slightly) falcate and ascending-spreading, adaxial face flat to becoming canaliculate, flat towards the apex, matt dark green to greyish-green (becoming reddish during the dry season), densely white-tuberculate in obscure transverse bands, abaxial face somewhat convex with a distinct eccentric keel, densely tuberculate, tubercles arranged in obscure transverse bands, margins denticulate to almost entire, apex acute or subacute, sometimes acuminate, mucronate; **Inf** racemose, to 40–55 cm, to 11-flowered; **Fl** secundly arranged, pendent, all open at the same time; **Ped** 8–12 mm, pink; **Per** 40–43 mm, stipitate for 5 mm, subcylindrical and curved, hardly gasteriform, orange-pink, upper  $\frac{1}{2}$  white with green striations, tips erect becoming erectly spreading, obtuse, margins of the **ITep** free and channelled at the base for 10–12 mm, diverging gradually towards the apex; **St** 34–37 mm; **Anth** 3  $\times$  1.5 mm, included or shortly exerted; **Ov** 8  $\times$  3 mm  $\varnothing$ , green; **Sty** 31 mm; **Sti** included or shortly exerted, curved upwards, minute; **Fr** 18–30  $\times$  7–8 mm  $\varnothing$ , narrowly obovoid, triangular in cross-section, with obtuse apex; **Se** 3.5–4  $\times$  1.5–2 mm, black.

**G. batesiana** G. D. Rowley (Nation. Cact. Succ. J. 10(2): 32, 1955). **Type** [neo]: RSA,



**Fig. 1** *Gasteria batesiana* var. *batesiana*. (Copyright: U. Eggli)

Mpumalanga (*Rowley* s.n. [RNG]). — **Distr:** RSA (Mpumalanga, KwaZulu-Natal).

**G. batesiana** var. *batesiana* — **Distr:** RSA (Mpumalanga, KwaZulu-Natal); S-facing cliff faces in river valleys, Valley Bushveld vegetation; flowers spring to mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 37). – Fig. 1.

[4] Acaulescent, decumbent to erect, 3–10  $\times$  8–30 cm, proliferating from the base to form small to large groups, rarely solitary; **L** distichous at first, becoming rosulate, 5–18  $\times$  1.5–4 cm, triangular-lanceolate to linear, erectly spreading, becoming recurved, dark green with white spots densely arranged in transverse bands, densely rugulose-tuberculate, margin cartilaginous, serrulate (rarely denticulate), tip acute, rarely obtuse, mucronate; juvenile **L** loriate, densely tuberculate, tip obtuse, mucronate; **Inf** racemose, 30–45 cm; **Bra** 6–12  $\times$  2–5 mm; **Ped** 9 mm; **Per** 35–40 m, stipitate for 3–5 mm, gasteriform part narrowly ellipsoid,  $\frac{1}{2}$

of the perianth length, 6–9 mm  $\varnothing$ , light pink, upper  $\frac{1}{2}$  of the perianth white with green striations, inflated to the same  $\varnothing$  as the lower portion, with a slight constriction in the middle, tips obtuse, white with green median stripes; **Sti** included or exerted for up to 5 mm; **Fr** 16–20 mm; **Se** 4–6  $\times$  2–3 mm.

**G. batesiana** var. **dolomitica** Van Jaarsveld & E. A. van Wyk (Aloe 36(4): 74, 2000). **Type:** RSA, Mpumalanga (*Van Jaarsveld & Hankey* 15081 [NBG]). — **Distr:** RSA (Mpumalanga); sheer dolomite cliffs in Origstad Mountain Bushveld vegetation. **I:** Jaarsveld (2008: 85).

[4] Differs from var. *batesiana*: **L** linear, 10  $\times$  1–2 cm, becoming biconvex when turgid, tip obtuse.

The distribution (disjunct from var. *batesiana*) represents the N-most within the genus.

**G. baylissiana** Rauh (J. South Afr. Bot. 43(3): 187–191, ill., 1977). **Type:** RSA, Eastern Cape (*Bayliss* s.n. [HEID 30517, PRE]). — **Distr:** RSA (Eastern Cape); Kowie Thicket vegetation on quartzitic sandstones along the Witterivier (Suurberg), spring-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 75).

[1] Acaulescent, decumbent to erect, 0.5–4 cm tall, proliferating from the base to form small dense groups to 8 cm  $\varnothing$ , rarely solitary; **L** distichous, 2.5–5.5  $\times$  2–2.3 cm, lorate, erectly spreading, often becoming patent or recurved, epidermis with dense white cartilaginous tubercles, these very dense, domed to globose and confluent forming a dense reticulation, margin crenulate, becoming continuous towards the tip, tip obtuse, truncate or retuse, mucronate; juvenile **L** lorate, tuberculate and slightly asperulous; **Inf** racemose, 8–35 cm, erectly spreading, occasionally with a pair of branches; **Per** 14–16 mm, stipitate for 1 mm, gasteriform part  $\frac{2}{3}$  of the perianth length, red-pink, 6–7.5 mm  $\varnothing$ , then abruptly constricted into a tube 3–4 mm  $\varnothing$ , tube white with green striations; **Sty** included; **Fr** 14–20 mm; **Se** oblong, 4  $\times$  3 mm.

**G. bicolor** Haworth (Philos. Mag. J. 1826: 275, 1826). **Type:** [neo — icono]: Salm-Dyck,



**Fig. 2** *Gasteria bicolor* var. *bicolor*. (Copyright: E. Van Jaarsveld)

Monogr. Gen. Aloes & Mesembr., fasc. 7, *Aloe* sect. 29, fig. 5, 1863, as *Aloe bicolor*. — **Distr:** RSA (Eastern Cape).

$\equiv$  *Aloe bicolor* (Haworth) Schultes (1829).

**G. bicolor** var. **bicolor** — **Distr:** RSA (Eastern Cape); Albany Thicket vegetation, flowers in spring and summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 69). – Figs. 2 and 3.

**Incl.** *Aloe maculata* Thunberg (1785) (*nom. illeg.*, Art. 53.1)  $\equiv$  *Gasteria maculata* (Thunberg) Haworth (1827)  $\equiv$  *Gasteria maculata* var. *maculata*; **incl.** *Aloe maculata* var. *obliqua* Aiton (1789) (*nom. inval.*, Art. 43.1); **incl.** *Aloe obliqua* Haworth (1802)  $\equiv$  *Gasteria obliqua* (Haworth) Duval (1809); **incl.** *Aloe lingua* Ker (1807) (*nom. illeg.*, Art. 53.1); **incl.** *Gasteria picta* Haworth (1827); **incl.** *Gasteria retata* Haworth (1827); **incl.** *Aloe dictyodes* Roemer & Schultes (1829); **incl.** *Aloe zeyheri* Salm-Dyck (1836)  $\equiv$  *Gasteria zeyheri* (Salm-Dyck) Baker (1880); **incl.** *Aloe planifolia* Baker (1870) (*nom. illeg.*, Art. 53.1)  $\equiv$  *Gasteria planifolia* (Baker) Baker (1880); **incl.** *Gasteria variolosa* Baker (1871); **incl.** *Gasteria colubrina* N. E. Brown (1877); **incl.** *Gasteria marmorata* Hort. Peacock ex Baker (1880); **incl.** *Gasteria spiralis* Baker (1880); **incl.** *Gasteria spiralis* var. *tortulata* Baker (1880); **incl.** *Gasteria maculata* var. *dregeana* A. Berger (1908); **incl.** *Gasteria caespitosa* Von Poellnitz (1937); **incl.** *Gasteria chamaegigas* Von Poellnitz (1937); **incl.** *Gasteria herreana* Von Poellnitz (1938); **incl.** *Gasteria longiana* Von



**Fig. 3** *Gasteria bicolor* var. *bicolor*. (Copyright: E. Van Jaarsveld)

Poellnitz (1938); **incl.** *Gasteria longibracteata* Von Poellnitz (1938); **incl.** *Gasteria salmdyckiana* Von Poellnitz (1938); **incl.** *Gasteria biformis* Von Poellnitz (1940); **incl.** *Gasteria kirsteana* Von Poellnitz (1940); **incl.** *Gasteria loeriensis* Von Poellnitz (1940); **incl.** *Gasteria multiplex* Von Poellnitz (1940).

[1] Decumbent to erect, 8–50 cm tall, with a short leafy stem to 20 cm, proliferating from the base to form small groups; **L** distichous or rosulate, 8–40 × 1.5–6 cm, lorate to linear, erectly spreading, slightly falcate and twisted sideways when distichous, with an asymmetrical keel when spirally arranged, dark green and with dense white spots arranged in obscure transverse bands, epidermis smooth, rarely slightly asperulous, margin entire, cartilaginous, serrulate, tubercles becoming confluent towards the tip, tip obtuse, rarely acuminate, with an asymmetrical mucro; juvenile **L** patent or erectly spreading, lorate, asperulous, obtuse, mucronate; **Inf** 16–150 cm, rarely simple or mostly branched from the middle, with up to 8 erectly spreading branches; **Per** 12–20 mm, stipitate for 1–2 mm, gasteriform part >½ of the perianth length, light pink (rarely white), globose to globose-ellipsoid, 6–9 mm Ø, then abruptly constricted into a tube 3–4 mm Ø, tube white with green striations; **Fr** 10–25 × 6–10 mm; **Se** oblong to rectangular, 2–4 mm.

A very variable taxon with many local forms. Three varieties are recognized that often grade into each other.

**G. bicolor** var. **fallax** (Haworth) Van Jaarsveld (*Aloe* 44(4): 98, ill. (pp. 98–99), 2008). **Type** [neo]: RSA, Eastern Cape (*Van Jaarsveld* 18794 [NBG]). — **Distr**: RSA (Eastern Cape); Kowie Thicket vegetation, spring-flowering. **I**: Jaarsveld (2008: 99).

≡ *Gasteria maculata* var. *fallax* Haworth (1827) ≡ *Aloe obliqua* var. *fallax* (Haworth) Roemer & Schultes (1829).

[1] Differs from var. *bicolor*: **L** linear, 13–15 × 1–1.2 cm.

The type specimen cited above is here **designated as neotype**.

**G. bicolor** var. **liliputana** (Von Poellnitz) Van Jaarsveld (*Aloe* 29(1): 21, 1992). **Type**: RSA, Eastern Cape (*Dyer & Britten* 508 [PRE]). — **Distr**: RSA (Eastern Cape); Great Fish Noorsveld vegetation, spring-flowering. **I**: Jaarsveld & Ward-Hilhorst (1994: 71).

≡ *Gasteria liliputana* Von Poellnitz (1938) ≡ *Gasteria maculata* var. *liliputana* (Von Poellnitz) Hort. Flevohof (s.a.) (*nom. inval.*, Art. 29.1).

[1] Differs from var. *bicolor*: **L** distichous or rosulate, 1.5–10 × 0.8–1.4 cm, epidermis smooth, rarely slightly tuberculate or somewhat asperulous, tip obtuse or acute; **Inf** simple racemes, 16–40 cm, occasionally with a pair of branches; **Per** 12–15 mm, diameter of the gasteriform part variable.

**G. brachyphylla** (Salm-Dyck) Van Jaarsveld (*Aloe* 29(1): 19, 1992). **Type**: [lecto — icono]: Salm-Dyck, Monogr. Gen. Aloes & Mesembr. 29, t. 8. — **Distr**: RSA (Western Cape).

≡ *Aloe brachyphylla* Salm-Dyck (1840).

**G. brachyphylla** var. **bayeri** Van Jaarsveld (*Aloe* 29(1): 20, Fig. 21 (p. 19), 1992). **Type**: RSA, Western Cape (*Bayer* 1751 [NBG]). — **Distr**: RSA (Western Cape: Little Karoo); Succulent Karoo and Renosterveld vegetations, flowers late spring to mid-summer. **I**: Jaarsveld & Ward-Hilhorst (1994: 67).

[1] Differs from var. *brachyphylla*: **L** shorter, 1.5–5 × 2.2–2.8 cm, at first erect, becoming patent and recurved, tips often incurved, truncate, epidermis smooth or slightly asperulous; **Inf** racemose, 25–28 cm; **Per** 18 mm.

**G. brachyphylla** var. **brachyphylla** — **Distr:** RSA (Western Cape); Succulent Karoo and Renosterveld vegetations, spring-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 65).

**Incl.** *Aloe nigricans* var. *marmorata* Salm-Dyck (1821); **incl.** *Gasteria nigricans* var. *marmorata* Haworth (1821); **incl.** *Gasteria nigricans* var. *platyphylla* Baker (1880); **incl.** *Gasteria angustiarum* Von Poellnitz (1937); **incl.** *Gasteria triebneriana* Von Poellnitz (1938); **incl.** *Gasteria joubertii* Von Poellnitz (1940); **incl.** *Gasteria vlaaktensis* Von Poellnitz (1940).

[1] Acaulescent, decumbent to erect, 9–23 × 7.5–23 cm, proliferating from the base to form small groups; **L** distichous, 8.5–23 × 2.2–8 cm, lorate, rarely triangular-lanceolate, epidermis smooth, dark green, both faces with densely arranged white spots in obscure transverse bands, margin crenulate, becoming continuous towards the tip, tip acute, obtuse or truncate; juvenile **L** lorate, asperulous, densely spotted, obtuse; **Inf** racemose, simple or with a pair of branches, 0.2–1.1 m; **Per** 12–22 mm, stipitate for 2–3 mm, gasteriform part >½ of the perianth length, pink, 5–7 mm Ø, globose or globose-ellipsoid, then constricted into a tube 3–4 mm Ø, tube white with green striations; **Sty** 7–10 mm, included; **Fr** oblong, 15–23 × 7 mm; **Se** 3–4 × 2–3 mm.

**G. carinata** (Miller) Duval (Pl. Succ. Horto Alencon., 6, 1809). **Type:** [lecto — icono]: Commelin, Hort. Med. Amstel., t. 9, 1701. — **Lit:** Jaarsveld (1998). **Distr:** RSA (Western Cape).

**Incl.** *Aloe disticha* var.  $\delta$  Linné (1753);  $\equiv$  *Aloe carinata* Miller (1768).

[4] Acaulescent, decumbent to erect, 3–18 cm tall, proliferating from the base to form small dense groups 15–80 cm Ø; **L** distichous at first, remaining distichous or becoming rosulate, 3–28 × 1–10 cm, triangular to triangular-lanceolate, erectly spreading, lower leaves spreading, both faces tuberculate or smooth, rarely asperulous, spotted with raised or immersed white domed tubercles in obscure transverse bands, margin cartilaginous, tuberculate-crenulate, rarely denticulate, tip acute, rarely obtuse, truncate or retuse, mucronate; juvenile **L** distichous, erectly spreading, tuberculate or smooth, lorate; **Inf** racemose,

12–90 cm, occasionally with a pair of side branches; **Per** variable, 16–27 mm, gasteriform part >½ of the perianth length, pink, narrowly ellipsoid to rarely globose-ellipsoid, above constricted into a tube 3–5 mm Ø, lobes light pink to white with central green stripes; **St** included; **Ov** 6–7 × 2.5 mm; **Sty** 14 mm; **Fr** 19–23 × 7 mm; **Se** oblong, 3–4 × 2 mm.

**G. carinata** var. **carinata** — **Distr:** RSA (Western Cape); Renosterveld vegetation and thickets on shale or quartz, spring-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 55).

**Incl.** *Aloe tristicha* Medikus (1786); **incl.** *Aloe carinata* var. *subglabra* Haworth (1804); **incl.** *Aloe lingua* var. *angulata* Haworth (1804); **incl.** *Aloe lingua* var. *multifaria* Haworth (1804); **incl.** *Aloe angulata* Willdenow (1811)  $\equiv$  *Gasteria angulata* (Willdenow) Haworth (1819)  $\equiv$  *Gasteria disticha* var. *angulata* (Willdenow) Baker (1880); **incl.** *Aloe excavata* Willdenow (1811)  $\equiv$  *Gasteria excavata* (Willdenow) Haworth (1827); **incl.** *Aloe laevis* Salm-Dyck (1817)  $\equiv$  *Aloe angustifolia* var. *laevis* (Salm-Dyck) Salm-Dyck (1821) (*nom. inval.*, Art. 43.1); **incl.** *Aloe obscura* var. *truncata* Salm-Dyck (1817); **incl.** *Aloe pseudoangulata* Salm-Dyck (1817); **incl.** *Aloe subcarinata* Salm-Dyck (1817)  $\equiv$  *Gasteria subcarinata* (Salm-Dyck) Haworth (1819); **incl.** *Gasteria latifolia* var. *multifaria* Haworth (1819); **incl.** *Aloe sulcata* Salm-Dyck (1821)  $\equiv$  *Gasteria sulcata* (Salm-Dyck) Haworth (1827); **incl.** *Gasteria laetepuncta* Haworth (1827)  $\equiv$  *Aloe laetepuncta* (Haworth) Roemer & Schultes (1829); **incl.** *Gasteria parva* Haworth (1827)  $\equiv$  *Gasteria carinata* var. *parva* (Haworth) Baker (1896); **incl.** *Gasteria strigata* Haworth (1827)  $\equiv$  *Gasteria carinata* var. *strigata* (Haworth) Baker (1896); **incl.** *Aloe carinata* var. *laevior* Salm-Dyck (1836); **incl.** *Gasteria pallescens* Baker (1880); **incl.** *Gasteria parvifolia* Baker (1880); **incl.** *Gasteria porphyrophylla* Baker (1880); **incl.** *Gasteria carinata* var. *falcata* A. Berger (1908); **incl.** *Gasteria carinata* var. *latifolia* A. Berger (1908); **incl.** *Gasteria trigona* var. *kewensis* A. Berger (1908); **incl.** *Gasteria humilis* Von Poellnitz (1929); **incl.** *Gasteria bijliae* Von Poellnitz (1937); **incl.** *Gasteria schweickerdtiana*



Von Poellnitz (1938); **incl.** *Gasteria patentissima* Von Poellnitz (1940).

[4] **L** first distichous, becoming rosulate or spirally arranged, 3–18 × 2.5–10 cm, triangular to triangular-lanceolate with a distinct keel, epidermis with raised white tubercles, tip acute or obtuse.

Differs from the other varieties by the triangular to triangular-lanceolate tuberculate and keeled leaves.

**G. carinata** var. **glabra** (Salm-Dyck) Van Jaarsveld (Cact. Succ. J. (US) 70(2): 70, ill. (p. 68), 1998). **Type:** [neo — icono]: Salm-Dyck, Monogr. Gen. Aloes & Mesembr., fasc. 5, *Aloe* sect. 29, fig. 19, 1849. — **Distr:** RSA (Western Cape: E of the Gouritz River, around Mossel Bay etc.); Mossel Bay Shale Renosterveld vegetation. **I:** Jaarsveld (2008: 88). — Fig. 4.

≡ *Aloe glabra* Salm-Dyck (1817) ≡ *Gasteria glabra* (Salm-Dyck) Haworth (1819); **incl.** *Aloe glabra* var. *brevifolia* Salm-Dyck (1817); **incl.** *Aloe glabra* var. *major* Salm-Dyck (1821) (*nom. illeg.*, Art. 52.1).

[4] Differs from var. *carinata*: **L** 3–18 × 2.5–10 cm, without tubercles.

**G. carinata** var. **verrucosa** (Miller) Van Jaarsveld (Aloe 29(1): 15, 1992). **Type:** [lecto — icono]: Boerhaave, Ind. Alter Hort. Lugd.-Bat., t. 2, p. 131 (no. 36), 1720. — **Distr:** RSA (Western Cape); Fynbos vegetation on limestone or shale, mainly spring-flowering.

≡ *Aloe verrucosa* Miller (1768) ≡ *Aloe linguiformis* var. *verrucosa* (Miller) De Candolle (1799) ≡ *Gasteria verrucosa* (Miller) Duval (1809); **incl.** *Aloe racemosa* Lamarck (1783); **incl.** *Aloe carinata* De Candolle (1799) (*nom. illeg.*, Art. 53.1); **incl.** *Aloe intermedia* Haworth (1804) ≡ *Gasteria intermedia* (Haworth) Haworth (1812); **incl.** *Aloe lingua* Ker (1810) (*nom. illeg.*, Art. 52.1); **incl.** *Aloe subverrucosa* Salm-Dyck (1817) ≡ *Gasteria subverrucosa* (Salm-Dyck) Haworth (1827); **incl.** *Aloe verrucosa* var. *striata* Salm-Dyck (1817) ≡ *Gasteria verrucosa* var. *striata* (Salm-Dyck) Von Poellnitz (1938); **incl.** *Aloe intermedia* var. *asperrima* Salm-Dyck (1821) ≡ *Gasteria intermedia* var. *asperrima* (Salm-Dyck)



**Fig. 4** *Gasteria carinata* var. **glabra**. (Copyright: E. Van Jaarsveld)

Haworth (1821) (*nom. inval.*, Art. 43.1) ≡ *Gasteria verrucosa* var. *asperrima* (Salm-Dyck) Von Poellnitz (1938) (*nom. inval.*, Art. 43.1); **incl.** *Aloe subverrucosa* var. *parvipunctata* Salm-Dyck (1821) ≡ *Gasteria subverrucosa* var. *parvipunctata* (Salm-Dyck) Haworth (1827); **incl.** *Aloe verrucosa* var. *latifolia* Salm-Dyck (1821) ≡ *Gasteria verrucosa* var. *latifolia* (Salm-Dyck) Haworth (1821); **incl.** *Gasteria repens* Haworth (1821); **incl.** *Aloe subverrucosa* var. *grandipunctata* Salm-Dyck (1821) (*nom. inval.*, Art. 26.1) ≡ *Gasteria subverrucosa* var. *grandipunctata* (Salm-Dyck) Haworth (1827) (*nom. inval.*, Art. 26.1); **incl.** *Gasteria intermedia* var. *laevior* Haworth (1827); **incl.** *Gasteria intermedia* var. *longior* Haworth (1827); **incl.** *Aloe scaberrima* Salm-Dyck (1834) ≡ *Gasteria verrucosa* var. *scaberrima* (Salm-Dyck) Baker (1880); **incl.** *Gasteria subverrucosa* var. *marginata* Baker (1880); **incl.** *Gasteria radulosa* Baker (1889).

[4] Differs from var. *carinata*: **L** distichous, rarely becoming rosulate, 3–28 × 1.5–3.5 cm, linear-lanceolate to lorate, distinctly tuberculate due to raised semitranslucent white or green domed tubercles, green to glaucous-green; **Inf** 12–30 cm; **Per** 20–25 mm.

Aymerich & Gustamante (2015) report that the taxon is likely to become naturalized in Spain, based on a small number of recent sightings at ruderal places.

**G. croucheri** (Hooker fil.) Baker (J. Linn. Soc., Bot. 18(109): 196, 1880). **Type:** RSA



(*Cooper* s.n. [K]). — **Distr:** RSA (KwaZulu-Natal, N Eastern Cape).

≡ *Aloe croucheri* Hooker *fil.* (1869).

**G. croucheri** ssp. **croucheri** — **Distr:** RSA (KwaZulu-Natal, N Eastern Cape); quartzitic sandstone cliff faces in Eastern Valley Bushveld vegetation, flowers mid-summer.

**Incl.** *Gasteria disticha* var. *natalensis* Baker (1880).

[4] Acaulescent, decumbent to erect, 25–40 × 60 cm Ø, solitary or dividing to form dense groups; **L** rosulate, 15–36 × 3–10 cm, triangular to linear-lanceolate, erectly spreading, rarely patent or recurved or pendent, both surfaces dark green, often glaucous, with dense white spots arranged in transverse bands, epidermis smooth, rarely slightly asperulous, margin tuberculate, serrulate, rarely denticulate, tip obtuse or acute, mucronate; juvenile **L** distichous, lorate, patent to erectly spreading, smooth or asperulous, tip acute, rarely obtuse, mucronate; **Inf** variable flat-topped panicles to 50 cm, or racemose, with or without a pair of branches; **Bra** 5 mm, piliferous; **Ped** 6–7 mm, pink; **Per** 28–40 mm, stipitate for up to 6 mm, gasteriform part narrowly ellipsoid, ½ of the perianth length, 5–9 mm Ø, pink, upper ½ of the perianth white with green striations, inflated to the same Ø as the lower part, lobes erect becoming erectly spreading, obtuse; **Sti** included or shortly exerted; **Fr** 18–25 mm, obtuse; **Se** 3–4 × 2–3 mm.

**G. croucheri** ssp. **pendulifolia** (Van Jaarsveld) Zonneveld (Pl. Syst. Evol. 251: 225, 2005). **Type:** RSA, KwaZulu-Natal (*Van Jaarsveld & al.* 9838 [NBG]). — **Distr:** RSA (KwaZulu-Natal); quartzitic sandstone cliff faces in Eastern Valley Bushveld vegetation. **I:** Jaarsveld & Ward-Hilhorst (1994: 39, as *G. croucheri*).

≡ *Gasteria pendulifolia* Van Jaarsveld (2001).

[4] Differs from ssp. *croucheri*: **L** linear-lanceolate to lorate-falcate, to 45 cm, basally to 4.5 cm broad, epidermis often glaucous.

**G. croucheri** ssp. **pondoensis** N. Crouch & al. (Bothalia 41(1): 183–184, ill., 2011). **Type:** RSA, Eastern Cape (*Crouch & Styles* 1149 [NH]). — **Lit:** Crouch & al. (2013). **Distr:** RSA (Eastern

Cape); on quartzitic sandstone cliff faces in Scarp Forest vegetation.

[4] Differs from ssp. *croucheri*: **L** 20–150 cm; **Per** 42–50 mm.

Both this subspecies and ssp. *pendulifolia* can have glaucous leaves. Zukulu & al. (2012: 12) report that the plants are used locally for protection against lightning strikes and misfortune through witchcraft.

**G. disticha** (Linné) Haworth (Philos. Mag. Ann. Chem. 1827: 352, 1827). **Type:** [lecto — icono]: Commelin, Hort. Med. Amstel., t. 8, 1701. — **Distr:** RSA (Western Cape); Succulent Karoo, Nama Karoo and Renosterveld vegetations, flowers spring to mid-summer.

≡ *Aloe disticha* Linné (1753).

**G. disticha** var. **disticha** — **Distr:** RSA (Western Cape: Robertson Karoo); in the shade of Karoo shrubs, spring-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 63).

**Incl.** *Aloe linguiformis* Miller (1768); **incl.** *Aloe lingua* var. *angustifolia* Aiton (1789) ≡ *Gasteria angustifolia* (Aiton) Duval (1809) ≡ *Aloe angustifolia* Salm-Dyck (1821) (*nom. illeg.*, Art. 53.1) ≡ *Aloe angustifolia* (Aiton) Salm-Dyck (1849) (*nom. illeg.*, Art. 53.1) ≡ *Gasteria disticha* var. *angustifolia* (Aiton) Baker (1880); **incl.** *Aloe lingua* var. *crassifolia* Aiton (1789) ≡ *Gasteria nigricans* var. *crassifolia* (Aiton) Haworth (1821) ≡ *Aloe crassifolia* (Aiton) Roemer & Schultes (1829); **incl.** *Aloe lingua* var. *latifolia* Haworth (1804) ≡ *Gasteria latifolia* (Haworth) Haworth (1812); **incl.** *Aloe lingua* var. *longifolia* Haworth (1804) ≡ *Gasteria longifolia* (Haworth) Duval (1809); **incl.** *Aloe nigricans* Haworth (1804) ≡ *Gasteria nigricans* (Haworth) Duval (1809); **incl.** *Aloe obscura* Willdenow (1811) (*nom. illeg.*, Art. 53.1); **incl.** *Aloe conspurcata* Salm-Dyck (1817) ≡ *Gasteria conspurcata* (Salm-Dyck) Haworth (1827) ≡ *Gasteria disticha* var. *conspurcata* (Salm-Dyck) Baker (1880); **incl.** *Aloe conspurcata* var. *truncata* Salm-Dyck (1817); **incl.** *Aloe conspurcata* var. *unilateralis* Salm-Dyck (1817); **incl.** *Aloe lingua* var. *brevifolia* Salm-Dyck (1817); **incl.** *Aloe nigricans* var. *denticulata* Salm-Dyck (1817) ≡ *Gasteria denticulata* (Salm-Dyck) Haworth (1819);

**incl.** *Aloe obtusifolia* Salm-Dyck (1821)  $\equiv$  *Gasteria obtusifolia* (Salm-Dyck) Haworth (1827); **incl.** *Gasteria mollis* Haworth (1821)  $\equiv$  *Aloe mollis* (Haworth) Roemer & Schultes (1829); **incl.** *Gasteria disticha* var. *major* Haworth (1827); **incl.** *Gasteria disticha* var. *minor* Baker (1880).

[1] Acaulescent, decumbent to erect, proliferating from the base to form small groups to 23 cm  $\varnothing$ ; **L** distichous, 6–17  $\times$  3–4.5 cm, lorate, erectly spreading, both faces with dense white spots arranged in irregular transverse bands, epidermis asperulous, margin irregularly undulating, tuberculate-crenulate, tip obtuse, rarely truncate, mucronate; juvenile **L** often patent or recurved, asperulous, truncate; **Inf** racemose, simple or with a pair of branches, 20–90 cm; **Per** 12–20 mm, stipitate for 2–3 mm, gasteriform part  $> \frac{1}{2}$  of the perianth length, globose-ellipsoid or narrowly ellipsoid, 6 mm  $\varnothing$ , pink to reddish-pink, then constricted into a tube of 3–4 mm  $\varnothing$ , white with green striations; **Fr** oblong, 15–23  $\times$  7 mm; **Se** 3–4  $\times$  2–3 mm.

**G. disticha** var. **langebergensis** Van Jaarsveld (*Aloe* 44(4): 99, ill., 2008). **Type:** RSA, Western Cape (*Van Jaarsveld & Visser* 19893 [N BG]). — **Distr:** RSA (Western Cape: Robertson Karoo: lower slopes of the Langeberg); spring-flowering.

[1] Differs from var. *disticha*: Forming small clusters; **L** linear-lorate, 3–5  $\times$  1–1.2 cm, margin denticulate.

**G. disticha** var. **robusta** Van Jaarsveld (*Aloe* 44(4): 99, ill., 2008). **Type:** RSA, Western Cape (*Smith* s.n. [PRE]). — **Distr:** RSA (Western Cape: Gamka Karoo); mid-summer-flowering.

[1] Differs from var. *disticha*: Proliferating to form small groups; **L** lorate, 5.5–10  $\times$  4.5–6.5 cm.

**G. doreeniae** Van Jaarsveld & A. E. van Wyk (*Aloe* 41(4): 81–82, ill., 2005). **Type:** RSA, Eastern Cape (*Court* 448 [N BG]). — **Distr:** RSA (Eastern Cape); on cliffs in Kowie Thicket vegetation, spring-flowering.

[1] Acaulescent, proliferating and forming clusters; **L** distichous, lorate, 3.5–8  $\times$  1.4–2.5 cm, surface asperulous, mottled with dark green and white spots; **Inf** racemose, 12–40 cm, usually unbranched;

**Per** 15–17 mm, globose-ovoid for the lower  $\frac{1}{3}$  of its length, pink, uppermost  $\frac{1}{3}$  pale pink with green striation; **Fr** 18 mm; **Se** 3–4  $\times$  2–3 mm.

Formerly classified as *G. bicolor* var. *liliputana*, e.g. by Jaarsveld & Ward-Hilhorst (1994).

**G. ellaphieae** Van Jaarsveld (*Cact. Succ. J. (US)* 63(1): 3–7, ill., 1991). **Type:** RSA, Eastern Cape (*Van Jaarsveld & al.* 9904 [N BG]). — **Distr:** RSA (Eastern Cape); Gamtoos Thicket vegetation, in rock crevices; flowers early to mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 51).

[4] Acaulescent, decumbent to erect, 1.5–4  $\times$  5–16 cm, solitary or proliferating from the base to form small groups; **L** first distichous, becoming rosulate, 2–5  $\times$  1–2 cm, triangular to triangular-lanceolate and falcate, the inner erectly spreading, the outer recurved, lower face with an asymmetrical keel, both faces dark green with dense white tubercles arranged in irregular transverse bands, epidermis tuberculate, margin tuberculate-denticulate, tip acute or acuminate, recurved, mucronate; juvenile **L** distichous, lorate, ascending at first, becoming patent or recurved; **Inf** erectly spreading racemes, 25–40 cm, unbranched or branched in the upper  $\frac{1}{3}$  and with 8–15 flowers; **Per** 22–27 mm, reddish-pink, stipitate for 2.5 mm, gasteriform for slightly  $> \frac{1}{2}$  of the perianth length, 7.5 mm  $\varnothing$ , narrowly ellipsoid, above constricted into a tube 4.5 mm  $\varnothing$ , lobes erectly spreading, obtuse, white with central green striae; **Sty** included; **Fr** 12–15  $\times$  5–6 mm; **Se** 3  $\times$  2 mm.

**G. excelsa** Baker (*J. Linn. Soc., Bot.* 18(109): 195, 1880). **Type:** RSA, Eastern Cape (*Cooper* s.n. [K]). — **Distr:** RSA (Eastern Cape); Valley Bushveld and Albany Thicket vegetations, rocky river valleys, flowers mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 43).

**Incl.** *Gasteria fuscopunctata* Baker (1880); **incl.** *Gasteria huttoniae* N. E. Brown (1908); **incl.** *Gasteria lutzii* Von Poellnitz (1933).

[4] Acaulescent, robust, decumbent to erect, solitary, 30–60  $\times$  60–75 cm; **L** in a dense **Ros**, 10–40  $\times$  10–18 cm, triangular to triangular-lanceolate, erectly spreading to somewhat recurved, both faces dark green with indistinct white spots

arranged in transverse bands, which (rarely) may be barely visible, rarely striate, epidermis smooth, margin often very sharp, cartilaginous, serrulate, tip acute or obtuse, mucronate; juvenile **L** distichous, densely white-spotted, patent, lorate, tuberculate; **Inf** very large spreading panicles, 1–3 per plant, 1–1.9 m, branches erectly (rarely horizontally) spreading; **Per** 22–26 mm, stipitate for 2–3 mm, gasteriform part  $> \frac{1}{2}$  of the perianth length, narrowly ellipsoid, tube constricted to 5 mm  $\varnothing$ , light pink (rarely white), 6–7 mm  $\varnothing$  at the widest point, lobes white with green mid-stripes; **Sty** included; **Fr** 17–20  $\times$  8–12 mm; **Se** 4–5  $\times$  2–3 mm.

Cumming (2003) counted the reproductive success of a population with 51 flowering-size plants. He found 116 racemes with 150–260 capsules each, with 10–85 seeds per capsule, resulting in the production of 1.132 million seeds in the study year. He observed only  $\pm 4$  seedling plants/year, resulting in an establishment rate of 1:300,000.

Crook & al. (2009) found, based on casual observation, that some seeds remain enclosed at the bottom of open capsules, but further studies are needed to establish whether this is a general feature, since the capsules do not differ from those of other species of the genus.

**G. glauca** Van Jaarsveld (Cact. Succ. J. (US) 70(2): 65–66, ills., 1998). **Type:** RSA, Eastern Cape (*Van Jaarsveld & Welsh* 14670 [PRE]). — **Lit:** Jaarsveld & Thomas (2003). **Distr:** RSA (Eastern Cape: Kouga River); sheer S-facing cliff-faces in Gamtoos Thicket vegetation, flowers in mid-summer.

[4] Acaulescent, decumbent to erect, proliferating from the base to form dense clusters to 30 cm  $\varnothing$ ; **L** rosulate, 5–7  $\times$  1.5–1.8 cm, lorate-lanceolate, upper face slightly canalicate in the upper  $\frac{1}{3}$ , lower face somewhat convex with a distinct asymmetrical keel, both surfaces glaucous, epidermis tuberculate-asperulous, margins tuberculate-dentate, tip acute, mucronate; **Inf** simple racemes to 25 cm with 10–20 flowers in the upper  $\frac{1}{2}$ ; **Per** 30–34 mm, reddish-pink, gasteriform basally for  $\pm \frac{1}{2}$  of its length or slightly less, globose-ellipsoid, then constricted into a

tube 5 mm wide; **St** to 32 mm; **Anth** yellow, included; **Ov** yellowish-green, 6  $\times$  2.5 mm; **Fr** oblong, 20  $\times$  8 mm; **Se** 3  $\times$  2 mm, black.

Closely related to *G. ellaphieae*, which also occurs along the Kouga River.

**G. glomerata** Van Jaarsveld (*Bradleya* 9: 100–104, ills., SEM-ills., 1991). **Type:** RSA, Eastern Cape (*Van Jaarsveld & Sardin* 11054 [NBG]). — **Distr:** RSA (Eastern Cape); on sheer sandstone cliff faces in Gamtoos Thicket vegetation, S aspects, spring-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 77).

[1] Acaulescent, decumbent to erect, 1.5–4  $\times$  2–8 cm, proliferating from the base to form dense globose clusters to 20 cm  $\varnothing$ ; **L** distichous, 1.5–5  $\times$  1.5–2.5 cm, lorate to widely ovate, the inner erectly spreading, the outer patent or recurved, biconvex in cross-section to almost terete, becoming flattened during the dry season, upper face often retuse in the upper  $\frac{1}{3}$ , both faces glaucous, unspotted, epidermis minutely tuberculate, asperulous, margin entire, minutely crenulate-tuberculate in the upper  $\frac{1}{4}$ , tip truncate or obtuse, mucronate; juvenile **L** distichous, lorate, ascending at first, becoming patent or recurved, asperulous, only slightly and obscurely tuberculate; **Inf** erectly spreading racemes, simple, 12–20 cm; **Per** 20–27 mm, gasteriform part slightly  $> \frac{1}{2}$  of the perianth length, reddish-pink, globose to globose-ellipsoid, 6–9 (–10) mm  $\varnothing$ , variable, then constricted into a tube 4 mm  $\varnothing$ ; **Fr** 16  $\times$  8 mm; **Se** 3  $\times$  2 mm.

**G. koenii** Van Jaarsveld (*Haseltonia* 23: 48, ills. (pp. 49–52), 2017). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 26922 [NBG]). — **Distr:** RSA (Western Cape: S foothills of the Osberg (Groot Swartberg)); in Eastern Valley Bushveld vegetation, 270 m; summer-flowering.

[1] Acaulescent, decumbent, 30  $\times$  to 35 cm  $\varnothing$ , proliferating from the base and forming clusters with 3–8 heads; **R** succulent, to 5 mm  $\varnothing$ ; **L** rosulate, deltoid-lanceolate to linear, 1.5–3  $\times$  2–4.5 cm, falcate and curving upwards, sometimes twisted and unevenly parallel, upper face flat to shallowly canalicate, plane towards the apex, faintly to densely white-spotted, lower face

somewhat convex with a distinct eccentric keel, faintly to densely spotted, spots arranged in obscure transverse bands, both faces shiny, light to dark green, with smooth epidermis, margins minutely denticulate to almost entire, apex acute or subacute, sometimes acuminate, mucronate; juvenile **L** distichous, lorate, patent to ascending, epidermis similar to adult leaves, densely white-spotted, spots arranged in transverse bands, apex obtuse, mucronate; **Inf** racemose, to 70 cm, flowers secundly arranged and open at the same time, bracteate; floral **Bra** 7 × 2 mm, piliferous; **Ped** 5 mm, pink; **Per** 20–21 mm, gasteriform, stipitate for 2 mm; **Tep** fused except for the tips and margins of the inner ones, perianth tube subcylindrical, curved in the upper 1/3, the lower 2/3 slightly decurved, inflated to ±5–6 mm Ø, pink, upper 1/2 white with green striations, tips erect becoming erectly spreading, obtuse; **St** 10–12 mm; **Anth** 2 × 1 mm, included; **Ov** 5–6 × 2–3 mm Ø, green; **Sty** 7 mm; **Sti** included, minute; **Fr** 22–30 × 6–8 mm Ø, narrowly obovoid, triangular in cross-section, obtuse at the apex; **Se** blackish.

**G. loedolffiae** Van Jaarsveld (Bradleya 32: 44–46, ills. (pp. 45–48), 2014). **Type:** RSA, Eastern Cape (*Van Jaarsveld & al.* 24626 [NBG]). — **Distr:** RSA (Eastern Cape); sheer shale cliffs, Eastern Valley Bushveld vegetation, 270 m, summer-flowering.

[3] Acaulescent, decumbent to ascending, to 38 cm Ø, solitary or proliferating from the base to form clusters of 3–5 heads; **L** rosulate (but distichous in juvenile plants), first ascending, then patent-spreading firm, lorate-lanceolate, 16.5–23 × 6–6.5 cm broad at the base, slightly falcate, adaxial face canaliculate, faintly white-spotted (spots in transverse bands in juvenile plants), abaxial face somewhat convex with a distinct asymmetrical keel, faintly spotted, both faces dull green with smooth, slightly minutely asperulous epidermis, margins minutely serrulate to almost entire, apex obtuse to subacute, mucronate; **Inf** ascending to flat-topped panicles (racemose in juvenile plants), to 1.15 m; **Ped** 4 mm, pink; **Per** 27–29 mm, stipitate for 3–4 mm, subcylindrical, curved in the middle, upper 1/2 inflated

to ±7 mm Ø; **Tep** fused for the greater part of their length, uniform dull pink; **St** 23–25 mm; **Anth** 3 × 1.5 mm, included; **Ov** 6.5 × 3 mm Ø, green; **Sty** 13 mm; **Sti** included, curved upwards, minute; **Fr** 16–25 × 7–10 mm, narrowly obovoid, triangular in cross-section, with obtuse apex; **Se** oblong, 5 × 3 mm, black.

**G. nitida** (Salm-Dyck) Haworth (Philos. Mag. Ann. Chem. 1827: 359, 1827). **Type:** [neo — icono]: Salm-Dyck, Monogr. Gen. Aloes & Mesembr., fasc. 4, *Aloe* sect. 29, t. 17, 1842. — **Distr:** RSA (Eastern Cape); Kouga Sandstone Fynbos and Bisho Thornveld vegetations, flowers in mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 47).

≡ *Aloe nitida* Salm-Dyck (1817); **incl.** *Aloe nitida* var. *major* Salm-Dyck (1817); **incl.** *Aloe nitida* var. *minor* Salm-Dyck (1817); **incl.** *Aloe nitida* var. *obtusata* Salm-Dyck (1817) ≡ *Gasteria obtusata* (Salm-Dyck) Haworth (1827); **incl.** *Aloe nitida* var. *grandipunctata* Salm-Dyck (1821) (*nom. illeg.*, Art. 52.1) ≡ *Gasteria nitida* var. *grandipunctata* (Salm-Dyck) A. Berger (1908) (*nom. illeg.*, Art. 52.1); **incl.** *Aloe nitida* var. *parvipunctata* Salm-Dyck (1821) (*nom. illeg.*, Art. 52.1) ≡ *Gasteria nitida* var. *parvipunctata* (Salm-Dyck) A. Berger (1908) (*nom. illeg.*, Art. 52.1); **incl.** *Aloe trigona* var. *obtusata* Salm-Dyck (1821) (*nom. illeg.*, Art. 52.1); **incl.** *Aloe nitida* Ker Gawler (1822) (*nom. illeg.*, Art. 53.1); **incl.** *Haworthia nigricans* Haworth (1824); **incl.** *Gasteria decipiens* Haworth (1827) ≡ *Aloe decipiens* (Haworth) Roemer & Schultes (1829); **incl.** *Gasteria beckeri* Schönland (1907); **incl.** *Gasteria stayneri* Von Poellnitz (1938).

[4] Acaulescent, decumbent to erect, 6–20 × 5–28 cm, solitary or proliferating from the base to form small groups; **R** somewhat fusiform, succulent, to 12 mm Ø; **L** first distichous, becoming rosulate, 1.6–18 × 2.5–8 cm, triangular-lanceolate, rarely lanceolate-acuminate, erectly spreading with a distinct asymmetrical keel, both faces dark green, with faint to dense white spots arranged in irregular transverse bands, epidermis smooth and shiny, margin entire or indistinctly tuberculate, tip acute, mucronate; juvenile **L** distichous, lorate, 2–4 × 2–3.5 cm, epidermis

tuberculate, rarely smooth, dark green, not or rarely spotted; **Inf** erectly spreading branched lax panicles 0.2–1.2 m; **Per** 20–25 mm, bright reddish-pink, stipitate for 2–3 mm, gasteriform for slightly  $> \frac{1}{2}$  of the perianth length, 5–8 mm  $\varnothing$ , narrowly ellipsoid, constricted above into a tube 4–5 mm  $\varnothing$ , lobes erectly spreading, obtuse, yellowish; **Sty** included; **Fr** oblong, 24–30  $\times$  8 mm; **Se** 3–4  $\times$  2 mm.

**G. pillansii** Kensit (Trans. Roy. Soc. South Africa 1: 163, 1909). **Type:** RSA, Northern Cape (*Pillans* 833 [BOL, PRE]). — **Distr:** S Namibia, NW RSA (Northern Cape).

**G. pillansii** var. **ernesti-ruschii** (Dinter & Von Poellnitz) Van Jaarsveld (Aloe 29(1): 17, 1992). **Type:** [lecto — icono]: Kakt. and. Sukk. (Berlin), 1938(2): ill. p. 36. — **Distr:** S Namibia, RSA (Northern Cape); Succulent Karoo vegetation, rocks, flowers mid-summer to autumn. **I:** Jaarsveld & Ward-Hilhorst (1994: 61). — Fig. 5.

≡ *Gasteria ernesti-ruschii* Dinter & Von Poellnitz (1938).

[2] Differs from var. *pillansii*: **L** 2–7 cm; **Inf** 6–30 cm; **Per** 25–30 mm; **St** shortly exserted.

**G. pillansii** var. **hallii** Van Jaarsveld (Aloe 44 (4): 94, ill., 2008). **Type:** RSA (*Van Jaarsveld & Duncan* 7912 [NBG]). — **Distr:** RSA (Northern Cape: Richtersveld); succulent shrubland, rocks, autumn-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 2, as *G. pillansii* var. *ernesti-ruschii*).

[2] Differs from var. *pillansii*: **L** 2–4  $\times$  1.5–2 cm; **Fl** shorter and in autumn; **St** shortly exserted.

**G. pillansii** var. **pillansii** — **Distr:** RSA (Northern Cape: Namaqualand); Succulent Karoo vegetation, flowers in mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 59). — Figs. 6 and 7.

**Incl.** *Gasteria neliana* Von Poellnitz (1930).

[2] Acaulescent, decumbent to erect, 5–20  $\times$  6–40 cm, proliferating from subterranean stolons and forming dense groups; **L** distichous, 2–20  $\times$  1.5–5 cm, lorate, erectly spreading or patent, both faces spotted with immersed tubercles in obscure transverse bands, epidermis asperulous, rarely with few domed tubercles, margin cartilaginous,



**Fig. 5** *Gasteria pillansii* var. *ernesti-ruschii*. (Copyright: U. Eggli)

tuberculate or crenulate, tip obtuse to acute, mucronate; **Inf** racemose, 1–3 per plant, spreading and slightly curved, 0.6–1.2 (–1.65) m, rarely with a pair of branches; **Fl** laxly arranged in the upper  $\frac{1}{2}$ ; **Per** 25–50  $\times$  6–8 mm, stipitate for 3 mm, obscurely gasteriform basally for  $\frac{1}{3}$  or less of the length, globose-ellipsoid to slightly constricted above the ovary, above gradually enlarging and rarely clavate, gasteriform part pink, tube white with green striations; **St** included or exserted to 5 mm; **Fr** oblong, 15–23  $\times$  7 mm; **Se** 4–5  $\times$  2.5 mm.

**G. polita** Van Jaarsveld (Cact. Succ. J. (US) 73 (3): 127–129, ills., 2001). **Type:** RSA, Western Cape (*Van Jaarsveld & Kok* 13742 [NBG]). — **Distr:** RSA (Western Cape); Tsitsikamma Sandstone Fynbos vegetation, rocky outcrops, spring-flowering. **I:** Retief (2015).

[4] Acaulescent, solitary or proliferating to form small groups, 12  $\times$  25 cm; **L** rosulate, ascending,





**Fig. 6** *Gasteria pillansii* var. *pillansii*. (Copyright: E. Van Jaarsveld)



**Fig. 7** *Gasteria pillansii* var. *pillansii*. (Copyright: E. Van Jaarsveld)

becoming spreading, strap-shaped, 6–12 × 3–4 cm, apex obtuse to subacute, mucronate, adaxial face canaliculate, abaxial face somewhat convex with a distinct asymmetrical keel, both faces dark green mottled with white spots in transverse pattern, epidermis smooth, shiny, margin tuberculate-crenate; juvenile **L** distichous, lorate, patent to ascending, smooth and shiny, apex obtuse, mucronate; **Inf** racemose, to 60 (–100) cm, spreading, simple or sometimes with 2 branches; **Per** 35 mm, stipitate for 4 mm, gasteriform basally, narrowly ellipsoid over ½ of the length, pink, upper ½ white with green striation; **Fr** oblong, 24–25 × 4–6 mm; **Se** 4–5 × 2 mm, black.

A new population with overall larger plants (inflorescences to 1 m) with somewhat earlier flowering time was recently discovered (Baard 2012a, Baard 2012b).

**G. pulchra** (Aiton) Haworth (Synops. Pl. Succ., 86, 1812). **Type:** [lecto — icono]: Miller, Gard. Dict., 1759, t. 292. — **Distr:** RSA (Eastern Cape); Gamtoos and Groot Thicket vegetations, on conglomerate, spring-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 45).

≡ *Aloe maculata* var. *pulchra* Aiton (1789) ≡ *Aloe pulchra* (Aiton) Haworth (1804); **incl.** *Aloe obliqua* De Candolle (1802) (*nom. illeg.*, Art. 53.1); **incl.** *Aloe pulchra* Jacquin (1805) (*nom. illeg.*, Art. 53.1); **incl.** *Gasteria poellnitziana* H. Jacobsen (1954) (*nom. inval.*, Art. 36.1).

[4] Acaulescent, decumbent to erect, 20–36 × 20–36 cm, solitary or proliferating from the base to

form small groups; **L** in a dense rosette, 24–36 × 2.5–4 cm, erectly spreading, often falcate, linear-ensiform to linear-acuminate, with an indistinct asymmetrical keel, both faces dark green with dense white spots in transverse bands, epidermis smooth, margin cartilaginous, serrulate, tip acute or acuminate, mucronate; juvenile **L** distichous, erectly spreading, lorate, acuminate, distinctly tuberculate, mucronate; **Inf** erect to erectly spreading lax panicles, 0.35–1.5 m, rarely simple or side branches erectly spreading; **Per** 18–25 mm, stipitate for 2 mm, gasteriform part >½ of the perianth length, globose-ellipsoid, reddish-pink, 6–7 mm Ø, then constricted into a tube of 4–4.5 mm Ø, light to dark pink, lobes white, rarely pink, erectly spreading, obtuse, with green median stripes; **Sty** included; **Fr** oblong, 12–27 × 7 mm; **Se** 2–5 × 2–3 mm.

**G. rawlinsonii** Obermeyer (Flow. Pl. Afr. 43 (3/4): t. 1701 + text, 1976). **Type:** RSA, Eastern Cape (*Rawlinson* s.n. [PRE 34421]). — **Distr:** RSA (Eastern Cape); Groot Thicket vegetation, sheer shady quartzitic sandstone cliff faces; spring-flowering. **I:** Jaarsveld & Ward-Hilhorst (1994: 79).

[1] Caulescent, pendulous, proliferating from the base; stems leafy, to 1 m, rarely branched, internodes 1–2 cm; **L** distichous or rosulate, 3–8 × 1–2.5 cm, linear, lorate, slightly falcate, tips recurved, lower face convex, without keel, both faces green, unspotted or with faint white spots, epidermis asperulous, margin sparingly denticulate, or sometimes unarmed, prickles



**Fig. 8** *Gasteria retusa*. (Copyright: E. Van Jaarsveld)

turning black with age, tip obtuse, mucronate; **Inf** racemose, 10–50 cm; **Bra** 5 × 2 mm at the base; **Per** variable, 16–25 mm, stipitate for 1–3 mm, gasteriform part  $> \frac{1}{2}$  of the length, globose-ellipsoid or globose, pink, then constricted into a tube 4–6 mm  $\varnothing$ , tube pink or white, occasionally with green striations; **Fr** 18 mm, oblong-ovoid; **Se** 3–4 mm.

A slow growing cliff-dweller with two forms grading into each other: One has the leaves remaining distichous and short inflorescences; the other is with rosulate leaves and longer inflorescences and a globose gasteriform perianth part.

**G. retusa** (Van Jaarsveld) Van Jaarsveld (Aloe 44(4): 100, ills., 2008). **Type:** RSA, Western Cape (Van Jaarsveld & Stayner 4656 [NBG]). — **Distr:** RSA (Western Cape): Robertson Karoo vegetation, on shale, spring-flowering. **I:** Jaarsveld & Weber (1994: as *G. carinata* var.). — Fig. 8.

≡ *Gasteria carinata* var. *retusa* Van Jaarsveld (1992).

[4] Acaulescent, decumbent to erect, proliferating from the base to form small groups 3–17 × 10–25 cm; **L** distichous, 3–15 (–17) × 1–3.5 cm, erectly spreading, lorate, both faces light to dark green, with raised semi-translucent white dome-shaped tubercles in transverse bands, margin cartilaginous often undulating, tuberculate-crenulate, rarely denticulate, tip retuse, truncate or obtuse, mucronate; juvenile **L** similar to adult leaves; **Inf** simple ascending racemes, 15–45 cm; **Ped** 8–9 mm; **Per** 17–22 mm, stipitate for 1–2 mm, gasteriform

part narrowly to globosely ellipsoid, making up  $> \frac{1}{2}$  of the perianth length, 5–8 mm  $\varnothing$ , pink, above constricted to a tube 4 mm  $\varnothing$ , white with green striation; **Sty** included; **Fr** oblong, 19–23 × 7 mm; **Se** 3–4 × 2 mm.

**G. thunbergii** N. E. Brown (Bothalia 1: 140, 1923). **Type:** RSA, Western Cape (*Thunberg* 8595 [UPS]). — **Distr:** RSA (Western Cape: Gouritz River Valley); Southern Cape Valley Thicket vegetation, on conglomerate, flowers mainly in autumn. **I:** Jaarsveld (2008: 93).

≡ *Gasteria carinata* var. *thunbergii* (N. E. Brown) Van Jaarsveld (1998); ≡ *Aloe disticha* Thunberg (1785) (*nom. illeg.*, Art. 53.1).

[4] Acaulescent, decumbent to erect, proliferating from the base to form small groups 6–20 × 10–30 cm; **L** distichous, 3–20 × 1–3 cm, ascending, acrose-subulate to linear-triangular, upper face deeply channelled, both faces green, with raised white to greenish tubercles in transverse bands, margin cartilaginous, denticulate, tip mucronate; juvenile **L** similar to adult leaves; **Inf** simple ascending racemes, 30–45 cm; **Per** variable, 18–20 mm, gasteriform at the base for  $\pm \frac{1}{2}$  of the perianth length, narrowly ellipsoid, pink, lobes white, rarely pink, erectly spreading, obtuse, with green median stripes; **Sty** included; **Fr** 20–22 × 6 mm; **Se** oblong, 6 × 2 mm.

**G. tukhelensis** Van Jaarsveld (Bothalia 35(2): 164–165, ills., 2005). **Type:** RSA, KwaZulu-Natal (Van Jaarsveld & al. 17996 [NBG]). — **Distr:** RSA (KwaZulu-Natal); cliffs along the Tukhela River, in Valley Bushveld vegetation, summer-flowering.

[3] Acaulescent, decumbent, to 25 × 70 cm  $\varnothing$ ; **L** rosulate, deltoid-lanceolate, 12–25 × 3–5 cm, falcate and curving upwards, adaxial face canaliculate, abaxial face somewhat convex with an asymmetrical keel, faintly spotted in obscure transverse bands, both surfaces shiny, dark green, margin minutely denticulate to almost entire, apex acute to subacute, mucronate; juvenile **L** distichous, lorate, patent to ascending, epidermis tuberculate; **Inf** racemose, to 56 cm, with up to 11 secundly arranged pendent flowers; **Per** pink, 40–43 mm, curved in the middle, basally only

very weakly elongate-gasteriform; **Fr** 23–32 mm; **Se** 5–7 × 2–3 mm.

**G. vlokii** Van Jaarsveld (Cact. Succ. J. (US) 58 (4): 170–174, ills., 1987). **Type:** RSA, Western Cape (*Vlok* 880 [NBG]). — **Dist:** RSA (Western Cape); South Swartberg Sandstone Fynbos vegetation, quartzitic sandstones, flowers in mid-summer. **I:** Jaarsveld & Ward-Hilhorst (1994: 53).

[4] Acaulescent, proliferating from the base to form small groups to 14 cm Ø; **R** succulent, to 8 mm Ø, fusiform; **L** distichous, ultimately becoming rosulate, 5–9 × 2–3 cm broad at the base, patent, lorate, lanceolate to triangular, falcate, with an asymmetrical keel in the upper ½, both faces green with dense white spots in obscure transverse bands, epidermis asperulous, margin acute, tuberculate, crenulate, becoming continuous towards the tip, tip acute or obtuse with an asymmetrical mucro; juvenile **L** lorate, tip obtuse, mucronate; **Inf** racemose, curved and spreading, 30–84 cm, rarely with a pair of branches; **Per** 29–33 mm, stipitate for 2–3 mm, gasteriform part slightly >½ of the perianth length, 6–7 mm Ø, dark reddish-pink, above constricted into a tube of 4 mm Ø, lobes white with green median striations; **Fr** 15–18 × 6 mm; **Se** oblong, 3–5 × 2 mm.

## References

- Aymerich, P. & Gustamante, L. (2015) Nuevas citas de plantas alóctonas de origen ornamental en el litoral meridional de Cataluña. *Bouteloua* 20: 22–41, ills.
- Baard, J. (2012a) Discovery on the Garden Route. Another population of the rare *Gasteria polita* found. *Veld Fl.* (1975+) 98(1): 20–21, ills., map.
- Baard, J. (2012b) *Gasteria polita*, an endangered succulent from South Africa. *CactusWorld* 30(3): 159–161, ills., map.
- Crook, I. [& al. 2009], Minors, D. M. & Minors, C. J. (2009) Observations on the seed dispersal strategy of *Gasteria excelsa*. *Haworthiad* 23(2): 52–54, ills.
- Crouch, N. R. [& al. 2000], Smith, G. F., Symmons, R. & Tomalin, M. (2000) *Gasteria croucheri* — the magic impundu of the Zulu. *Brit. Cact. Succ. J.* 18(2): 70–78, ills., map.
- Crouch, N. R. [& al. 2013], Smith, G. F. & Condy, G. (2013) *Gasteria croucheri* subsp. *pondoensis*. *Flow. Pl. Afr.* 63: 22–30, t. 2284, ill., map.
- Cumming, D. (2003) The army needs you! A matter of recruitment in *Gasteria excelsa* Baker. *Alsterworthia Int.* 3(3): 21.
- Daru, B. H. [& al. 2013], Manning, J. C., Boatwright, J. S., Maurin, O., Mclean, N., Schaefer, H., Kuzmina, M. & Bank, M. van der (2013) Molecular and morphological analysis of subfamily *Aloioideae* (*Asphodelaceae*) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62(1): 62–76, ills. **URL:** <http://www.jstor.org/stable/24389313>.
- Grace, O. M. & Rønsted, N. (2013) Unlocking the secrets of DNA in the classification of aloes. *Aloe* 50(1-2): 22–23.
- Jaarsveld, E. J van (1992) The genus *Gasteria*, a synoptic review. *Aloe* 29(1): 5–30, ills., maps, key, (2): 49 [erratum].
- Jaarsveld, E. J van (1998) A new taxon and new combinations in the *Gasteria carinata* complex. *Cact. Succ. J. (US)* 70(2): 65–71, ills., map, key.
- Jaarsveld, E. J van (2008) The genus *Gasteria*: A synoptic review (new taxa and combinations). *Aloe* 44(4): 84–103, ills.
- Jaarsveld, E. J van (2009) New *Gasteria* cultivars. *Aloe* 45(3): 52–55, ills.
- Jaarsveld, E. J van & Thomas, V. (2003) *Gasteria glauca*. *Flow. Pl. Afr.* 58: 16–21, t. 2184, map.
- Jaarsveld, E. J van & Ward-Hilhorst, E. (1994) *Gasterias* of South Africa. A new revision of a major succulent group. Vlaeberg (ZA): Fernwood Press in association with the National Botanical Institute.
- Jaarsveld, E. J van & Weber, R. (1994) *Gasteria carinata* var. *retusa*. *Flow. Pl. Afr.* 53: 86–89, t. 2097, map.
- Manning, J. C. [& al. 2014a], Boatwright, J. S., Daru, B. H., Maurin, O. & Bank, M. van der (2014) A molecular phylogeny and generic classification of *Asphodelaceae* subfamily *Aloioideae*: A final resolution of the prickly issue of polyphyly in the Alooids. *Syst. Bot.* 39(1): 55–74, key. <https://doi.org/10.1600/036364414X678044>
- Mays, H. (2009) Hybrids & cultivars of the succulent *Asphodelaceae*. Volume 1. *Aloe, Astroloba, Bulbine, Gasteria* & nothogenera. St. Michaels on Wyre (GB): Harry Mays.
- Raimondo, D. [& al. 2009], Staden, L. von, Foden, W., Victor, J. E., Helme, N. A., Turner, R. C., Kamundi, D. A. & Manyama, P. A. (eds.) (2009) Red List of South African plants 2009. Pretoria (ZA): South African National Biodiversity Institute SANBI (= *Strelitzia* No. 25).
- Retief, K. (2015) *Gasterias* at Nature's Valley. *Aloe* 51(2): 41–45, ills.
- Zonneveld, B. J. M. & Jaarsveld, E. J van (2005) Taxonomic implications of genome size for all species of the genus *Gasteria* Duval (*Aloaceae*). *Pl. Syst. Evol.* 251: 217–227, maps. <https://doi.org/10.1007/s00606-004-0244-x>
- Zukulu, S. [& al. 2012], Dold, T., Abbott, T. & Raimondo, D. (2012) Medicinal and charm plants of Pondoland. Pretoria (ZA): South African National Biodiversity Institute SANBI.



## × *Gastroloba* ASPHODELACEAE

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× *Gastroloba* D. M. Cumming (Bull. Afr. Succ. Pl. Soc. 9: 36, 1974). — *Alooidae*.

≡ *Gasteria* × *Astroloba*. Rowley (1982: 76) lists two known combinations, one of them formally named as *G. apicroides* (Baker) G. D. Rowley (≡ *Gasteria apicroides* Baker). Two further cultivars are described and illustrated by Mays (2009: 59).

### References

- Mays, H. (2009) Hybrids & cultivars of the succulent *Asphodelaceae*. Volume 1. *Aloe, Astroloba, Bulbine, Gasteria* & nothogenera. St. Michaels on Wyre (GB): Harry Mays.
- Rowley, G. D. (1982) Intergeneric hybrids in succulents. *Nation. Cact. Succ. J.* 37(1): 2–6, (2): 45–49, (3): 76–80, (4): 119, ills.

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## Haworthia ASPHODELACEAE

M. B. Bayer and E. Van Jaarsveld

**Haworthia** Duval (Pl. Succ. Horto Alencon., [7], 1809). **Type:** *Aloe pumila* var. *arachnoidea* Linné. — **Alooiidae** — **Lit:** Bayer (1982: ill. synopsis); Scott (1985: ill. synopsis); Breuer & Metzger (1997: typification); Breuer (1998a: bibliography); Breuer (1998b: synopsis); Bayer (1999: revision); Battista (2009: ill. synopsis); Schulz (2009: ill. synopsis); Mays (2013: cultivar synopsis); Zonneveld (2015: sectional classification); Gildenhuis & Klopper (2016: classification *Haworthiopsis*); Gildenhuis (2017: illustrated synopsis *Haworthiopsis*). **Distr:** S Namibia, RSA (predominantly Western Cape, Eastern Cape, but also Northern Cape, Free State, KwaZulu-Natal and Mpumalanga), Swaziland, S Moçambique; mainly Succulent Karoo, Nama Karoo and Albany Thicket vegetations, and to a lesser extent savanna, mostly in rocky places in the shade of grasses or shrubs. **Etym:** For Adrian H. Haworth (1768–1833), English zoologist and botanist and succulent plant specialist.

**Incl.** *Catevala* Medikus (1786) (*nomen rejiciendum*, Art. 56.1). **Type:** *Aloe retusa* Linné [Pfeiffer,

Nomencl. Bot., 1871–74 (cf. P. V. Heath, *Calyx* 4(3): 83, 1994)].

**Incl.** *Apicra* Willdenow (1811). **Type:** not typified.

**Incl.** *Aprica* D. Dietrich (1840). **Type:** not typified.

**Incl.** *Tulista* Rafinesque (1840). **Type:** *Aloe pumila* var. *margaritifera* Linné.

**Incl.** *Haworthiopsis* G. D. Rowley (2013). **Type:** *Haworthia coarctata* Haworth.

**Incl.** ×*Hawiopsis* G. D. Rowley (2014).

**Incl.** ×*Tulworthia* G. D. Rowley (2014).

**Incl.** ×*Tulworthiopsis* G. D. Rowley (2014).

Dwarf rosulate perennials, acaulescent to caulescent, solitary or proliferating to form dense tight clusters; **R** fibrous to succulent, sometimes fusiform; **Ros** sessile or caulescent, 2–15 cm Ø, flat to globose or elongate; **L** erect, spreading to recurved, sometimes highly reduced, laxly to densely spirally arranged, rarely distichous or somewhat tristichous, triangular-lanceolate to linear, usually firm, often drying back from the tip and becoming papery, surfaces often tuberculate and variously marked, glabrous to rarely pubescent, often with translucent windows, and with various patterns, markings and reticulations, very pale green, blue-green to dark (blackish-) green, upper face flat, or channelled to convex, lower face convex, often keeled towards the tip, margin entire, denticulate, ciliate, with bristly **Sp** or tuberculate, tip acute, or acuminate to mucronate, sometimes retuse or truncate; **Inf** 1–5 racemes from near the rosette centre, erect, simple or branched, firm to wiry, bracteate, peduncle brownish-green, often

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with a powdery bloom; **Bra** small; **Fl** small, zygomorphic, bilabiate, 5–50 per inflorescence,  $\pm 15$  mm, tube curved or straight, slightly swollen towards the base; **Tep** 6, white to pink, often with central green or brownish striations, tips spreading to recurved with green, brownish or occasionally yellow median colouration; **Fil** 6, included; **Ov** oblong to oblong-ovoid, 3-chambered, with 6 grooves; **Sty** subulate; **Sti** apical, minute, trilobate or rounded; **Fr** erect oblong-ovoid woody capsules, dehiscing longitudinally; **Se** black to grey, compressed, irregularly angled or flattish.

**Classification:** Treutlein & al. (2003b) found evidence that *Haworthia* in the traditional circumscription is not monophyletic, and this was corroborated by Ramdhani & al. (2009) and Ramdhani & al. (2011), as well as Daru & al. (2013) and Manning & al. (2014a) in their detailed studies of the whole subfamily *Aloioideae*. These last-mentioned authors recovered three well-supported clades of *Haworthia* that conform to the traditionally accepted subgenera, with the exception of *H. koelmaniorum*, which occupies an enigmatic position separate from all other *Haworthias*. The typical subgen. *Haworthia* has been found in a polytomy amongst *Aloe* sect. *Kumara*, *Aloe* sect. *Macrifolia* and a clade composed of the “true Aloes” and the remaining alooid genera. Subgen. *Robustipedunculares* is sister a clade that includes *Aloe aristata*, *A. variegata* and the genus *Astroloba*, and subgen. *Hexangulares* is sister to *Gasteria*. Rowley (2013a) formalized this phylogeny by accepting the genus *Tulista* for subgen. *Robustipedunculares*, and by describing the new genus *Haworthiopsis* for subgen. *Hexangulares*. *Tulista* in the sense of Rowley (l.c.) also includes *Astroloba*, *Poellnitzia* and *Aloe aristata*, a circumscription that is based on the phylogeny presented by Daru & al. (2013). Manning & al. (2014a) also accept the break-up of *Haworthia* into the three genera just mentioned, but recircumscribe *Tulista* by excluding *Aloe aristata* (recognized as monotypic genus *Aristaloe*). The cytogenetic work by Zonneveld (2015) also supports breaking up *Haworthia* s.l.

Editorial comment by U. Eggli: Despite the good support for many branches in the phylogenies of Daru & al. (2013) and Manning & al. (2014a), it

is argued that it is still premature to split *Haworthia* s.l., until a full and complete picture of the alooid genera is available — even though a good proportion of *Aloe* species have already been included in the phylogenetic studies cited above, taxa so far omitted could well cause surprising new interpretations when they are finally also investigated.

*Haworthia* s.l. has its centre of diversity in the Western Cape. Species definition is notoriously difficult because many species are highly variable and phenotypically plastic. To account for this Bayer (2002a: 59), Vosa (2005) and Bayer (2007a: 162–164) formulated a “superspecies” concept. It is well known that there are few reproductive barriers and natural hybrids are common within all three subgenera. In addition both *H. pumila* and *H. minima* hybridize naturally with *Astroloba corrugata*. [Editorial comment by U. Eggli: In fact, Ramdhani & al. (2011) proposed ancient hybridization (also with species from other alooid genera) to explain the phylogeny that resulted from their DNA study. These authors also found evidence that interspecific hybridization is still on-going, esp. in subgen. *Haworthia*, and they argue that the absence of reproductive barriers supports such an assumption].

It is commonly known that environmental and growing conditions determine physical appearance of *Haworthias* to a great degree, and Bayer & Dold (2003) discuss the role of geology and habitat in determining ecotypes.

The difficulties to diagnostically circumscribe taxa in *Haworthia* have led to differing views on how many and which species should be recognized, culminating in the vast over-splitting as advocated by Hayashi (2008) (4 subgenera, 546 species of which 234 were only provisionally named) or Breuer (2010) and Breuer (2011) (3 subgenera, 366 species in 108 “aggregates”, also with numerous provisional names).

Here, species definitions take into account morphological data supplemented with data from geographical distribution, with due notion of sympatric occurrences. We follow the classification concept of Bayer & Manning (2012a) and Bayer & Manning (2012b), which are based on the earlier synoptical work of Bayer (1982), the monograph of Bayer (1999), and subsequent new evidence

(Bayer 2002a, Bayer 2006, Bayer 2007a, Bayer 2008, Bayer 2009, Bayer 2010a, Bayer 2012a, Bayer 2012b). The following three subgenera are recognized:

- [1] Subgen. *Haworthia*: Base of the **Fl** triangular or rounded-triangular, tube obclavate, curved; **OTep** free; **Sty** upcurved; **Se** irregularly angled. — 37 species.
- [2] Subgen. *Hexangulares* Uitewaal ex M. B. Bayer 1971: Base of the **Fl** 6-angular, gradually narrowing to the junction with the **Ped**; tube obcapitate, curved; **OTep** partly fused to the **ITep**; **Sty** straight; **Se** irregularly angled. — 17 species.
- [3] Subgen. *Robustipedunculares* Uitewaal ex M. B. Bayer 1971: Base of the **Fl** 6-angular, rounded, abruptly joined to the **Ped**; **OTep** partly fused to the **ITep**, tube obcapitate, straight; **Sty** straight; **Se** flattish. — 4 species.

**Ecology:** North & al. (2008) report contractile roots for *Haworthia*, and this helps to explain the growth habit of the retuse-leaved species. Contraction is the result of radial expansion and longitudinal shrinkage of cells in the inner and/or middle root cortex layers.

**Pollination Biology:** Smith & al. (2002) found an interesting difference in nectar sugar concentrations: Species of subgen. *Haworthia* have <50% sucrose, while those of subgen. *Hexangulares* and subgen. *Robustipedunculares* (as well as those of the genera *Astroloba* and *Chortolirion*) have >60% sucrose. The significance of this difference is unknown, as our knowledge of pollinators of *Haworthia* is very incomplete. Bayer (2013b) reports an unidentified anthophorid solitary bee as frequent visitor, and Bayer (2013c) presents photographs of the bombylid solitary bee fly *Australoechus hirtus* on *Haworthia* flowers. In addition, a lycaenid butterfly is also sometimes visiting *Haworthia* flowers (Bayer, pers. obs.) Grenier (2013) also illustrates *Australoechus* and in addition *Amegilla* as flower visitors of *Haworthia* species and observed that pollinators do not discriminate between three concurrently flowering species. Marx (2013b) observed a tabanid horse-fly

(probably *Philoliche aethiopica*) as regular pollinator of *H. arachnoidea*.

**Horticulture:** Haworthias are popular amongst succulent plant collectors, and many can tolerate relatively shaded growing conditions. Propagation is usually from offsets, but also possible from detached whole leaves or in some taxa even from detached roots, as well as from seed or via tissue culture. In the list of names of unresolved application below, many are of horticultural derivation.

Over the course of the years, numerous forms have been selected, propagated, and named as cultivars, esp. in Japan (Hayashi 2013), where special oddities are highly prized. Some species occasionally produce variegated offspring, and some of these have also been formally named as cultivars. Hildyard (2016a) has a short synopsis on variegated forms in the genus.

**Acknowledgment:** We are indebted to Sean Gildenhuis for his help with placing some of the synonyms.

The following names are of unresolved application but are referred to this genus:

*Aloe anomala* Haworth (1804) ≡ *Apicra anomala* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4); *Aloe aspera* Haworth (1804) ≡ *Apicra aspera* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Astroloba aspera* (Haworth) Uitewaal (1947); *Aloe cylindrica* Lamarck ex Poiret (1810); *Aloe cylindrica* var. *rigida* Lamarck (1783) ≡ *Aloe rigida* (Lamarck) De Candolle (1799) ≡ *Apicra rigida* (Lamarck) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia rigida* (Lamarck) Haworth (1821) ≡ *Haworthiopsis* × *rigida* (Lamarck) Gildenhuis & Klopper (2016); *Aloe* × *expansa* Haworth pro sp. (1804) ≡ *Haworthia expansa* (Haworth) Haworth (1812) ≡ *Aloe rigida* var. *expansa* (Haworth) Salm-Dyck (1836) ≡ *Haworthia rigida* var. *expansa* (Haworth) Baker (1880) ≡ *Haworthiopsis* × *expansa* (Haworth) Gildenhuis & Klopper (2016); *Aloe expansa* var. *major* Haworth (1804); *Aloe glabrata* var. *concolor* Salm-Dyck (1849) ≡ *Haworthia*

*glabrata* var. *concolor* (Salm-Dyck) Baker (1880); *Aloe glabrata* var. *perviridis* Salm-Dyck (1849)  $\equiv$  *Haworthia glabrata* var. *perviridis* (Salm-Dyck) Baker (1880); *Aloe*  $\times$  *hybrida* Salm-Dyck *pro sp.* (1817)  $\equiv$  *Haworthia*  $\times$  *hybrida* (Salm-Dyck) Haworth (1821)  $\equiv$  *Haworthiopsis*  $\times$  *hybrida* (Salm-Dyck) Gildenhuis & Klopper (2016); *Aloe*  $\times$  *pseudorigida* Salm-Dyck *pro sp.* (1817)  $\equiv$  *Apicra pseudorigida* (Salm-Dyck) Haworth (1819)  $\equiv$  *Haworthia pseudorigida* (Salm-Dyck) Haworth (1819)  $\equiv$  *Haworthia tortuosa* var. *pseudorigida* (Salm-Dyck) A. Berger (1908)  $\equiv$  *Haworthiopsis*  $\times$  *pseudorigida* (Salm-Dyck) Gildenhuis & Klopper (2017); *Aloe pumila* Thunberg (1785) (*nom. illeg.*, Art. 53.1); *Aloe radula* var. *major* Salm-Dyck (1817); *Aloe radula* var. *media* Salm-Dyck (1817); *Aloe radula* var. *minor* Salm-Dyck (1817); *Aloe rigida* var. *paulo-major* Salm-Dyck (1817); *Aloe rugosa* Salm-Dyck (1834)  $\equiv$  *Haworthia rugosa* (Salm-Dyck) Baker (1880); *Aloe rugosa* var. *laetevirens* Salm-Dyck (1834); *Aloe rugosa* var. *perviridis* Salm-Dyck (1834)  $\equiv$  *Haworthia rugosa* var. *perviridis* (Salm-Dyck) A. Berger (1908); *Aloe semimargaritifera* var. *glabrata* Salm-Dyck (1834); *Aloe semimargaritifera* var. *major* Salm-Dyck (1817)  $\equiv$  *Haworthia semimargaritifera* var. *major* (Salm-Dyck) Haworth (1819)  $\equiv$  *Haworthia margaritifera* subvar. *major* (Haworth) A. Berger (1908); *Aloe semimargaritifera* var. *minor* Salm-Dyck (1817)  $\equiv$  *Haworthia semimargaritifera* var. *minor* (Salm-Dyck) Haworth (1819); *Aloe semimargaritifera* var. *mutipapillosa* Salm-Dyck (1834)  $\equiv$  *Haworthia margaritifera* subvar. *mutipapillosa* (Salm-Dyck) A. Berger (1908); *Aloe subalbicans* Salm-Dyck (1854)  $\equiv$  *Haworthia margaritifera* var. *subalbicans* (Salm-Dyck) A. Berger (1908); *Aloe subalbicans* var. *acuminata* Salm-Dyck (1854)  $\equiv$  *Haworthia margaritifera* subvar. *acuminata* (Salm-Dyck) A. Berger (1908); *Aloe subalbicans* var. *laevior* Salm-Dyck (1854)  $\equiv$  *Haworthia margaritifera* subvar. *laevior* (Salm-Dyck) A. Berger (1908); *Aloe subattenuata* Salm-Dyck (1834)  $\equiv$  *Haworthia subattenuata* (Salm-Dyck) Baker (1880); *Aloe subfasciata* Salm-Dyck (1825) (*nom. illeg.*, Art. 52.1)  $\equiv$  *Haworthia subfasciata* (Salm-Dyck) Baker (1880) (*nom. illeg.*, Art. 52.1); *Aloe*  $\times$  *subrigida*

Roemer & Schultes *fil. pro sp.* (1829)  $\equiv$  *Haworthiopsis*  $\times$  *subrigida* (Roemer & Schultes *fil.*) Gildenhuis & Klopper (2016); *Aloe subulata* Salm-Dyck (1822); *Aloe subulata* Salm-Dyck (1829) (*nom. illeg.*, Art. 52.1?)  $\equiv$  *Haworthia subulata* (Salm-Dyck) Baker (1880); *Aloe tortuosa* var. *major* Salm-Dyck (1837)  $\equiv$  *Haworthia tortuosa* var. *major* (Salm-Dyck) Baker (1896)  $\equiv$  *Haworthiopsis*  $\times$  *major* (Salm-Dyck) Gildenhuis & Klopper (2016); *Apicra aspera* var. *major* Haworth (1819) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Astroloba aspera* var. *major* (Haworth) Uitewaal (1947)  $\equiv$  *Haworthia aspera* var. *major* (Haworth) Parr (1971); *Apicra patula* Willdenow (1811) (*incorrect name*, ICN Art. 11.4); *Haworthia affinis* Baker (1880)  $\equiv$  *Haworthia bilineata* var. *affinis* (Baker) Von Poellnitz (1938); *Haworthia altilinea* Haworth (1824)  $\equiv$  *Aloe altilinea* (Haworth) Roemer & Schultes *fil.* (1829)  $\equiv$  *Haworthia mucronata* var. *altilinea* (Haworth) Halda (1997); *Haworthia altilinea* fa. *acuminata* Von Poellnitz (1938)  $\equiv$  *Haworthia mucronata* fa. *acuminata* (Von Poellnitz) Von Poellnitz (1940); *Haworthia altilinea* fa. *minor* Triebner (1938)  $\equiv$  *Haworthia mucronata* fa. *minor* (Triebner) Von Poellnitz (1940); *Haworthia altilinea* fa. *subglauca* Von Poellnitz (1938)  $\equiv$  *Haworthia mucronata* fa. *subglauca* (Von Poellnitz) Von Poellnitz (1940); *Haworthia altilinea* var. *bicarinata* Triebner (1938)  $\equiv$  *Haworthia mucronata* var. *bicarinata* (Triebner) Von Poellnitz (1940); *Haworthia altilinea* var. *brevisetata* Von Poellnitz (1937); *Haworthia altilinea* var. *setulifera* Triebner & Von Poellnitz (1938)  $\equiv$  *Haworthia mucronata* var. *setulifera* (Triebner & Von Poellnitz) Von Poellnitz (1940); *Haworthia altilinea* var. *typica* Von Poellnitz (1937) (*nom. inval.*, ICN Art. 24.3); *Haworthia argyrostigma* Baker (1896) (*nom. inval.*, Art. 32.1)  $\equiv$  *Haworthia attenuata* var. *argyrostigma* (Baker) A. Berger (1908) (*nom. inval.*, Art. 32.1); *Haworthia aspera* Haworth (1812); *Haworthia asperula* Haworth (1824)  $\equiv$  *Aloe asperula* (Haworth) Roemer & Schultes *fil.* (1829)  $\equiv$  *Haworthia retusa* ssp. *asperula* (Haworth) Halda (1997)  $\equiv$  *Haworthia retusa* var. *asperula* (Haworth) Halda (1997)  $\equiv$  *Haworthia magnifica* var. *asperula* (Haworth) Breuer (2016) (*incorrect name*, ICN Art. 11.4); *Haworthia baccata* G. G. Smith (1944); *Haworthia*



*bijliana* Von Poellnitz (1929)  $\equiv$  *Haworthia setata* var. *bijliana* (Von Poellnitz) Von Poellnitz (1938); *Haworthia bilineata* Baker (1880); *Haworthia*  $\times$  *cassytha* Baker pro sp. (1896)  $\equiv$  *Haworthiopsis*  $\times$  *cassytha* (Baker) Gildenhuis & Klopper (2016); *Haworthia coarctata* var. *sampaiana* Resende (1938)  $\equiv$  *Haworthia*  $\times$  *sampaiana* (Resende) Resende pro sp. (1940)  $\equiv$  *Haworthiopsis*  $\times$  *sampaiana* (Resende) Gildenhuis & Klopper (2016); *Haworthia*  $\times$  *coarctatoides* Resende & Viveiros (1948); *Haworthia columnaris* Baker (1889)  $\equiv$  *Haworthia pilifera* var. *columnaris* (Baker) Von Poellnitz (1938)  $\equiv$  *Haworthia obtusa* var. *columnaris* (Baker) Uitewaal (1948); *Haworthia confusa* Von Poellnitz (1933)  $\equiv$  *Haworthia minima* var. *confusa* (Von Poellnitz) Von Poellnitz (1938) (incorrect name, ICN Art. 11.4)  $\equiv$  *Haworthia tenera* var. *confusa* (Von Poellnitz) Uitewaal (1948); *Haworthia*  $\times$  *curta* Haworth pro sp. (1819)  $\equiv$  *Aloe curta* (Haworth) Sprengel (1825)  $\equiv$  *Haworthia tortuosa* var. *curta* (Haworth) Baker (1896)  $\equiv$  *Haworthiopsis*  $\times$  *curta* (Haworth) Gildenhuis & Klopper (2016); *Haworthia cuspidata* Haworth (1819)  $\equiv$  *Aloe cuspidata* (Haworth) Roemer & Schultes fil. (1829); *Haworthia fergusoniae* Von Poellnitz (1930); *Haworthia ferox* Von Poellnitz (1933); *Haworthia ferox* var. *armata* Von Poellnitz (1937); *Haworthia fukuyae* M. Hayashi (2007); *Haworthia gracilidelineata* Von Poellnitz (1933)  $\equiv$  *Haworthia bilineata* var. *gracilidelineata* (Von Poellnitz) Von Poellnitz (1938)  $\equiv$  *Haworthia cymbiformis* fa. *gracilidelineata* (Von Poellnitz) Pilbeam (1983); *Haworthia helmiae* Von Poellnitz (1937)  $\equiv$  *Haworthia unicolor* var. *helmiae* (Von Poellnitz) M. B. Bayer (1976)  $\equiv$  *Haworthia aristata* var. *helmiae* (Von Poellnitz) Pilbeam (1983) (nom. inval., ICN Art. 41.4)  $\equiv$  *Haworthia aristata* ssp. *helmiae* (Von Poellnitz) Halda (1997); *Haworthia henriquesii* Resende (1941); *Haworthia icosiphylla* Baker (1880); *Haworthia janseana* Uitewaal (1940); *Haworthia krausiana* Hort. Haage & Schmidt (s.a.) (nom. inval., ICN Art. 29.1, 38.1a); *Haworthia*  $\times$  *krausii* hort. ex J. R. Brown (1957); *Haworthia*  $\times$  *lisbonensis* Resende pro sp. (1946)  $\equiv$  *Haworthiopsis*  $\times$  *lisbonensis* (Resende) Gildenhuis & Klopper (2016); *Haworthia longifolia* Farden (1939); *Haworthia multifaria* Haworth (1824)  $\equiv$  *Aloe multifaria* (Haworth) Roemer & Schultes fil. (1829); *Haworthia obscura* Breuer (2010) (nom. inval., ICN Art. 36.1b, 38.1a); *Haworthia ollasonii* G. R. Hayes (1971) (nom. inval., ICN Art. 39.1, 40.1); *Haworthia pearsonii* C. H. Wright (1907)  $\equiv$  *Haworthia arachnoidea* ssp. *pearsonii* (C. H. Wright) Halda (1997)  $\equiv$  *Haworthia arachnoidea* var. *pearsonii* (C. H. Wright) Halda (1997); *Haworthia pellucens* var. *delicatula* A. Berger (1908)  $\equiv$  *Haworthia translucens* var. *delicatula* (A. Berger) Von Poellnitz (1938); *Haworthia perplexa* Von Poellnitz (1938); *Haworthia platinosa* M. Hayashi (2010) (nom. inval., ICN Art. 39.1, 40.1); *Haworthia polyphylla* Baker (1880)  $\equiv$  *Haworthia altilinea* var. *polyphylla* (Baker) Von Poellnitz (1938)  $\equiv$  *Haworthia mucronata* var. *polyphylla* (Baker) Von Poellnitz (1940); *Haworthia pseudogranulata* Von Poellnitz (1937); *Haworthia radula* var. *asperior* Haworth (1821); *Haworthia radula* var. *laevior* Haworth (1821); *Haworthia radula* var. *magniperlata* Haworth (1821); *Haworthia reinwardtii* var. *minor* hort. ex Baker (1880); *Haworthia*  $\times$  *resendeana* Von Poellnitz pro sp. (1938)  $\equiv$  *Haworthiopsis*  $\times$  *resendeana* (Von Poellnitz) Gildenhuis & Klopper (2016); *Haworthia*  $\times$  *revendettii* Uitewaal (1940)  $\equiv$  *Haworthiopsis*  $\times$  *revendettii* (Uitewaal) Gildenhuis & Klopper (2016); *Haworthia*  $\times$  *rubrobrunnea* Von Poellnitz pro sp. (1940)  $\equiv$  *Haworthiopsis*  $\times$  *rubrobrunnea* (Von Poellnitz) Gildenhuis & Klopper (2016); *Haworthia ryderiana* Von Poellnitz (1937); *Haworthia semiglabrata* Haworth (1819)  $\equiv$  *Aloe semiglabrata* (Haworth) Roemer & Schultes fil. (1829); *Haworthia semimargaritifera* var. *multi-perlata* Haworth (1819)  $\equiv$  *Aloe semimargaritifera* var. *multi-perlata* (Haworth) Roemer & Schultes fil. (1829)  $\equiv$  *Haworthia margaritifera* subvar. *multi-perlata* (Haworth) Von Poellnitz (1938); *Haworthia sessiliflora* Baker (1896); *Haworthia setata* var. *subinermis* Von Poellnitz (1936); *Haworthia similis* M. Hayashi (2010) (nom. inval., ICN Art. 39.1, 40.1); *Haworthia stiemiei* Von Poellnitz (1938); *Haworthia tislei* Baker (1880); *Haworthia*  $\times$  *tortella* Haworth pro sp. (1819)  $\equiv$  *Haworthia tortuosa* var. *tortella* (Haworth) Baker (1896)  $\equiv$  *Haworthiopsis*  $\times$  *tortella* (Haworth) Gildenhuis & Klopper (2016); *Haworthia triebneriana* var.



*lanceolata* Triebner & Von Poellnitz (1938); *Haworthia triebneriana* var. *nitida* Von Poellnitz (1940); *Haworthia uitewaaliana* Von Poellnitz (1939); *Haworthia vitris* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7); *Haworthia walmsleyi* Hort. Haage & Schmidt (s.a.) (*nom. inval.*, ICN Art. 29.1, 38.1a); *Haworthia yarrowa* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1).

**H. angustifolia** Haworth (Philos. Mag. J. 66: 283, 1825). **Type** [neo]: RSA, Eastern Cape (Bruyns 1653 [NBG 120 017]). — **Distr:** RSA (Eastern Cape).

≡ *Haworthia chloracantha* ssp. *angustifolia* (Haworth) Halda (1997) ≡ *Haworthia chloracantha* var. *angustifolia* (Haworth) Halda (1997).

**H. angustifolia** var. **altissima** M. B. Bayer (Haworthia Revisited, 26, ill. (p. 27), 1999). **Type:** RSA, Eastern Cape (Smith 5220 [NBG]). — **Distr:** RSA (Eastern Cape: Grahamstown Distr.); in Bisho Thornveld and savanna vegetations.

≡ *Haworthia altissima* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *angustifolia*: **Ros** proliferous; **L** slender, erect, to 15 × 1 cm, finely denticulate along margins and keel, colour tending to greyish-green rather than darkish green.

**H. angustifolia** var. **angustifolia** — **Distr:** RSA (Eastern Cape); in savanna. **I:** Bayer (1982: fig. 1a); Scott (1985: 55).

**Incl.** *Aloe stenophylla* Roemer & Schultes *fil.* (1829); **incl.** *Haworthia albanensis* Schönland (1912) ≡ *Haworthia angustifolia* var. *albanensis* (Schönland) Von Poellnitz (1937); **incl.** *Haworthia angustifolia* var. *grandis* G. G. Smith (1943) ≡ *Haworthia angustifolia* fa. *grandis* (G. G. Smith) Pilbeam (1983); **incl.** *Haworthia grandis* M. Hayashi (2000) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia anna* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia cocksia* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia viridula* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] **Ros** to 4 cm Ø, proliferous, stemless; **L** 10–40, slender, erect, to 10 × 1 cm, lanceolate-acuminate, somewhat flaccid, brownish to

dark green, margins and keel finely denticulate; **Inf** to 20 cm, lax; **Fl** 8–10, white to dull pinkish-white.

**H. angustifolia** var. **baylissii** (C. L. Scott) M. B. Bayer (Haworthia Revisited, 27, ill., 1999). **Type:** RSA (Scott 796 [PRE, NBG]). — **Distr:** RSA (Eastern Cape: Oudekraal); in Albany Thicket vegetation. **I:** Bayer (1982: Fig. 1b, as fa.); Scott (1985: 102, as *H. baylissii*).

≡ *Haworthia baylissii* C. L. Scott (1968) ≡ *Haworthia angustifolia* fa. *baylissii* (C. L. Scott) M. B. Bayer (1982) ≡ *Haworthia chloracantha* ssp. *baylissii* (C. L. Scott) Halda (1997).

[1] Differs from var. *angustifolia*: **L** deltoid, recurving.

**H. angustifolia** var. **paucifolia** G. G. Smith (J. South Afr. Bot. 14: 48, ill. (p. 58), 1948). **Type:** RSA, Eastern Cape (Smith 6819 [NBG]). — **Distr:** RSA (Eastern Cape: Frazer's Camp to Kaffir drift); in savanna.

≡ *Haworthia angustifolia* fa. *paucifolia* (G. G. Smith) Pilbeam (1983) ≡ *Haworthia paucifolia* (G. G. Smith) M. Hayashi (2010).

[1] Differs from var. *angustifolia*: **L** only 3–4, to 3 cm.

**H. arachnoidea** (Linné) Duval (Pl. Succ. Horto Alencon., 7, 1809). **Type:** [lecto — icono]: Commelin, Praeludia Bot., t. 27, 1703. — **Lit:** Bayer (2003b); Bayer (2004b); Bayer (2010g). **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape); mainly in Succulent Karoo vegetation.

≡ *Aloe pumila* var. *arachnoidea* Linné (1753) ≡ *Aloe arachnoidea* (Linné) Burman *fil.* (1768) ≡ *Catevala arachnoidea* (Linné) Medikus (1786) ≡ *Apicra arachnoidea* (Linné) Willdenow (1811) (*incorrect name*, ICN Art. 11.4); **incl.** *Aloe arachnoidea* Thunberg (1785); **incl.** *Aloe arachnoidea* var. *communis* Aiton (1789) (*nom. inval.*, ICN Art. 26.1).

**H. arachnoidea** var. **arachnoidea** — **Distr:** RSA (Western Cape: Little Karoo). **I:** Bayer (1982: Fig. 2). — Fig. 1.

**Incl.** *Haworthia arachnoidea* var. *minor* Haworth (1819); **incl.** *Haworthia joubertii* M. Hayashi



**Fig. 1** *Haworthia arachnoidea* var. *arachnoidea*. (Copyright: E. J. Van Jaarsveld)

(2005) (*nom. inval.*, ICN Art. 40.7)  $\equiv$  *Haworthia arachnoidea* var. *joubertii* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia laxa* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7)  $\equiv$  *Haworthia arachnoidea* var. *laxa* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia limbata* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7)  $\equiv$  *Haworthia arachnoidea* var. *limbata* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia gilva* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia isomorpha* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **R** slender, succulent; **Ros** stemless, variable in size from 6 to exceptionally 12 cm  $\varnothing$ , solitary or forming small clusters; **L** 25–80, dense, incurving, uniformly light to dark green, not translucent and only occasionally faintly reticulate, flattened and often drying grey-white to brownish at the tips forming a protective cover, triangular-lanceolate to ovate-lanceolate, 2–7  $\times$  1–1.5 cm, keeled, margin and keels with translucent bristly **Sp** to 12 mm, tip acuminate-aristate; **Inf** to 30 cm; **Fl** 20–30, white.

**H. arachnoidea** var. **aranaea** (A. Berger) M. B. Bayer (Haworthia Revisited, 30, ill. (p. 31), 1999). **Type**: [lecto — icono]: A. Berger in Engler, A. & Prantl, K. (eds.), Pflanzenr. 4(38 = Heft 33): 114, Fig. 39A–E, 1908. — **Distr**: RSA (Western Cape: Little Karoo); dry Mountain Fynbos vegetation. **I**: Bayer (1982: Fig. 3, as *H. aranea*).

$\equiv$  *Haworthia bolusii* var. *aranaea* A. Berger (1908)  $\equiv$  *Haworthia aranea* (A. Berger) M. B.

Bayer (1976); **incl.** *Haworthia araneoides* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] Differs from var. *arachnoidea*: **Ros** smaller, to 6 cm  $\varnothing$ ; **L** softer in texture.

**H. arachnoidea** var. **namaquensis** M. B. Bayer (Haworthia Revisited, 31, ills., 1999). **Type**: RSA, Northern Cape (Bayer 1674 [NBG]). — **Distr**: RSA (Northern Cape, Western Cape); Succulent Karoo vegetation.

$\equiv$  *Haworthia namaquensis* (M. B. Bayer) Breuer (2010).

[1] Differs from var. *arachnoidea*: **Ros** to 6 cm  $\varnothing$ ; **L** paler green.

**H. arachnoidea** var. **nigricans** (Haworth) M. B. Bayer (Haworthia Revisited, 32, ill., 1999). **Type** [neo]: RSA (Bayer 2419 [NBG]). — **Lit**: Bayer (2002b). **Distr**: RSA (Western Cape: Little Karoo); Succulent Karoo vegetation. **I**: Scott (1985: 100, as *H. helmiae*).

$\equiv$  *Haworthia setata* var. *nigricans* Haworth (1821)  $\equiv$  *Aloe setata* var. *nigricans* (Haworth) Roemer & Schultes fil. (1829); **incl.** *Haworthia venterii* Von Poellnitz (1939)  $\equiv$  *Haworthia unicolor* var. *venterii* (Von Poellnitz) M. B. Bayer (1976); **incl.** *Haworthia scottii* Breuer (2003); **incl.** *Haworthia nigrata* M. Hayashi (2006); **incl.** *Haworthia apta* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia formosa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia kuromisa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia regens* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *arachnoidea*: **L** with dark purplish coloration.

**H. arachnoidea** var. **scabrispina** M. B. Bayer (Haworthia Revisited, 34, ills., 1999). **Type**: RSA, Western Cape (Bayer 2105 [NBG]). — **Distr**: RSA (Western Cape); Nama Karoo vegetation.

$\equiv$  *Haworthia scabrispina* (M. B. Bayer) Breuer (2010); **incl.** *Haworthia matjiesta* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *arachnoidea*: **Ros** roundish, raised above ground-level; **L** with firm rigid brownish spines.

**H. arachnoidea** var. **setata** (Haworth) M. B. Bayer (Haworthia Revisited, 34, ills. (p. 35), 1999). **Type:** RSA, Western Cape (*Makrill* s.n. [[lecto — icono]: K [drawing]]). — **Distr:** RSA (Western Cape, W Eastern Cape: Little Karoo). **I:** Scott (1985: 69, as *H. setata*).

≡ *Haworthia setata* Haworth (1819) ≡ *Aloe setata* (Haworth) Roemer & Schultes fil. (1829) ≡ *Haworthia arachnoidea* ssp. *setata* (Haworth) Halda (1997); **incl.** *Haworthia setata* var. *major* Haworth (1821) ≡ *Aloe setata* var. *major* (Haworth) Roemer & Schultes fil. (1829); **incl.** *Haworthia setata* var. *media* Haworth (1821) ≡ *Aloe setata* var. *media* (Haworth) Roemer & Schultes fil. (1829); **incl.** *Aloe setosa* Roemer & Schultes fil. (1829); **incl.** *Haworthia gigas* Von Poellnitz (1933) ≡ *Haworthia setata* var. *gigas* (Von Poellnitz) Von Poellnitz (1938) ≡ *Haworthia arachnoidea* var. *gigas* (Von Poellnitz) M. Hayashi (2000); **incl.** *Haworthia minima* var. *major* Von Poellnitz (1938) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia tenera* var. *major* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia pectinis* M. Hayashi (2003) ≡ *Haworthia tetryrensis* var. *pectinis* (M. Hayashi) Breuer (2016); **incl.** *Haworthia tetryrensis* Breuer (2003); **incl.** *Haworthia angiras* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7) ≡ *Haworthia arachnoidea* var. *angiras* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia cangoensis* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia kogmanensis* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7) ≡ *Haworthia cangoensis* var. *kogmanensis* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 35.1, 40.7); **incl.** *Haworthia royalis* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7) ≡ *Haworthia cangoensis* var. *royalis* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 35.1, 40.7); **incl.** *Haworthia candida* M. Hayashi (2006) ≡ *Haworthia aranea* var. *candida* (M. Hayashi) Breuer (2016).

[1] Differs from var. *arachnoidea*: **Ros** variable; **L** white-spined.

**H. aristata** Haworth (Suppl. Pl. Succ., 51, 1819). **Type:** K [lecto — icono]. — **Distr:** RSA (Eastern Cape); Albany Thicket vegetation. — Fig. 2.



**Fig. 2** *Haworthia aristata*. (Bayer 7697b: N of Swartkop, Kaboega.) (Copyright: M. B. Bayer)

≡ *Aloe aristata* (Haworth) Roemer & Schultes fil. (1829) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Haworthia denticulata* Haworth (1821) ≡ *Aloe denticulata* (Haworth) Roemer & Schultes fil. (1829) ≡ *Aloe altilinea* var. *denticulata* (Haworth) Salm-Dyck (1842) ≡ *Haworthia altilinea* var. *denticulata* (Haworth) Von Poellnitz (1938); **incl.** *Haworthia lapis* Breuer & M. Hayashi (2004); **incl.** *Haworthia dura* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia rava* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7) ≡ *Haworthia lapis* var. *rava* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7).

[1] **Ros** stemless, proliferating slowly, to 6 cm Ø; **L** slender, erect, incurved, dark green, hardly translucent and faintly reticulated, margins and keel entire or minutely spined; **Inf** to 15 cm, lax; **Fl** 10–15, white.

Growing in close vicinity with *H. cooperi* at times, with occasional occurrence of intermediate plants (Bayer 2010b).

**H. attenuata** (Haworth) Haworth (Synops. Pl. Succ., 92, 1812). **Type** [neo]: RSA, Eastern Cape (*Perry* 660 [NBG 144 672]). — **Distr:** RSA (Eastern Cape).

≡ *Aloe attenuata* Haworth (1804) ≡ *Apicra attenuata* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia pumila* ssp.



*attenuata* (Haworth) Halda (1997) ≡ *Haworthiopsis attenuata* (Haworth) G. D. Rowley (2015).

**H. attenuata** var. **attenuata** — **Distr:** RSA (Eastern Cape); Albany Thicket vegetation. **I:** Bayer (1982: Fig. 46); Gildenhuis (2017: 15–16, as *Haworthiopsis*).

**Incl.** *Haworthia clariperla* Haworth (1826) ≡ *Aloe clariperla* (Haworth) Roemer & Schultes fil. (1829) ≡ *Aloe attenuata* var. *clariperla* (Haworth) Salm-Dyck (1836) ≡ *Haworthia attenuata* var. *clariperla* (Haworth) Baker (1880) ≡ *Haworthia attenuata* fa. *clariperla* (Haworth) M. B. Bayer (1976); **incl.** *Haworthia fasciata* var. *caespitosa* A. Berger (1908) ≡ *Haworthia attenuata* var. *caespitosa* (A. Berger) R. S. Farden (1939) ≡ *Haworthia attenuata* fa. *caespitosa* (A. Berger) Pilbeam (1983) (*nom. inval.*, ICN Art. 41.4); **incl.** *Haworthia britteniana* Von Poellnitz (1937) ≡ *Haworthia attenuata* var. *britteniana* (Von Poellnitz) Von Poellnitz (1937) ≡ *Haworthia attenuata* fa. *britteniana* (Von Poellnitz) M. B. Bayer (1982); **incl.** *Haworthia attenuata* var. *deltoidea* R. S. Farden (1939); **incl.** *Haworthia attenuata* var. *linearis* R. S. Farden (1939); **incl.** *Haworthia attenuata* var. *minissima* R. S. Farden (1939); **incl.** *Haworthia attenuata* var. *odonoghueana* R. S. Farden (1939); **incl.** *Haworthia attenuata* var. *inusitata* R. S. Farden (1939) (*nom. inval.*, ICN Art. 39.1); **incl.** *Haworthia attenuata* var. *uitewaaliana* R. S. Farden (1939) (*nom. inval.*, ICN Art. 39.1).

[2] **Ros** stemless, proliferous, to 13 cm tall and 10 cm Ø; **L** to 13 × 1.5 cm, attenuate, spreading, lanceolate-deltoid, surfaces scabrid with distinct raised non-confluent tubercles; **Inf** sparsely branched, 24–28 cm, lax; **Fl** tube obcapitate, **Tep** revolute.

**H. attenuata** var. **glabrata** (Salm-Dyck) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 37, 2012). **Type:** [neo — icono]: Salm-Dyck, Monogr. Gen. Aloes & Mesembr. 3: Aloe t. 7 [sect. 6: 13], 1840. — **Distr:** RSA (Eastern Cape: former Transkei); Eastern Valley Bushveld vegetation. **I:** Bayer (1982: Fig. 50, as *H. glabrata*); Gildenhuis (2017: 17, as *Haworthiopsis*).

≡ *Aloe glabrata* Salm-Dyck (1834) ≡ *Haworthia glabrata* (Salm-Dyck) Baker (1880) ≡

*Haworthiopsis attenuata* var. *glabrata* (Salm-Dyck) G. D. Rowley (2015).

[2] Differs from var. *attenuata*: **L** scabrid and more turgid.

**H. attenuata** var. **radula** (Jacquin) M. B. Bayer (Haworthia Revisited, 167, ill., 1999). **Type:** [lecto — icono]: Jacquin, Pl. Hort. Schoenbr. 4: t. 422, 1804. — **Distr:** RSA (Eastern Cape: Baviaanskloof); Gamtoos Thicket vegetation. **I:** Bayer (1982: Fig. 56, as *H. radula*); Gildenhuis (2017: 18, as *Haworthiopsis*).

≡ *Aloe radula* Jacquin (1804) ≡ *Apicra radula* (Jacquin) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia radula* (Jacquin) Haworth (1812) ≡ *Haworthia pumila* ssp. *radula* (Jacquin) Halda (1997) ≡ *Haworthiopsis attenuata* var. *radula* (Jacquin) G. D. Rowley (2015); **incl.** *Haworthia radula* var. *pluriperlata* Haworth (1821).

[2] Differs from var. *attenuata*: **L** with many minute crowded white tubercles.

**H. bayeri** J. D. Venter & S. A. Hammer (Cact. Succ. J. (US) 69(2): 75–76, ill., 1997). **Type:** RSA, Western Cape (*Stayner* s.n. in *Karoo Garden* 164/69 [NBG]). — **Distr:** RSA (Western Cape: Little Karoo); Succulent Karoo vegetation.

**Incl.** *Haworthia uniondalensis* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Haworthia hayashii* M. Hayashi (2002) ≡ *Haworthia bayeri* var. *hayashii* (M. Hayashi) Breuer (2016); **incl.** *Haworthia bayeri* var. *scabrifolia* Breuer (2002) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia indigoa* M. Hayashi (2005); **incl.** *Haworthia jadea* M. Hayashi (2005) ≡ *Haworthia bayeri* var. *jadea* (M. Hayashi) Breuer (2016); **incl.** *Haworthia laeta* M. Hayashi (2005); **incl.** *Haworthia truterorum* Breuer & Marx (2011) ≡ *Haworthia indigoa* var. *truterorum* (Breuer & Marx) Breuer (2016).

[1] **Ros** stemless, to 8 cm Ø; **L** 15–20, retuse, dark brownish-green to blackish-green, slightly scabrid, keels and margins with minute **Sp** or smooth, tip rounded and not pointed, the end-area opaque, cloudy-transparent, with sparse reticulate patterning or longitudinal lines; **Inf** to 30 cm; **Fl** 15–25.

Here belongs *H. willowmorensis* in the sense of Scott (1985). The recently described *H. truterorum*

is provisionally synonymized here and appears to fall between *H. bayeri* and *H. emelyae*.

**H. blackburniae** W. F. Barker (J. South Afr. Bot. 3: 93, 1937). **Type:** RSA, Western Cape (*Reynolds* 1842 [NBG, BOL, PRE]). — **Distr:** RSA (Western Cape); Succulent Karoo and Fynbos vegetations.

**Incl.** *Haworthia blackburniana* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1).

**H. blackburniae** var. **blackburniae** — **Distr:** RSA (Western Cape: mountains of the C Little Karoo). **I:** Bayer (1982: Fig. 6).

**R** fusiform; **Ros** stemless, basally 1–1.5 cm Ø, clumping; **L** 10–15, erect, long, slender, to 40 cm × 3–5 mm, bright green to brownish-green or dark greyish-green, upper face channelled, margins glabrous or finely spined; **Inf** to 30 cm; **Fl** 15–20, white with green veins.

**H. blackburniae** var. **derustensis** M. B. Bayer (*Haworthia Revisited*, 41, ill., 1999). **Type:** RSA, Western Cape (*Vlok* s.n. in *Venter* 93/24 [NBG]). — **Distr:** RSA (Western Cape: Oudtshoorn Distr.).

≡ *Haworthia derustensis* (M. B. Bayer) M. Hayashi (2000) ≡ *Haworthia graminifolia* var. *derustensis* (M. B. Bayer) Breuer (2016).

[1] Differs from var. *blackburniae*: **Ros** robust, to 1.8 cm Ø; **L** very long, to 45 cm, to 3 mm broad, brownish-green at the base, green above.

**H. blackburniae** var. **graminifolia** (G. G. Smith) M. B. Bayer (*Haworthia Revisited*, 42, ills., 1999). **Type:** RSA, Western Cape (*Smith* 5222 [NBG]). — **Distr:** RSA (Western Cape: Swartberg Mts.). **I:** Bayer (1982: Fig. 16, as *H. graminifolia*).

≡ *Haworthia graminifolia* G. G. Smith (1942) ≡ *Haworthia blackburniae* ssp. *graminifolia* (G. G. Smith) Halda (1997).

[1] Differs from var. *blackburniae*: **L** <3 mm broad, dark greyish-green.

**H. bolusii** Baker (J. Linn. Soc., Bot. 18(109): 215–216, 1880). **Type:** RSA, Eastern Cape (*Bolus* 158 [K, BOL]). — **Distr:** RSA (Eastern Cape, S Free State); Nama Karoo vegetation.

≡ *Haworthia arachnoidea* var. *bolusii* (Baker) Halda (1997).



**Fig. 3** *Haworthia bolusii* var. *blackbeardiana*. (Copyright: U. Eggli)

**H. bolusii** var. **blackbeardiana** (Von Poellnitz) M. B. Bayer (*New Haworthia Handb.*, 31, 1982). **Type:** Cult. (*Anonymus* s.n. [B]). — **Lit:** Zietsman & Smith (2010). **Distr:** RSA (interior of the Eastern Cape, S Free State). **I:** Bayer (1982: Fig. 7b). – Fig. 3.

≡ *Haworthia blackbeardiana* Von Poellnitz (1933); **incl.** *Haworthia inermis* Von Poellnitz (1933) ≡ *Haworthia altilinea* var. *inermis* (Von Poellnitz) Von Poellnitz (1937) ≡ *Haworthia altilinea* fa. *inermis* (Von Poellnitz) Von Poellnitz (1940) ≡ *Haworthia mucronata* fa. *inermis* (Von Poellnitz) Von Poellnitz (1940); **incl.** *Haworthia blackbeardiana* var. *major* Von Poellnitz (1937); **incl.** *Haworthia batteniae* C. L. Scott (1979) ≡ *Haworthia cooperi* ssp. *batteniae* (C. L. Scott) Halda (1997); **incl.** *Haworthia calaensis* Breuer (2004) ≡ *Haworthia blackbeardiana* var. *calaensis* (Breuer) Breuer (2016); **incl.** *Haworthia specksii* Breuer (2004) ≡ *Haworthia blackbeardiana* var. *specksii* (Breuer) Breuer (2016); **incl.** *Haworthia villosa* M. Hayashi (2005); **incl.** *Haworthia hogsia* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia malvina* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia speciosa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *bolusii*: **Ros** generally larger, to 15 cm Ø; **L** with sparse **Sp** >2 mm.

**H. bolusii** var. **bolusii** — **Distr:** RSA (interior of the Eastern Cape). **I:** Scott (1985: 72).

**Incl.** *Haworthia odetteae* Breuer (2003); **incl.** *Haworthia odyseii* M. Hayashi (2005) (*nom.*



*inval.*, ICN Art. 40.7)  $\equiv$  *Haworthia odetteae* var. *odyssei* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia capillaris* M. Hayashi (2006); **incl.** *Haworthia sapphaia* M. Hayashi (2007).

[1] **Ros** 4–8 cm  $\varnothing$ , slowly proliferating; **L** oblong-lanceolate, incurved, translucent bluish-green, margins and keel with **Sp** >2 mm; **Inf** robust, to 30 cm; **Fl** broad and flat across the base of the tube.

**H. bolusii** var. **pringlei** (C. L. Scott) M. B. Bayer (Haworthiad 16(2): 62, 2002). **Type:** RSA, Eastern Cape (*Pringle* s.n. in *Scott* 8970 [PRE]). — **Distr:** RSA (Eastern Cape). **I:** Scott (1994b: as *H. pringlei*).

$\equiv$  *Haworthia pringlei* C. L. Scott (1994)  $\equiv$  *Haworthia decipiens* var. *pringlei* (C. L. Scott) M. B. Bayer (1999); **incl.** *Haworthia aquamarina* M. Hayashi (2003); **incl.** *Haworthia hastata* M. Hayashi (2005)  $\equiv$  *Haworthia pringlei* var. *hastata* (M. Hayashi) Breuer (2016); **incl.** *Haworthia hisui* M. Hayashi (2005)  $\equiv$  *Haworthia cooperi* var. *hisui* (M. Hayashi) Breuer (2016); **incl.** *Haworthia lazulis* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7).

[1] Differs from var. *bolusii*: **L**  $\pm$  lanceolate, incurved and erect to suberect, bright green, margins and keel with white **Sp**.

**H. bruynsii** M. B. Bayer (J. South Afr. Bot. 47: 789, 1981). **Type:** RSA, Eastern Cape (*Rossouw* 456 [NBG]). — **Distr:** RSA (Eastern Cape: Great Karoo); Nama Karoo vegetation. **I:** Bayer (1982: Fig. 47); Gildenhuys (2017: 63, as *Haworthiopsis*).

$\equiv$  *Haworthia retusa* var. *bruynsii* (M. B. Bayer) Halda (1997)  $\equiv$  *Haworthiopsis bruynsii* (M. B. Bayer) G. D. Rowley (2013).

[2] **Ros** stemless, solitary, to 6 cm  $\varnothing$ ; **L** 5–11, 2–3 cm, brownish-green, with flat retuse end-area, opaque and slightly scabrid with small raised tubercles; **Inf** simple, slender; **Fl** distant, slender, tube obcapitate; **Tep** fused, tips revolute.

**H. chloracantha** Haworth (Revis. Pl. Succ., 57, 1821). **Type** [lecto]: RSA, Western Cape (*Bowie* s.n. [[lecto — icono]: K [drawing]]). — **Distr:** RSA (Western Cape); Fynbos vegetation.

$\equiv$  *Aloe chloracantha* (Haworth) Roemer & Schultes *fil.* (1829).

**H. chloracantha** var. **chloracantha** — **Distr:** RSA (Western Cape). **I:** Bayer (1982: Fig. 8a).

[1] **Ros** 2.5–4 cm  $\varnothing$ , proliferous; **L** 18–25, 0.5–1.5 cm long, erectly spreading, light green, faintly reticulate, firm to slightly scabrid, triangular in cross-section, margins and keel with translucent **Sp** to 0.3 mm; **Inf** lax, to 25 cm; **Fl** small.

**H. chloracantha** var. **denticulifera** (Von Poellnitz) M. B. Bayer (Haworthia Handb., 112, 1976). **Type:** B [lecto: unpubl. ill.]. — **Distr:** RSA (Western Cape: Mosselbay). **I:** Bayer (1982: Fig. 8b).

$\equiv$  *Haworthia angustifolia* var. *denticulifera* Von Poellnitz (1937)  $\equiv$  *Haworthia denticulifera* (Von Poellnitz) M. Hayashi (2000); **incl.** *Haworthia angustifolia* var. *liliputana* Uitewaal (1953).

[1] Differs from var. *chloracantha*: **L** 2.5–3.5 cm long, dark green.

**H. chloracantha** var. **subglauca** Von Poellnitz (Kakteenkunde 9: 135, 1937). **Type** [neo]: RSA, Western Cape (*Hurling & Neil* s.n. [BOL]). — **Distr:** RSA (Western Cape: Mosselbay). **I:** Bayer (1982: Fig. 8c).

$\equiv$  *Haworthia subglauca* (Von Poellnitz) M. Hayashi (2000).

[1] Differs from var. *chloracantha*: **L** bluish-green, **Sp** larger and sparser.

**H. coarctata** Haworth (Philos. Mag. J. 64: 301, 1824). **Type** [neo]: RSA, Eastern Cape (*Smith* 7092 [NBG 68473]). — **Distr:** RSA (Eastern Cape); Fynbos and thickets.

$\equiv$  *Aloe coarctata* (Haworth) Roemer & Schultes *fil.* (1829)  $\equiv$  *Haworthia reinwardtii* ssp. *coarctata* (Haworth) Halda (1997)  $\equiv$  *Haworthia reinwardtii* var. *coarctata* (Haworth) Halda (1997)  $\equiv$  *Haworthiopsis coarctata* (Haworth) G. D. Rowley (2013)  $\equiv$  *Haworthiopsis reinwardtii* var. *coarctata* (Haworth) Breuer (2016).

**H. coarctata** fa. **greenii** (Baker) M. B. Bayer (Haworthia Revisited, 172, ill., 1999). **Type:** RSA, Eastern Cape (*Cooper* s.n. [K]). — **Distr:** RSA

(Eastern Cape: Grahamstown). **I:** Bayer (1982: Fig. 48b, as var.).

≡ *Haworthia greenii* Baker (1880) ≡ *Haworthia coarctata* var. *greenii* (Baker) M. B. Bayer (1973) ≡ *Haworthia reinwardtii* var. *greenii* (Baker) Halda (1997) ≡ *Haworthiopsis reinwardtii* var. *greenii* (Baker) Breuer (2016); **incl.** *Haworthia peacockii* Baker (1880); **incl.** *Haworthia greenii* fa. *minor* Resende (1943); **incl.** *Haworthia greenii* fa. *bakeri* Resende (1943) (*nom. illeg.*, Art. 52.1, 26.1).

[2] Differs from var. *coarctata*: **L** without tubercles.

**H. coarctata** var. **adelaidensis** (Von Poellnitz)

M. B. Bayer (*Haworthia Revisited*, 172, ills., 1999). **Type:** RSA, Eastern Cape (*Armstrong* s.n. [B [lecto: unpubl. ill.]]). — **Distr:** RSA (Eastern Cape: Grahamstown). **I:** Bayer (1982: Fig. 48d, as ssp.); Gildenhuis (2017: 21, as *Haworthiopsis*).

≡ *Haworthia reinwardtii* var. *adelaidensis* Von Poellnitz (1940) ≡ *Haworthia coarctata* ssp. *adelaidensis* (Von Poellnitz) M. B. Bayer (1973) ≡ *Haworthia adelaidensis* (Von Poellnitz) Breuer (2010) ≡ *Haworthiopsis coarctata* var. *adelaidensis* (Von Poellnitz) G. D. Rowley (2013); **incl.** *Haworthia reinwardtii* var. *riebeekensis* G. G. Smith (1944); **incl.** *Haworthia reinwardtii* var. *bellula* G. G. Smith (1945) ≡ *Haworthia coarctata* fa. *bellula* (G. G. Smith) Pilbeam (1983).

[2] Differs from var. *coarctata*: **Ros** smaller, stems to 15 cm, 3 cm Ø; **L** 3.2 × 1 cm.

**H. coarctata** var. **coarctata** — **Distr:** RSA (Eastern Cape). **I:** Bayer (1982: Fig. 48a); Gildenhuis (2017: 19–20, as *Haworthiopsis*).

**Incl.** *Haworthia chalwinii* Marloth & A. Berger (1906) ≡ *Haworthia reinwardtii* var. *chalwinii* (Marloth & A. Berger) Resende (1943) ≡ *Haworthia coarctata* fa. *chalwinii* (Marloth & A. Berger) Pilbeam (1983); **incl.** *Haworthia fallax* Von Poellnitz (1933) ≡ *Haworthia reinwardtii* var. *fallax* (Von Poellnitz) Von Poellnitz (1937); **incl.** *Haworthia reinwardtii* var. *conspicua* Von Poellnitz (1937) ≡ *Haworthia coarctata* fa. *conspicua* (Von Poellnitz) Pilbeam (1983); **incl.** *Haworthia reinwardtii* var. *pseudocoarctata* Von Poellnitz (1940) ≡ *Haworthia coarctata* fa. *pseudocoarctata*

(Von Poellnitz) Resende (1943) ≡ *Haworthia greenii* fa. *pseudocoarctata* (Von Poellnitz) Resende & Pinto-Lopes (1946); **incl.** *Haworthia coarctata* fa. *major* Resende (1943); **incl.** *Haworthia coarctata* var. *kraussii* Resende (1943); **incl.** *Haworthia fulva* G. G. Smith (1943); **incl.** *Haworthia greenii* var. *silvicola* G. G. Smith (1943); **incl.** *Haworthia reinwardtii* var. *committeesensis* G. G. Smith (1943); **incl.** *Haworthia coarctata* var. *haworthii* Resende (1943) (*nom. illeg.*, ICN Art. 52.1, 26.1); **incl.** *Haworthia reinwardtii* var. *huntsdriftensis* G. G. Smith (1944); **incl.** *Haworthia musculina* G. G. Smith (1948).

[2] **Ros** to 12 cm Ø, caulescent, proliferating; **L** numerous, to 7 × 2 cm, ratio stem diameter : leaf width = 1:1.7, erect-spreading or incurved, scabrid, both faces brownish-green, usually with rounded tubercles; **Inf** simple or occasionally compound, to 60 cm; **Fl** tube obcapitate; **Te** revolute.

Not always easily separated from *H. reinwardtii* and its forms. The ratio between stem diameter and leaf width is a good help.

**H. coarctata** var. **tenuis** (G. G. Smith) M. B. Bayer (*Nation. Cact. Succ. J.* 28: 80, 1973). **Type:** RSA, Eastern Cape (*Smith* 3420 [NBG]). — **Distr:** RSA (Eastern Cape: Alexandria). **I:** Bayer (1982: Fig. 48c); Gildenhuis (2017: 22, as *Haworthiopsis*).

≡ *Haworthia reinwardtii* var. *tenuis* G. G. Smith (1948) ≡ *Haworthia tenuis* (G. G. Smith) Breuer (2010) ≡ *Haworthiopsis coarctata* var. *tenuis* (G. G. Smith) G. D. Rowley (2013) ≡ *Haworthiopsis reinwardtii* var. *tenuis* (G. G. Smith) Breuer (2016).

[2] Differs from var. *coarctata*: **Ros** with elongated narrow stems to 40 cm, 2.5 cm Ø; **L** 3.5 × 0.8 cm.

**H. cooperi** Baker (*Refug. Bot.* 4: t. 233 + text, 1871). **Type:** RSA, Eastern Cape (*Cooper* s.n. [K]). — **Distr:** RSA (Eastern Cape).

**H. cooperi** var. **cooperi** — **Distr:** RSA (Eastern Cape); mainly Fynbos, grassland and Albany Thicket vegetations. **I:** Bayer (1982: Fig. 10a); Bayer (2010c).

**Incl.** *Haworthia vittata* Baker (1871); **incl.** *Haworthia subularis* M. Hayashi (2003); **incl.** *Haworthia pallens* Breuer & M. Hayashi (2004) ≡ *Haworthia caerulea* var. *pallens* (Breuer & M. Hayashi) Breuer (2016); **incl.** *Haworthia calva* M. Hayashi (2005) ≡ *Haworthia venetia* var. *calva* (M. Hayashi) Breuer (2016); **incl.** *Haworthia cooperi* var. *cymbiformoides* M. B. Bayer (2008) (*nom. inval.*, ICN Art. 36.1b); **incl.** *Haworthia elegans* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia foeda* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia turcosa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia yocans* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** to 12 cm Ø, often proliferous, stemless; **L** 20–40, fleshy, swollen, erect, oblong-lanceolate, quickly tapering, acuminate or truncate, bluish-green, slightly translucent, with veins usually reddening and leaves becoming purplish in exposed situations, marginal **Sp** <2 mm when present; **Inf** compact, firm, to 20 cm; **Fl** 20–30, closely arranged, white.

**H. cooperi** var. **dielsiana** (Von Poellnitz) M. B. Bayer (*Haworthia Revisited*, 51, ill., 1999). **Type** [neo]: RSA, Eastern Cape (*van der Merwe* s.n. in *Smith* 1140 [NBG]). — **Distr**: RSA (Eastern Cape: Cookhouse); Great Fish Thicket vegetation. **I**: Scott (1995: as *H. joeyae*).

≡ *Haworthia dielsiana* Von Poellnitz (1930) ≡ *Haworthia cooperi* f. *dielsiana* (Von Poellnitz) hort. (s.a.) (*nom. inval.*, ICN Art. 29.1) ≡ *Haworthia pilifera* var. *dielsiana* (Von Poellnitz) Von Poellnitz (1940) ≡ *Haworthia obtusa* var. *dielsiana* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia joeyae* C. L. Scott (1995).

[1] Differs from var. *cooperi*: **L** obtuse, truncate, not acuminate, conspicuously veined.

**H. cooperi** var. **doldii** M. B. Bayer (*Haworthiad* 16(2): 65–66, ills. (p. 71), 2002). **Type**: RSA, Eastern Cape (*Dold* 3961 [GRA]). — **Distr**: RSA (Eastern Cape: Tyolomnqa, Chalumna); Buffels Thicket vegetation.

≡ *Haworthia doldii* (M. B. Bayer) M. Hayashi (2005) ≡ *Haworthia tenera* var. *doldii* (M. B. Bayer) Breuer (2016); **incl.** *Haworthia leightonii*

var. *doldii* Breuer (2002) (*nom. inval.*, ICN Art. 39.1, 40.1).

Differs from var. *cooperi*: **Ros** small, to 4 cm Ø; **L** slender, erect, acuminate, margins and keel spinose.

**H. cooperi** var. **gordoniana** (Von Poellnitz) M. B. Bayer (*Haworthia Revisited*, 52, ills., 1999). **Type** [neo]: RSA, Eastern Cape (*Smith* 3028 [NBG]). — **Distr**: RSA (Eastern Cape: Baviaanskloof); Groot Thicket vegetation.

≡ *Haworthia gordoniana* Von Poellnitz (1937) ≡ *Haworthia pilifera* var. *gordoniana* (Von Poellnitz) Von Poellnitz (1938) ≡ *Haworthia obtusa* var. *gordoniana* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia harryi* M. Hayashi (2005); **incl.** *Haworthia jeffreis* M. Hayashi (2005) ≡ *Haworthia venetia* var. *jeffreis* (M. Hayashi) Breuer (2016); **incl.** *Haworthia ligulata* M. Hayashi (2005) ≡ *Haworthia isabellae* var. *ligulata* (M. Hayashi) Breuer (2016); **incl.** *Haworthia pusilla* M. Hayashi (2005) ≡ *Haworthia picturata* var. *pusilla* (M. Hayashi) Breuer (2016); **incl.** *Haworthia venetia* M. Hayashi (2005); **incl.** *Haworthia brandea* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia cineraria* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia compressa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia gelatina* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia ionandra* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia neritica* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia silvicola* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia tomentosa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *cooperi*: **Ros** small, to 6 cm Ø; **L** erect, acuminate, not truncate.

**H. cooperi** var. **gracilis** (Von Poellnitz) M. B. Bayer (*Haworthiad* 16(2): 64, 2002). **Type**: B [lecto: unpubl. photograph of the type collection]. — **Distr**: RSA (Eastern Cape); Albany Thicket vegetation.

≡ *Haworthia gracilis* Von Poellnitz (1930) ≡ *Haworthia arachnoidea* var. *gracilis* (Von Poellnitz) Halda (1997); **incl.** *Haworthia bella* M. Hayashi (2005) ≡ *Haworthia isabellae* var.

*bella* (M. Hayashi) Breuer (2016); **incl.** *Haworthia caerulea* M. Hayashi & Breuer (2005); **incl.** *Haworthia teres* M. Hayashi (2005) ≡ *Haworthia venetia* var. *teres* (M. Hayashi) Breuer (2016).

[1] Differs from var. *cooperi*: **Ros** proliferous; **L** 30–40, lanceolate-acuminate, incurved, pale greyish-green, upper face translucent between the veins, margins with sparse slender short spines.

Here belongs *H. translucens* in the sense of Bayer (1976).

**H. cooperi** var. **isabellae** (Von Poellnitz) M. B. Bayer (Haworthiad 16(2): 65, 2002). **Type** [neo]: RSA, Eastern Cape (*Hall* s.n. in *NBG* 68799 [NBG]). — **Distr**: RSA (Eastern Cape: Baviaanskloof); Groot and Gamtoos Thicket vegetations. **I**: Bayer (1982: Fig. 38a, as *H. translucens*).

≡ *Haworthia isabellae* Von Poellnitz (1938) ≡ *Haworthia gracilis* var. *isabellae* (Von Poellnitz) M. B. Bayer (1999); **incl.** *Haworthia azurea* M. Hayashi (2003); **incl.** *Haworthia arabesqua* M. Hayashi (2005) ≡ *Haworthia isabellae* var. *arabesqua* (M. Hayashi) Breuer (2016); **incl.** *Haworthia florens* M. Hayashi (2005) ≡ *Haworthia transiens* var. *florens* (M. Hayashi) Breuer (2016); **incl.** *Haworthia pilosa* M. Hayashi (2005); **incl.** *Haworthia ciliata* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7) ≡ *Haworthia pilosa* var. *ciliata* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia bathylis* M. Hayashi (2006); **incl.** *Haworthia lachnosa* M. Hayashi (2006) ≡ *Haworthia pilosa* var. *lachnosa* (M. Hayashi) Breuer (2016); **incl.** *Haworthia cuprina* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia dasyllis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia kromia* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia patriae* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] Differs from var. *cooperi*: **Ros** more proliferous; **L** spreading, greyish-green, margins and keel finely and more densely spined.

The **neotype** listed above is **formally designated here** for *Haworthia isabellae*, but was previously already listed as such, though

ineffectively under the ICN, in the first edition of this handbook.

**H. cooperi** var. **leightonii** (G. G. Smith) M. B. Bayer (Haworthia Handb., 128, 1976). **Type**: RSA, Eastern Cape (*Smith* 6938 [NBG]). — **Distr**: RSA (Eastern Cape: between Chalumna and East London); Albany Coastal Belt vegetation. **I**: Bayer (1982: Fig. 10b).

≡ *Haworthia leightonii* G. G. Smith (1950); **incl.** *Haworthia leightonii* var. *davidii* Breuer (2003) ≡ *Haworthia davidii* (Breuer) M. Hayashi & Breuer ex M. Hayashi (2005); **incl.** *Haworthia sabita* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *cooperi*: **Ros** very proliferous; **L** lanceolate-acuminate.

**H. cooperi** var. **picturata** (M. B. Bayer) M. B. Bayer (Haworthiad 16(2): 65, 2002). **Type**: RSA, Eastern Cape (*Thode* 21507 [NBG]). — **Distr**: RSA (Eastern Cape: Baviaanskloof); Groot Thicket vegetation.

≡ *Haworthia gracilis* var. *picturata* M. B. Bayer (1999) ≡ *Haworthia picturata* (M. B. Bayer) M. Hayashi (2000); **incl.** *Haworthia oculata* M. Hayashi (2005); **incl.** *Haworthia florida* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia imperialis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia kubusie* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *cooperi*: **L** glabrous, bright green, translucent areas contrasting with the dark green opaque reticulation.

**H. cooperi** var. **pilifera** (Baker) M. B. Bayer (Haworthia Revisited, 54, ills., 1999). **Type**: [lecto — icono]: Refug. Bot. 4: t. 234, 1871. — **Distr**: RSA (Eastern Cape); Albany Thicket vegetation. **I**: Scott (1985: 105, as *H. pilifera*).

≡ *Haworthia pilifera* Baker (1871) ≡ *Haworthia obtusa* var. *pilifera* (Baker) Uitewaal (1948) ≡ *Haworthia cooperi* fa. *pilifera* (Baker) Pilbeam (1983); **incl.** *Haworthia stayneri* Von Poellnitz (1937) ≡ *Haworthia pilifera* var. *stayneri* (Von Poellnitz) Von Poellnitz (1938) ≡ *Haworthia obtusa* var. *stayneri* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia stayneri* var. *salina* Von Poellnitz (1937) ≡ *Haworthia pilifera* var. *salina*



(Von Poellnitz) Von Poellnitz (1938) ≡ *Haworthia obtusa* var. *salina* (Von Poellnitz) Uitewaal (1948) ≡ *Haworthia salina* (Von Poellnitz) M. Hayashi (2010); **incl.** *Haworthia pilifera* fa. *acuminata* Von Poellnitz (1940) ≡ *Haworthia obtusa* fa. *acuminata* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia luri* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia sabrina* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *cooperi*: **L** obtusely acuminate, margins and keel acute, with small bristly hairs, tips becoming truncate, contracting and flattening as exposure to light increases.

**H. cooperi** var. **tenera** (Von Poellnitz) M. B. Bayer (Haworthiad 16(2): 65, 2002). **Type** [neo]: RSA, Eastern Cape (*Smith* 5416 [NBG 115210]). — **Distr**: RSA (Eastern Cape: Fish River Valley); Great Fish Noorsveld vegetation. **I**: Bayer (1982: Fig. 38b, as *H. translucens* ssp. *tenera*).

≡ *Haworthia tenera* Von Poellnitz (1933) ≡ *Haworthia translucens* ssp. *tenera* (Von Poellnitz) M. B. Bayer (1976) ≡ *Haworthia arachnoidea* ssp. *tenera* (Von Poellnitz) Halda (1997) ≡ *Haworthia arachnoidea* var. *tenera* (Von Poellnitz) Halda (1997) ≡ *Haworthia gracilis* var. *tenera* (Von Poellnitz) M. B. Bayer (1999); **incl.** *Haworthia minima* Baker (1880) (*nom. illeg.*, Art. 53.1); **incl.** *Haworthia cummingii* Breuer & M. Hayashi (2003) ≡ *Haworthia tenera* var. *cummingii* (Breuer & M. Hayashi) Breuer (2016); **incl.** *Haworthia cooperi* var. *minima* M. B. Bayer (2012) (*nom. inval.*, ICN Art. 41.5).

Differs from var. *cooperi*: **Ros** smaller, more compact; **L** closely incurved.

**H. cooperi** var. **truncata** (H. Jacobsen) M. B. Bayer (Haworthia Revisited, 55, ill. (p. 56), 1999). **Type**: [neo — icono]: H. Jacobsen, Handb. Sukk. Pfl. 2: 724, Fig. 644, 1956. — **Distr**: RSA (Eastern Cape); Albany Thicket vegetation. **I**: Jacobsen (1960: 2: Fig. 756, as *H. obtusa* fa.).

≡ *Haworthia obtusa* fa. *truncata* H. Jacobsen (1955); **incl.** *Haworthia ikra* Breuer (2010).

[1] Differs from var. *cooperi*: **Ros** very profliferous, to 7 cm Ø; **L** 20–25, 20–25 × 8 mm,

pale blue-green, erect, truncate, translucent and lightly veined above.

**H. cooperi** var. **venusta** (C. L. Scott) M. B. Bayer (Haworthia Revisited, 56, ills., 1999). **Type**: RSA, Eastern Cape (*Britten* 781 [GRA]). — **Distr**: RSA (Eastern Cape: Alexandria); Albany Coastal Belt vegetation. **I**: Scott (1996: as *H. venusta*).

≡ *Haworthia venusta* C. L. Scott (1996) ≡ *Haworthia salina* var. *venusta* (C. L. Scott) Breuer (2016) (*incorrect name*, ICN Art. 11.4).

[1] Differs from var. *cooperi*: **L** shortly pilose.

**H. cooperi** var. **viridis** (M. B. Bayer) M. B. Bayer (Haworthiad 16(2): 65, 2002). **Type**: RSA, Eastern Cape (*Smith* 6867 [NBG]). — **Distr**: RSA (Eastern Cape: Winterhoek Mts.); Fynbos vegetation.

≡ *Haworthia gracilis* var. *viridis* M. B. Bayer (1999); **incl.** *Haworthia hamata* M. Hayashi (2003); **incl.** *Haworthia subhamata* M. Hayashi (2005) ≡ *Haworthia hamata* var. *subhamata* (M. Hayashi) Breuer (2016); **incl.** *Haworthia velutina* M. Hayashi (2005); **incl.** *Haworthia swanea* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] Differs from var. *cooperi*: **L** with brighter green colouration.

**H. cymbiformis** (Haworth) Duval (Pl. Succ. Horto Alencon., 7, 1809). **Type** [neo]: RSA, Eastern Cape (*Smith* 2844 [NBG 68015]). — **Distr**: RSA (Eastern Cape); often on cliffs in Albany Thicket and Eastern Valley Bushveld vegetations.

≡ *Aloe cymbiformis* Haworth (1804); **incl.** *Aloe cymbaefolia* Schrader (1807) ≡ *Apicra cymbaefolia* (Schrader) Willdenow (1811) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia concava* Haworth (1821); **incl.** *Aloe hebes* Roemer & Schultes fil. (1829).

**H. cymbiformis** var. **cymbiformis** — **Distr**: RSA (Eastern Cape); Albany Thicket vegetation. **I**: Bayer (1982: Fig. 11a). — Fig. 4.

**Incl.** *Haworthia planifolia* Haworth (1825) ≡ *Aloe planifolia* (Haworth) Roemer & Schultes fil. (1829) ≡ *Haworthia cymbiformis* var. *planifolia* (Haworth) Baker (1880) ≡ *Haworthia cymbiformis*





**Fig. 4** *Haworthia cymbiformis* var. *cymbiformis*. (Copyright: E. J. Van Jaarsveld)

fa. *planifolia* (Haworth) Pilbeam (1983); **incl.** *Haworthia cymbiformis* fa. *subarmata* Von Poellnitz (1938)  $\equiv$  *Haworthia cymbiformis* subvar. *subarmata* (Von Poellnitz) M. B. Bayer (1982) (*nom. inval.*, ICN Art. 41.5); **incl.** *Haworthia cymbiformis* var. *angustata* Von Poellnitz (1938)  $\equiv$  *Haworthia angustata* (Poellnitz) Breuer (2010); **incl.** *Haworthia cymbiformis* var. *compacta* Triebner (1938)  $\equiv$  *Haworthia compacta* (Triebner) Breuer (2010); **incl.** *Haworthia planifolia* fa. *agavoides* Triebner & Von Poellnitz (1938); **incl.** *Haworthia planifolia* fa. *alta* Triebner & Von Poellnitz (1938); **incl.** *Haworthia planifolia* fa. *calochlora* Triebner & Von Poellnitz (1938); **incl.** *Haworthia planifolia* fa. *olivacea* Triebner & Von Poellnitz (1938); **incl.** *Haworthia planifolia* fa. *robusta* Triebner & Von Poellnitz (1938); **incl.** *Haworthia planifolia* subvar. *agavoides* Triebner & Von Poellnitz (1938); **incl.** *Haworthia planifolia* var. *exulata* Von Poellnitz (1938); **incl.** *Haworthia planifolia* var. *incrassata* Von Poellnitz (1938); **incl.** *Haworthia planifolia*

var. *longifolia* Triebner & Von Poellnitz (1938); **incl.** *Haworthia planifolia* var. *sublaevis* Von Poellnitz (1938); **incl.** *Haworthia planifolia* var. *poellnitziana* Resende (1940); **incl.** *Haworthia lepida* G. G. Smith (1944)  $\equiv$  *Haworthia batesiana* var. *lepida* (G. G. Smith) Breuer (2016); **incl.** *Haworthia emeralda* M. Hayashi (2005); **incl.** *Haworthia cana* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia ingens* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia plena* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia rosea* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** to 13 cm  $\varnothing$ , usually stemless, proliferous; **L** broadly ovate to lanceolate, flat to slightly concave, generally  $< \frac{1}{3}$  as thick as wide, usually opaque, green turning yellowish or developing a pink hue in full sun; **Inf** to 25 cm, lax; **Fl** 10–15, white.

**H. cymbiformis** var. **incurvula** (Von Poellnitz) M. B. Bayer (*Haworthia* Handb., 124, 1976). **Type** [neo]: RSA, Eastern Cape (*Britten* s.n. [BOL 71307]). — **Distr**: RSA (Eastern Cape: E Grahams-town); Albany Thicket vegetation. **I**: Bayer (1982: Fig. 11c).

$\equiv$  *Haworthia incurvula* Von Poellnitz (1933).

[1] Differs from var. *cymbiformis*: **Ros** smaller, to 5 cm  $\varnothing$ ; **L** narrow, acuminate, incurved, tip obtuse.

**H. cymbiformis** var. **obtusata** (Haworth) Baker (J. Linn. Soc., Bot. 18(109): 209, 1880). **Type**: K [lecto — icono, publ. *Succulenta* 1948: 49]. — **Distr**: RSA (Eastern Cape: Fort Beaufort); Albany Thicket vegetation. **I**: Bayer (1982: Fig. 11e, as *H. umbraticola*).

$\equiv$  *Haworthia obtusata* Haworth (1825); **incl.** *Haworthia hilliana* Von Poellnitz (1937)  $\equiv$  *Haworthia umbraticola* var. *hilliana* (Von Poellnitz) Von Poellnitz (1938); **incl.** *Haworthia umbraticola* Von Poellnitz (1937)  $\equiv$  *Haworthia cymbiformis* var. *umbraticola* (Von Poellnitz) M. B. Bayer (1976); **incl.** *Haworthia blinkia* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *cymbiformis*: **Ros** proliferous, not contracting into the soil; **L** obtuse, venation subdued.

**H. cymbiformis** var. **ramosa** (G. G. Smith) M. B. Bayer (Haworthia Revisited, 60, ill., 1999). **Type:** RSA, Eastern Cape (*Smith* 3168 [NBG, PRE]). — **Distr:** RSA (Eastern Cape: Peddie); Albany Thicket vegetation. **I:** Bayer (1982: Fig. 11b, as fa.).

≡ *Haworthia ramosa* G. G. Smith (1940) ≡ *Haworthia cymbiformis* fa. *ramosa* (G. G. Smith) M. B. Bayer (1976).

[1] Differs from var. *cymbiformis*: **Ros** developing long leafy stems.

**H. cymbiformis** var. **setulifera** (Von Poellnitz) M. B. Bayer (Haworthia Revisited, 62, ills., 1999). **Type** [lecto]: RSA, Eastern Cape (*Anonymus* s.n. in *Stellenbosch Univ. Garden* 3332 [[lecto — icono]: *Kakteenkunde* 1938: 54]). — **Distr:** RSA (SE Eastern Cape); Eastern Valley Bushveld vegetation.

≡ *Haworthia planifolia* var. *setulifera* Von Poellnitz (1938) ≡ *Haworthia setulifera* (Von Poellnitz) Breuer (2010); **incl.** *Haworthia cymbiformis* var. *obesa* Von Poellnitz (1938) ≡ *Haworthia cymbiformis* fa. *obesa* (Von Poellnitz) Pilbeam (1983) ≡ *Haworthia obesa* (Von Poellnitz) Breuer (2010) ≡ *Haworthia umbraticola* var. *obesa* (Von Poellnitz) Breuer (2016); **incl.** *Haworthia sarcoidea* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *cymbiformis*: **L** deltoid, margins spiny.

**H. decipiens** Von Poellnitz (Repert. Spec. Nov. Regni Veg. 28: 103, 1930). **Type** [neo]: RSA, Western Cape (*Fourcade* 4637 [BOL]). — **Distr:** RSA (Western Cape, Eastern Cape: S Karoo); mainly Nama Karoo vegetation.

**H. decipiens** var. **cyanea** M. B. Bayer (Haworthia Revisited, 65, ills. (pp. 65–66), 1999). **Type:** RSA, Eastern Cape (*Bayer* 4180 [NBG]). — **Distr:** RSA (Western Cape, Eastern Cape).

≡ *Haworthia cyanea* (M. B. Bayer) M. Hayashi (2000); **incl.** *Haworthia amethysta* M. Hayashi (2003) ≡ *Haworthia cyanea* var. *amethysta* (M. Hayashi) Breuer (2016); **incl.** *Haworthia caesia* M. Hayashi (2003); **incl.** *Haworthia succinea* M. Hayashi (2003) ≡ *Haworthia cyanea* var. *succinea* (M. Hayashi) Breuer (2016); **incl.**

*Haworthia ianthina* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7) ≡ *Haworthia cyanea* var. *ianthina* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia virginea* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *decipiens*: **Ros** smaller with more **L**; **L** slender, incurving, bluish-green.

**H. decipiens** var. **decipiens** — **Distr:** RSA (Western Cape, Eastern Cape: S Karoo). **I:** Bayer (1982: Fig. 12).

**Incl.** *Haworthia exilis* M. Hayashi (2003) ≡ *Haworthia decipiens* var. *exilis* (M. Hayashi) Breuer (2016); **incl.** *Haworthia decipiens* var. *scottiana* M. Hayashi (2003) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia incrassa* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7) ≡ *Haworthia decipiens* var. *incrassa* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia studis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia tooris* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, slowly proliferous, to 20 cm Ø; **L** ascending, broadly ovate, sometimes acuminate, relatively thin, bright green, marginal **Sp** sparse but broad at their base; **Inf** robust, to 40 cm; **Fl** numerous, densely arranged, broad and flat across the upper base of the tube.

**H. decipiens** var. **minor** M. B. Bayer (Haworthia Revisited, 66, ills., 1999). **Type:** RSA, Eastern Cape (*Smith* 3588 [NBG]). — **Distr:** RSA (Eastern Cape).

≡ *Haworthia gracilis* var. *minor* (M. B. Bayer) M. Hayashi (2003) (*nom. inval.*, ICN Art. 41.5); **incl.** *Haworthia tenmari* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *decipiens*: **Ros** smaller, to 6 cm Ø; **L** broad, incurved, light green.

**H. decipiens** var. **virella** M. B. Bayer (Haworthiad 16(2): 63–64, ills. (p. 66–70), 2002). **Type:** RSA, Eastern Cape (*Bayer* 2070 [NBG]). — **Distr:** RSA (Eastern Cape).

≡ *Haworthia virella* (M. B. Bayer) M. Hayashi (2003); **incl.** *Haworthia crinita* M. Hayashi (2003) ≡ *Haworthia jansenvillensis* var. *crinita* (M.

Hayashi) Breuer (2016) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia eminens* M. Hayashi (2003)  $\equiv$  *Haworthia jansenvillensis* var. *eminens* (M. Hayashi) Breuer (2016) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia floccosa* M. Hayashi (2003)  $\equiv$  *Haworthia bolusii* var. *floccosa* (M. Hayashi) Breuer (2016); **incl.** *Haworthia kemari* M. Hayashi (2003); **incl.** *Haworthia mollis* M. Hayashi (2003)  $\equiv$  *Haworthia jansenvillensis* var. *mollis* (M. Hayashi) Breuer (2016) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia regalis* M. Hayashi (2003); **incl.** *Haworthia regina* M. Hayashi (2003)  $\equiv$  *Haworthia jansenvillensis* var. *regina* (M. Hayashi) Breuer (2016) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia jansenvillensis* Breuer (2004); **incl.** *Haworthia fluffa* M. Hayashi (2005)  $\equiv$  *Haworthia jansenvillensis* var. *fluffa* (M. Hayashi) Breuer (2016); **incl.** *Haworthia pellucida* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia delicata* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia ionides* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia lanceata* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia stewartia* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

Differs from var. *decipiens*: **L** brighter green.

**H. decipiens** var. **xiphiophylla** (Baker) M. B. Bayer (Haworthiad 16(2): 63, 2002). **Incorrect name**, ICN Art. 11.4. **Type**: RSA, Eastern Cape (Howlett s.n. [K]). — **Distr**: RSA (Eastern Cape). **I**: Bayer (1982: Fig. 44, as *H. xiphiophylla*).

$\equiv$  *Haworthia xiphiophylla* Baker (1896)  $\equiv$  *Haworthia setata* var. *xiphiophylla* (Baker) Von Poellnitz (1938)  $\equiv$  *Haworthia arachnoidea* var. *xiphiophylla* (Baker) Halda (1997); **incl.** *Haworthia longiaristata* Von Poellnitz (1937); **incl.** *Haworthia flavida* M. Hayashi (2003)  $\equiv$  *Haworthia jansenvillensis* var. *flavida* (M. Hayashi) Breuer (2016) (*incorrect name*, ICN Art. 11.4 Ex. 10); **incl.** *Haworthia auraria* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia kammaensis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

Differs from var. *decipiens*: **L** bright green, long, slender, with broad but short marginal **Sp**.

Editorial note [U. Eggli]: *H. xiphiophylla* has priority over *H. decipiens* at species rank, which makes *H. decipiens* var. *xiphiophylla* incorrect, but the name is preferably used here because it illustrates that var. *xiphiophylla* is part of a far greater *H. decipiens* alliance (Bayer 2013a).

**H. emelyae** Von Poellnitz (Repert. Spec. Nov. Regni Veg. 42: 271, 1937). **Type**: B [lecto: unpubl. ill.]. — **Lit**: Marx (2016a). **Distr**: RSA (Western Cape, Eastern Cape); Fynbos and Succulent Karoo vegetations.

$\equiv$  *Haworthia retusa* ssp. *emelyae* (Von Poellnitz) Halda (1997)  $\equiv$  *Haworthia retusa* var. *emelyae* (Von Poellnitz) Halda (1997).

**H. emelyae** var. **comptoniana** (G. G. Smith) J. D. Venter & S. A. Hammer (Cact. Succ. J. (US) 69(2): 77, 1997). **Type**: RSA, Eastern Cape (*Malherbe* s.n. in Smith 3433 [NBG]). — **Distr**: RSA (Eastern Cape: E Little Karoo); Willowmore Gwarrieveld vegetation. **I**: Bayer (1982: Fig. 9, as *H. comptoniana*). — Fig. 5.

$\equiv$  *Haworthia comptoniana* G. G. Smith (1945)  $\equiv$  *Haworthia retusa* var. *comptoniana* (G. G. Smith) Halda (1997)  $\equiv$  *Haworthia picta* var. *comptoniana* (G. G. Smith) Breuer (2016); **incl.** *Haworthia comptoniana* fa. *brevifolia* Hort. Sheilam (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Haworthia comptoniana* fa. *major* Pilbeam (1983) (*nom. inval.*, ICN Art. 40.1).

[1] Differs from var. *emelyae*: **Ros** to 12 cm  $\varnothing$ ; upper face of **L** smooth and markedly reticulate.



**Fig. 5** *Haworthia emelyae* var. *comptoniana*. (Copyright: U. Eggli)



**H. emelyae** var. **emelyae** — **Lit:** Marx (2009a). **Distr:** RSA (Western Cape: Little Karoo); Fynbos and Succulent Karoo vegetations. **I:** Bayer (1982: Fig. 14a); Marx (2014a).

**Incl.** *Haworthia blackburniae* Von Poellnitz (1937) (*nom. illeg.*, Art. 53.1); **incl.** *Haworthia correctata* Von Poellnitz (1938); **incl.** *Haworthia picta* Von Poellnitz (1938); **incl.** *Haworthia breueri* M. Hayashi (2002)  $\equiv$  *Haworthia multifolia* var. *breueri* (M. Hayashi) Breuer (2016); **incl.** *Haworthia correctata* var. *lucida* M. Hayashi (2002); **incl.** *Haworthia multifolia* var. *sandkraalensis* Breuer (2002) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia picta* var. *janvlokii* Breuer (2003)  $\equiv$  *Haworthia janvlokii* (Breuer) Breuer (2010); **incl.** *Haworthia picta* var. *tricolor* Breuer (2003)  $\equiv$  *Haworthia tricolor* (Breuer) M. Hayashi (2010).

[1] **Ros** to 10 cm  $\varnothing$ , rarely proliferous; **L** 15–20, distinctly retuse, pointed, barely translucent, dark green, with scattered elongate small flecks, with obscure raised tubercles, sometimes with lines and with reddish-brown hue; **Inf** to 30 cm; **Fl** 15–20, white.

**H. emelyae** var. **major** (G. G. Smith) M. B. Bayer (Aloe 34(1–2): 6, 1997). **Type:** RSA, Western Cape (*Smith* 5370 [NBG]). — **Distr:** RSA (Western Cape: S Little Karoo); Fynbos vegetation. **I:** Bayer (1982: Fig. 22c, as *H. magnifica* var.).

$\equiv$  *Haworthia schuldtiana* var. *major* G. G. Smith (1946)  $\equiv$  *Haworthia maraisii* var. *major* (G. G. Smith) M. B. Bayer (1976)  $\equiv$  *Haworthia magnifica* var. *major* (G. G. Smith) M. B. Bayer (1977)  $\equiv$  *Haworthia multifolia* var. *major* (G. G. Smith) Breuer (2016); **incl.** *Haworthia wimii* M. Hayashi (2000).

[1] Differs from var. *emelyae*: **L** acuminate, tubercles with an apical **Sp**.

**H. emelyae** var. **multifolia** M. B. Bayer (Nation. Cact. Succ. J. 34(2): 28–31, ills., 1979). **Type:** RSA, Western Cape (*Bayer* 1558 [NBG]). — **Distr:** RSA (Western Cape: S Little Karoo); Succulent Karoo vegetation. **I:** Bayer (1982: Fig. 14b).

$\equiv$  *Haworthia multifolia* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *emelyae*: **L** 25–30, erect.



**Fig. 6** *Haworthia fasciata*. (Copyright: E. J. Van Jaarsveld)

**H. fasciata** (Willdenow) Haworth (Revis. Pl. Succ., 54, 1821). **Type** [neo]: RSA, Eastern Cape (*Stayner* s.n. [NBG 110 360]). — **Distr:** RSA (Eastern Cape); naturalized in Spain. **I:** Bayer (1982: Fig. 49a); Gildenhuis (2017: 22–23, as *Haworthiopsis*). – Fig. 6.

$\equiv$  *Apicra fasciata* Willdenow (1811) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Aloe fasciata* (Willdenow) Salm-Dyck (1834)  $\equiv$  *Haworthia pumila* ssp. *fasciata* (Willdenow) Halda (1997)  $\equiv$  *Haworthiopsis fasciata* (Willdenow) G. D. Rowley (2013); **incl.** *Aloe fasciata* var. *major* Salm-Dyck (1817)  $\equiv$  *Haworthia fasciata* var. *major* (Salm-Dyck) Haworth (1819)  $\equiv$  *Haworthia fasciata* fa. *major* (Salm-Dyck) Von Poellnitz (1938); **incl.** *Aloe fasciata* var. *minor* Salm-Dyck (1834); **incl.** *Haworthia browniana* Von Poellnitz (1937)  $\equiv$  *Haworthia fasciata* fa. *browniana* (Von Poellnitz) M. B. Bayer (1976)  $\equiv$  *Haworthia fasciata* var. *browniana* (Von Poellnitz) C. L. Scott (1985)  $\equiv$  *Haworthiopsis fasciata* var. *browniana* (Von Poellnitz) Gildenhuis & Klopper (2016); **incl.**

*Haworthia fasciata* var. *subconfluens* Von Poellnitz (1937)  $\equiv$  *Haworthia fasciata* f.a. *subconfluens* (Von Poellnitz) Von Poellnitz (1938); **incl.** *Haworthia fasciata* f.a. *ovato-lanceolata* Von Poellnitz (1938); **incl.** *Haworthia fasciata* f.a. *sparsa* Von Poellnitz (1938); **incl.** *Haworthia fasciata* f.a. *vanstaadensis* Von Poellnitz (1938); **incl.** *Haworthia fasciata* f.a. *variabilis* Von Poellnitz (1938).

[2] **Ros** to 15 cm  $\varnothing$  and 18 cm tall, stemless, proliferating; **L** 60–80, erect, to 6  $\times$  1.5 cm, incurved, scabrid, with white tubercles on the lower face only; **Inf** simple or occasionally compound, to 30 cm; **Fl** tube obcapitate, curved; **Tep** tips revolute.

The species is used as a talisman by the Xhosa (similar to the use of *H. limifolia* by the Zulu), and the occurrence of *H. fasciata* in S and N KwaZulu-Natal is anthropogenic (Bayer 2010d).

Guillot & Laguna Lumbreras (2012) report the species as locally naturalized in Valencia Province, Spain. Gildenhuys (2017: 24, with ill, as *Haworthiopsis*) also accepts *H. fasciata* var. *browniana* because a small population is located outside the distribution area of var. *fasciata*.

**H. floribunda** Von Poellnitz (Repert. Spec. Nov. Regni Veg. 40: 149, 1936). **Type:** B [lecto: unpubl. ill.]. — **Distr:** RSA (Western Cape); Fynbos vegetation.

$\equiv$  *Haworthia chloracantha* var. *floribunda* (Von Poellnitz) Halda (1997).

**H. floribunda** var. *dentata* M. B. Bayer (Haworthia Revisited, 73, ill., 1999). **Type:** RSA, Western Cape (*Dekenah* 90 in *Smith* 5502 [NBG]). — **Distr:** RSA (Western Cape: Bredasdorp and Riversdale Distr.); Silcrete Renosterveld vegetation (Fynbos).

$\equiv$  *Haworthia dentata* (M. B. Bayer) M. Hayashi (2000)  $\equiv$  *Haworthia parksiana* var. *dentata* (M. B. Bayer) Breuer (2016).

[1] Differs from var. *floribunda*: **Ros** to 4 cm  $\varnothing$ ; **L** very dark green, slightly scabrid, margins spiny.

**H. floribunda** var. *floribunda* — **Distr:** RSA (Western Cape: Bredasdorp Distr.). **I:** Bayer (1982: Fig. 15); Scott (1985: 58).

**Incl.** *Haworthia henda* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, to 3 cm  $\varnothing$ , slowly proliferating; **L** 20–30, ovate-lanceolate, spreading, twisted with flattened rounded tip, dark green, opaque, glabrous, margins scabrid to dentate; **Inf** to 25 cm; **Fl** 10–15, greenish-white, few open together.

**H. floribunda** var. *major* M. B. Bayer (Haworthia Revisited, 74, ill., 1999). **Type:** RSA, Western Cape (*De Kok* s.n. [NBG]). — **Distr:** RSA (Western Cape: Bredasdorp Distr.); Fynbos vegetation.

$\equiv$  *Haworthia kondoi* M. Hayashi (2000).

[1] Differs from var. *floribunda*: Plants more robust (esp. in cultivation); **L** very green with darker colouration at the basal margins, relatively glabrous.

**H. glauca** Baker (J. Linn. Soc., Bot. 18(109): 203, 1880). **Type:** RSA, Eastern Cape (*Cooper* s.n. [K]). — **Distr:** RSA (Eastern Cape).

$\equiv$  *Haworthia reinwardtii* ssp. *glauca* (Baker) Halda (1997)  $\equiv$  *Haworthia reinwardtii* var. *glauca* (Baker) Halda (1997)  $\equiv$  *Haworthiopsis glauca* (Baker) G. D. Rowley (2013).

**H. glauca** var. *glauca* — **Distr:** RSA (Eastern Cape: Zuurberg Mts.); Fynbos and Albany Thicket vegetations. **I:** Bayer (1982: Fig. 51a); Gildenhuys (2017: 25–26, as *Haworthiopsis*).

**Incl.** *Haworthia carrissoi* Resende (1941).

[2] **Ros** to 8 cm  $\varnothing$ , caulescent, proliferating; **L** numerous, to 6  $\times$  1.5 cm, erectly spreading or incurved, scabrid, glaucous grey-green, surfaces without tubercles; **Inf** simple or occasionally compound, to 30 cm; **Fl** tube obcapitate, curved; **Tep** revolute.

**H. glauca** var. *herrei* (Von Poellnitz) M. B. Bayer (Haworthia Handb., 122, 1976). **Type** [neo]: RSA, Eastern Cape (*Barker* 5069 [NBG 68132]). — **Distr:** RSA (Eastern Cape: Little Karoo); Albany Thicket vegetation. **I:** Bayer (1982: Fig. 51b).

$\equiv$  *Haworthia herrei* Von Poellnitz (1929)  $\equiv$  *Haworthia reinwardtii* var. *herrei* (Von Poellnitz) Halda (1997)  $\equiv$  *Haworthiopsis glauca* var. *herrei*



(Von Poellnitz) G. D. Rowley (2013); **incl.** *Haworthia herrei* var. *depauperata* Von Poellnitz (1933); **incl.** *Haworthia armstrongii* Von Poellnitz (1937)  $\equiv$  *Haworthia glauca* fa. *armstrongii* (Von Poellnitz) M. B. Bayer (1976); **incl.** *Haworthia eilyae* Von Poellnitz (1937); **incl.** *Haworthia jacobseniana* Von Poellnitz (1937)  $\equiv$  *Haworthia glauca* fa. *jacobseniana* (Von Poellnitz) Pilbeam (1983); **incl.** *Haworthia jonesiae* Von Poellnitz (1937)  $\equiv$  *Haworthia glauca* fa. *jonesiae* (Von Poellnitz) Pilbeam (1983); **incl.** *Haworthia herrei* var. *poellnitzii* Resende (1941) (*nom. illeg.*, Art. 52.1, 26.1); **incl.** *Haworthia eilyae* var. *zantneriana* Resende (1943); **incl.** *Haworthia eilyae* var. *poellnitziana* Resende (1943) (*nom. illeg.*, ICN Art. 52.1, 26.1).

[2] Differs from var. *glauca*: **L** lanceolate, spreading, tuberculate.

**H. granulata** Marloth (Trans. Roy. Soc. South Africa 2: 39, 1910). **Type:** RSA, Northern Cape (*Marloth* 4217 [BOL]). — **Distr:** RSA (S Northern Cape, Western Cape): Tanqua Karoo and W Little Karoo, in Succulent Karoo vegetation. **I:** Bayer (1982: Fig. 61b, as *H. venosa* ssp.); Gildenhuis (2017: 42–43, as *Haworthiopsis*).

$\equiv$  *Haworthia venosa* ssp. *granulata* (Marloth) M. B. Bayer (1976)  $\equiv$  *Haworthia scabra* ssp. *granulata* (Marloth) Halda (1997)  $\equiv$  *Haworthiopsis granulata* (Marloth) G. D. Rowley (2013)  $\equiv$  *Haworthiopsis venosa* var. *granulata* (Marloth) G. D. Rowley (2013) (*nom. inval.*, ICN Art. 36.2); **incl.** *Haworthia schoemaniai* M. Hayashi (2003)  $\equiv$  *Haworthiopsis granulata* var. *schoemaniai* (M. Hayashi) Breuer (2016).

[2] **Ros** caulescent, to 15 cm, slowly proliferating; **L** 12–20, to 10  $\times$  1.5 cm, ovate-deltoid, suberect to erect, more scabrid than in *H. tessellata*; **Inf** sparsely branched, lax, to 35 cm; **Fl** 15–20, tube obcapitate; **ITep** revolute.

Closely similar to (and previously treated as variety of) *H. venosa*, but species rank is warranted due to the completely allopatric occurrences of the two taxa. *H. granulata* differs in its roughish leaves and a tendency to develop a short stem with age.

**H. grenieri** Breuer (*Alsterworthia* Int. 17(3): 14, ill. (pp. 17–21), 2017). **Type:** RSA, Western Cape (*Marx* 793 [GRA]). — **Distr:** RSA (Western Cape: N & W Little Karoo); in Fynbos vegetation among quartzitic sandstone rocks, flowers in autumn.

[1] **Ros** acaulescent, 1–2 cm  $\varnothing$ ; **L** 40–52, to 15  $\times$  2–3 mm, 3- to 4-angled, surface dark green, tessellate, tip with inward-curving awn, margin and keels ciliate; **Inf** simple, solitary or sometimes 2, 10–15 cm, 2- to 4-flowered, peduncle  $\pm$  1 mm  $\varnothing$ ; **Fl** similar to those of *H. monticola*.

The flowers show close similarity to those of *H. monticola* and *H. zantneriana*. — [E. Van Jaarsveld]

**H. herbacea** (Miller) Stearn (*Cact. J.* (Croydon) 7: 40, 1938). **Type:** [lecto — icono]: Boerhaave, Ind. Alter Hort. Lugd.-Bat., 2: t. ad p. 131, 1720. — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo); Succulent Karoo vegetation.

$\equiv$  *Aloe herbacea* Miller (1768); **incl.** *Aloe pumila* var.  $\varepsilon$  Linné (1753); **incl.** *Catevala atroviridis* Medikus (1786)  $\equiv$  *Haworthia atroviridis* (Medikus) M. Hayashi (2007); **incl.** *Aloe arachnoidea* var. *pumila* Aiton (1789)  $\equiv$  *Aloe pumila* (Aiton) Haworth (1804) (*nom. illeg.*, Art. 53.1)  $\equiv$  *Haworthia pumila* (Aiton) Duval (1809); **incl.** *Aloe arachnoidea* var. *pumila* Willdenow (1799) (*nom. illeg.*, Art. 53.1); **incl.** *Aloe atrovirens* De Candolle (1799) (*nom. illeg.*, Art. 52.1)  $\equiv$  *Apicra atrovirens* (De Candolle) Willdenow (1811) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Haworthia atrovirens* (De Candolle) Haworth (1821) (*nom. illeg.*, Art. 52.1); **incl.** *Aloe bradlyana* Jacquin (1804); **incl.** *Aloe translucens* Haworth (1804)  $\equiv$  *Aloe arachnoidea* var. *translucens* (Haworth) Ker Gawler (1811)  $\equiv$  *Apicra translucens* (Haworth) Willdenow (1811)  $\equiv$  *Haworthia translucens* (Haworth) Haworth (1819) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Haworthia arachnoidea* var. *translucens* (Haworth) Halda (1997); **incl.** *Haworthia pellucens* Haworth (1812)  $\equiv$  *Aloe arachnoidea* var. *pellucens* (Haworth) Salm-Dyck (1817); **incl.** *Aloe papillosa* Salm-Dyck (1817)  $\equiv$  *Haworthia papillosa* (Salm-Dyck) Haworth (1819); **incl.** *Haworthia pallida* Haworth (1821)  $\equiv$  *Aloe pallida* (Haworth) Roemer & Schultes fil. (1829); **incl.** *Haworthia papillosa*

var. *semipapillosa* Haworth (1821)  $\equiv$  *Aloe papillosa* var. *semipapillosa* (Haworth) Roemer & Schultes *fil.* (1829); **incl.** *Haworthia aegrota* Von Poellnitz (1939); **incl.** *Haworthia luteorosea* Uitewaal (1939); **incl.** *Haworthia submaculata* Von Poellnitz (1939).

Here belongs *H. arachnoidea* in the sense of Scott (1977) and Scott (1985).

**H. herbacea** var. **flaccida** M. B. Bayer (Haworthia Revisited, 86, ills., 1999). **Type:** RSA, Western Cape (*Bruyns* 7114 [NBG]). — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo).

$\equiv$  *Haworthia pallida* var. *flaccida* (M. B. Bayer) M. Hayashi (2000)  $\equiv$  *Haworthia flaccida* (M. B. Bayer) Breuer (2010).

[1] Differs from var. *herbacea*: **Ros** small and delicate.

**H. herbacea** var. **herbacea** — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo). **I:** Bayer (1982: Fig. 19). — Fig. 7.

[1] **Ros** stemless, proliferating, to 8 cm  $\varnothing$ ; **L** erect, incurved, ovate-lanceolate, to 6  $\times$  1 cm, greenish-yellow, with reticulate pattern with translucent areas between the veins, scabrid, margins and keel with firm spines; **Inf** to 30 cm; **Fl** 30–40, large, beige with pinkish tips, buds with an S-bend.

**H. herbacea** var. **lupula** M. B. Bayer (Haworthia Revisited, 86, ills. (pp. 86–87),



**Fig. 7** *Haworthia herbacea* var. *herbacea*. (Copyright: E. J. Van Jaarsveld)

1999). **Type:** RSA, Western Cape (*Esterhuysen* s.n. [NBG]). — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo).

$\equiv$  *Haworthia lupula* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *herbacea*: **L** broader, shorter, finely flecked, less scabrid; **Fl** larger, pink.

**H. herbacea** var. **paynei** (Von Poellnitz) M. B. Bayer (Haworthia Revisited, 87, ills., 1999). **Type:** RSA, Western Cape (*Payne* s.n. [B [lecto, unpubl. ill.]]). — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo).

$\equiv$  *Haworthia paynei* Von Poellnitz (1937)  $\equiv$  *Haworthia pallida* var. *paynei* (Von Poellnitz) Von Poellnitz (1937).

[1] Differs from typical *H. herbacea*: Plants small-sized; **Fl** bicoloured, pink above and white below.

**H. kingiana** Von Poellnitz (Repert. Spec. Nov. Regni Veg. 41: 203, 1937). **Type** [neo]: RSA, Western Cape (*Dekenah* 201 [NBG 68719]). — **Lit:** Bayer (2010f); Molteno & Smith (2017). **Distr:** RSA (Western Cape); Fynbos vegetation. **I:** Bayer (1982: Fig. 64).

$\equiv$  *Haworthia subfasciata* var. *kingiana* (Von Poellnitz) Von Poellnitz (1938)  $\equiv$  *Haworthia pumila* var. *kingiana* (Von Poellnitz) Halda (1997)  $\equiv$  *Tulista kingiana* (Von Poellnitz) Gideon F. Smith & Molteno (2017); **incl.** *Haworthia zenigata* M. Hayashi (2001)  $\equiv$  *Tulista opalina* var. *zenigata* (M. Hayashi) Breuer (2016).

[3] **Ros** stemless, slowly proliferating, to 18 cm tall; **L** to 16  $\times$  1.8 cm, nearly as thick as wide, yellowish-green, lanceolate-deltoid, attenuate, spreading, surfaces scabrid with raised rounded non-confluent tubercles; **Inf** sparsely branched, lax; **Fl** 30–40, tube obcapitate; **Tep** lobes short, veins pinkish.

Molteno & Smith (2017: as *Tulista*) describe the variability and distribution of the taxon, and also discuss a population that includes both tubercle-leaved and smooth-leaved plants.

**H. koelmaniorum** Obermeyer & D. S. Hardy (Flow. Pl. Afr. 1967: t. 1502 + text, 1967). **Type:** RSA, Mpumalanga (*Hardy & Mauve* 2267

[PRE]). — **Lit:** Bosch (2004); Craib (2007).  
**Distr:** RSA (Mpumalanga).

≡ *Haworthia limifolia* ssp. *koelmaniorum* (Obermeyer & D. S. Hardy) Halda (1997) ≡ *Tulista koelmaniorum* (Obermeyer & D. S. Hardy) G. D. Rowley (2013) ≡ *Haworthiopsis koelmaniorum* (Obermeyer & D. S. Hardy) Boatwright & J. C. Manning (2014).

Bosch (2004) studied the overall variability of the two varieties and concludes that they merely represent ecotypes determined by the geology of the substrate. Craib (2007) also found overlap in characters and distribution area between the two varieties. The species is adapted to grass fires in rocky areas. Recruitment is slow, as flowering/fruiting probably only occur in one to two out of 10 years, and seedlings are vulnerable as long as the leaves are not flush with the surrounding ground (Craib 2007).

**H. koelmaniorum** var. **koelmaniorum** — **Distr:** RSA (Mpumalanga); savanna. **I:** Bayer (1982: Fig. 52); Gildenhuis (2017: 36–37, as *Haworthiopsis*).

[2] **Ros** stemless, slowly proliferating, 5–7 cm Ø; **L** 14–20, ovate, 7 × 2 cm, dark brownish-green, opaque, somewhat recurved, scabrid with small raised tubercles, margins and keel with small **Sp**; **Inf** slender, to 35 cm; **Fl** 10–15, slender, **Tip** tips revolute.

**H. koelmaniorum** var. **mcmurtryi** (C. L. Scott) M. B. Bayer (*Haworthia Revisited*, 181, ills., 1999). **Type:** RSA, Mpumalanga (*McMurtry* 5247 [PRE]). — **Distr:** RSA (Mpumalanga); Loskop Mountain Bushveld vegetation. **I:** Scott (1985: 141, as *H. mcmurtryi*); Gildenhuis (2017: 37–38, as *Haworthiopsis*).

≡ *Haworthia mcmurtryi* C. L. Scott (1984) ≡ *Tulista koelmaniorum* var. *mcmurtryi* (C. L. Scott) G. D. Rowley (2013) ≡ *Haworthiopsis mcmurtryi* (C. L. Scott) Zonneveld (2014) ≡ *Haworthiopsis koelmaniorum* var. *mcmurtryi* (C. L. Scott) Gildenhuis & Klopper (2016); **incl.** *Haworthia mcmurtryi* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1).

[2] Differs from var. *koelmaniorum*: **Ros** smaller, 4–5 cm Ø; **L** with more prominent surface markings.

This variety is only known from two populations in the Highveld on red rhyolite of the Selons River formation. In one of the study populations, 84% of the almost 1300 plants counted were adults, 12% juveniles, and 4% seedlings (Biko'o & al. 2011).

**H. limifolia** Marloth (Trans. Roy. Soc. South Africa 1: 409, 1908). **Type:** RSA (*Marloth* 4678 [PRE]). — **Lit:** Bayer (2003a). **Distr:** S Moçambique, Swaziland, RSA (Mpumalanga, KwaZulu-Natal); savanna.

≡ *Haworthiopsis limifolia* (Marloth) G. D. Rowley (2013).

Used as a talisman by the Zulu under the name of “umathithibala” (= creator of harmony) (Bayer 2010d) and by the Swasi under the name “indvololwane”. The species is also used in traditional medicine as blood purifier and against coughs, sun burns and skin diseases. Coopoosamy & Naidoo (2011) found evidence that leaf extracts have antibacterial and antifungal properties.

**H. limifolia** var. **arcana** Gideon F. Smith & N. Crouch (*Bradleya* 19: 118–119, ills., 2001). **Type:** RSA, Mpumalanga (*Crouch & Smith* 7 [PRE]). — **Distr:** RSA (Mpumalanga); Swaziland Sour Bushveld vegetation. **I:** Gildenhuis (2017: 40, as *Haworthiopsis*).

≡ *Haworthia arcana* (Gideon F. Smith & N. Crouch) Breuer (2010) ≡ *Haworthiopsis limifolia* var. *arcana* (Gideon F. Smith & N. Crouch) G. D. Rowley (2013).

[2] Differs from var. *limifolia*: **L** with fewer transverse ridges, olive in colour.

**H. limifolia** var. **gigantea** M. B. Bayer (*J. South Afr. Bot.* 28: 215–216, 1962). **Type:** RSA, KwaZulu-Natal (*Bayer* 112 [PRE]). — **Distr:** RSA (Mpumalanga, N KwaZulu-Natal). **I:** Bayer (1982: Fig. 53b); Gildenhuis (2017: 40, as *Haworthiopsis*).

≡ *Haworthia gigantea* (M. B. Bayer) M. Hayashi (2000) ≡ *Haworthiopsis limifolia* var. *gigantea* (M. B. Bayer) G. D. Rowley (2013).

[2] Differs from var. *limifolia*: **Ros** larger, to 20 cm Ø; **L** to 13 × 5 cm, finely tuberculate, often with white tubercles or tubercular striations.

**H. limifolia** var. **glaucophylla** M. B. Bayer (Aloe 40(2): 50, ills. (pp. 44, 49), 2003). **Type:** RSA, Mpumalanga (*Venter* 13700 [NBG]). — **Distr:** RSA (Mpumalanga); savanna. **I:** Gildenhuis (2017: 40–41, as *Haworthiopsis*).

≡ *Haworthia glaucophylla* (M. B. Bayer) Breuer (2010) ≡ *Haworthiopsis limifolia* var. *glaucophylla* (M. B. Bayer) G. D. Rowley (2013).

Differs from var. *limifolia*: **L** slightly broader, paler green.

**H. limifolia** var. **limifolia** — **Distr:** S Moçambique, Swaziland, RSA (Mpumalanga, KwaZulu-Natal); savanna. **I:** Bayer (1982: Fig. 53a); Gildenhuis (2017: 39, as *Haworthiopsis*).

**Incl.** *Haworthia limifolia* fa. *variegata* Hort. Huntington (s.a.) (*nom. inval.*, ICN Art. 29.1, 38.1a); **incl.** *Haworthia limifolia* fa. *diploidea* Resende (1940); **incl.** *Haworthia limifolia* fa. *schuldtiana* Resende (1940) ≡ *Haworthia limifolia* var. *schuldtiana* (Resende) Resende (1943); **incl.** *Haworthia limifolia* fa. *tetraploidea* Resende (1940); **incl.** *Haworthia limifolia* var. *diploidea* Resende (1940); **incl.** *Haworthia limifolia* var. *tetraploidea* Resende (1940); **incl.** *Haworthia limifolia* fa. *marlothiana* Resende (1941) ≡ *Haworthia limifolia* var. *marlothiana* (Resende) Resende (1943); **incl.** *Haworthia limifolia* fa. *major* Resende (1943); **incl.** *Haworthia limifolia* fa. *pimentelii* Resende (1943); **incl.** *Haworthia limifolia* var. *stolonifera* Resende (1943); **incl.** *Haworthia limifolia* var. *keithii* G. G. Smith (1950) ≡ *Haworthia keithii* (G. G. Smith) M. Hayashi (2000); **incl.** *Haworthia limifolia* var. *striata* Pilbeam (1983) (*nom. inval.*, ICN Art. 40.1) ≡ *Haworthiopsis limifolia* var. *striata* (Pilbeam) Breuer (2016) (*nom. inval.*, ICN Art. 40.1); **incl.** *Haworthia striata* M. Hayashi (2000) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia gideonii* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[2] **Ros** stemless, slowly proliferating, with or without stolons, 5–7 cm Ø; **L** 12–30, ovate-lanceolate, to 6 × 2 cm, spreading, light to very dark green and even brownish-green, opaque, scabrid with white or concolorous tubercles or with confluent transverse ridges, margins and

keel scabrid; **Inf** slender, to 35 cm; **Fl** 15–20, slender, **Tep** tips revolute.

**H. limifolia** var. **ubomboensis** (I. Verdoorn) G. G. Smith (J. South Afr. Bot. 16: 4, 1950). **Type:** Swaziland (*Keith* s.n. [PRE]). — **Distr:** E Swaziland; savanna. **I:** Bayer (1982: Fig. 53c); Gildenhuis (2017: 41, as *Haworthiopsis*).

≡ *Haworthia ubomboensis* I. Verdoorn (1941) ≡ *Haworthiopsis limifolia* var. *ubomboensis* (I. Verdoorn) G. D. Rowley (2013).

[2] Differs from var. *limifolia*: **L** bright green, glabrous.

**H. lockwoodii** Archibald (Flow. Pl. South Afr. 20: t. 792 + text, 1940). **Type:** RSA, Western Cape (*Lockwood Hill* 215 [GRA]). — **Distr:** RSA (Western Cape: SW Great Karoo); Succulent Karoo vegetation. **I:** Bayer (1982: Fig. 20).

≡ *Haworthia mucronata* ssp. *lockwoodii* (Archibald) Halda (1997) ≡ *Haworthia inconfluens* var. *lockwoodii* (Archibald) Breuer (2016) (*incorrect name*, ICN Art. 11.4).

[1] **Ros** stemless, to 10 cm Ø, slowly proliferating, withdrawn into the soil in habitat; **L** many, ovate, 7 × 2 cm, incurved, smooth, usually spineless and dying back at the tips, pale green, translucent towards the tips; **Inf** robust; **Fl** numerous, large, appressed to the inflorescence axis, broad across and flat at the base of the tube.

**H. longiana** Von Poellnitz (Repert. Spec. Nov. Regni Veg. 41: 203–204, 1937). **Type:** B [lecto: unpubl. ill.]. — **Distr:** RSA (Eastern Cape: Baviaanskloof); Albany Thicket vegetation. **I:** Bayer (1982: Fig. 54); Gildenhuis (2017: 28, as *Haworthiopsis*).

≡ *Haworthia pumila* ssp. *longiana* (Von Poellnitz) Halda (1997) ≡ *Haworthiopsis longiana* (Von Poellnitz) G. D. Rowley (2013); **incl.** *Haworthia longiana* var. *albinota* G. G. Smith (1948).

[2] **Ros** stemless, slowly proliferating, to 30 cm tall and 6 cm Ø; **L** to 30 × 2 cm, narrowly long attenuate, erect, incurving, surfaces minutely scabrid with small indistinctly raised tubercles (occasionally with small white tubercles); **Inf**



sparsely branched, lax; **Fl** tube obovate, curved; **ITep** tips revolute.

**H. maculata** (Von Poellnitz) M. B. Bayer (Haworthia Handb., 130, 1976). **Type** [lecto]: RSA, Western Cape (*Venter* 6 [BOL]). — **Distr**: RSA (Western Cape); Succulent Karoo vegetation.

≡ *Haworthia schuldiana* var. *maculata* Von Poellnitz (1940) ≡ *Haworthia intermedia* var. *maculata* (Von Poellnitz) J. Esterhuizen (2003).

**H. maculata** var. **livida** (M. B. Bayer) M. B. Bayer (Haworthia Nomenclator, 10, 2012). **Type**: RSA, Western Cape (*Bayer* 1128 [NBG]). — **Distr**: RSA (Western Cape: Robertson Karoo: S of Worcester).

≡ *Haworthia pubescens* var. *livida* M. B. Bayer (1999) ≡ *Haworthia maraisii* var. *livida* (M. B. Bayer) M. Hayashi (2000) ≡ *Haworthia intermedia* var. *livida* (M. B. Bayer) J. Esterhuizen (2003); **incl.** *Haworthia livida* Breuer (2011) (*nom. inval.*, ICN Art. 38.1a, 41.5).

[1] Differs from var. *maculata*: **Ros** smaller; **L** less spotted.

**H. maculata** var. **maculata** — **Distr**: RSA (Western Cape: Worcester-Robertson Karoo). **I**: Bayer (1982: Fig. 21).

**Incl.** *Haworthia audens* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, proliferous, to 8 cm Ø; **L** numerous, ovate-lanceolate, 6 × 1 cm, suberect to spreading, purplish-green, spotted with colourless dots, margins and keel with short spines; **Inf** slender; **Fl** 15–20, only a few open together, white with yellowish throat and green veins.

**H. × mantelii** Uitewaal (Succulenta 1947(4): 37–38, ill., 1947). **Type**: not typified.

This is the garden hybrid *H. truncata* × *H. cuspidata* according to the protologue. *H. cuspidata* is treated as unresolved name here. The often asymmetrical rosettes with truncate leaves clearly show the influence of *H. truncata* as one parent. — [U. Eggl]

**H. margaritifera** (Linné) Haworth (Suppl. Pl. Succ., 55, 1819). **Type**: [lecto — icono]: Commelin, Horti Med. Amstelod. 2: t. 10, 1701. — **Lit**: Scott (2011: as *H. maxima*). **Distr**: RSA (Western Cape: Worcester-Robertson Karoo, W Little Karoo); Succulent Karoo vegetation. **I**: Bayer (1982: Fig. 68, as *H. pumila*).

≡ *Aloe pumila* var. *margaritifera* Linné (1753) ≡ *Aloe margaritifera* (Linné) Miller (1768) ≡ *Apicra margaritifera* (Linné) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Tulista margaritifera* (Linné) Rafinesque (1840); **incl.** *Aloe margaritifera* var. *maxima* Haworth (1804); ≡ *Aloe pumila* var. *margaritifera* Linné (1753); **incl.** *Aloe margaritifera* var. *maxima* Haworth (1804) ≡ *Haworthia maxima* (Haworth) Duval (1809) ≡ *Apicra margaritifera* var. *maxima* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Aloe semimargaritifera* var. *maxima* (Haworth) Salm-Dyck (1817) ≡ *Haworthia semimargaritifera* var. *maxima* (Haworth) Haworth (1819) ≡ *Apicra maxima* (Haworth) Steudel (1821) (*incorrect name*, Art. 11.4) ≡ *Haworthia margaritifera* subvar. *maxima* (Haworth) A. Berger (1908) ≡ *Haworthia margaritifera* var. *maxima* (Haworth) Uitewaal (1947); **incl.** *Aloe pumila* Linné (1753) ≡ *Tulista pumila* (Linné) G. D. Rowley (2013); **incl.** *Aloe pumila* Burman fil. (1768) (*nom. illeg.*, Art. 53.1); **incl.** *Aloe semimargaritifera* Salm-Dyck (1817) ≡ *Haworthia semimargaritifera* (Salm-Dyck) Haworth (1819) ≡ *Haworthia margaritifera* var. *semimargaritifera* (Salm-Dyck) Baker (1880); **incl.** *Haworthia ao-onii* M. Hayashi (2006); **incl.** *Haworthia ohkuwae* M. Hayashi (2006) ≡ *Tulista pumila* var. *ohkuwae* (M. Hayashi) Breuer (2016); **incl.** *Haworthia sparsa* M. Hayashi (2006) ≡ *Tulista pumila* var. *sparsa* (M. Hayashi) Breuer (2016).

[3] **Ros** stemless, slowly proliferating, to 25 cm tall; **L** 14 × 2 cm, almost as thick as wide, lanceolate-deltoid, attenuate, spreading, brownish-green to olive-green, surfaces scabrid with raised rounded non-confluent tubercles; **Inf** sparsely branched, lax, to 60 cm; **Fl** tube straight; **Tep** short, veins brownish-green.

Editorial comment [U. Eggl]: The nomenclatural status of this name was differently interpreted



over the course of time. In the first edition of this handbook, this species is covered as *H. maxima*, while Bayer & Manning (2012a) and Bayer & Manning (2012b) used the name *H. pumila*, following its usage by Scott (1985), who followed advice by L. E. Codd. While the oldest name for this taxon is *Aloe pumila* Linné 1753, it unfortunately cannot be transferred to *Haworthia* for purely nomenclatural reasons because of the name *H. pumila* (Aiton) Haworth 1804, based on *Aloe arachnoidea* var. *pumila* Aiton 1789, which is a different taxon that is treated as a synonym of *Haworthia herbacea* (Miller) Stearn 1938 (Manning 2013). *H. margaritifera* is based on one of Linné's varieties of his *A. pumila*, and has the same type as *A. pumila* (Jarvis 2007).

Bayer (2010e) reports (under *H. pumila*) a casual find of a natural hybrid with *Astroloba muricata*/*congregata* (= ×*Astroworthia skinneri*).

**H. marginata** (Lamarck) Stearn (Cact. J. (Croydon) 7(2): 39, 1938). **Type:** [lecto — icono]: Commelin, *Praecludia Bot.*, t. 30, 1703. — **Distr:** RSA (Western Cape: Heidelberg); Fynbos vegetation. **I:** Bayer (1982: Fig. 65).

≡ *Aloe marginata* Lamarck (1783) ≡ *Tulista marginata* (Lamarck) G. D. Rowley (2013); **incl.** *Aloe albicans* Haworth (1804) ≡ *Apicra albicans* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia albicans* (Haworth) Haworth (1812); **incl.** *Haworthia laevis* Haworth (1821) ≡ *Haworthia marginata* var. *laevis* (Haworth) H. Jacobsen (1955); **incl.** *Haworthia ramifera* Haworth (1821) ≡ *Aloe ramifera* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthia marginata* var. *ramifera* (Haworth) H. Jacobsen (1955); **incl.** *Haworthia virescens* Haworth (1821) ≡ *Aloe virescens* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthia albicans* var. *virescens* (Haworth) Baker (1896) ≡ *Haworthia marginata* var. *virescens* (Haworth) Uitewaal (1939); **incl.** *Haworthia virescens* var. *minor* Haworth (1821).

[3] **Ros** stemless, slowly proliferating, to 20 cm tall; **L** 50–60, to 18 × 2 cm, lanceolate-deltoid, attenuate, spreading, pale brownish-green, smooth without tubercles; **Inf** sparsely branched, lax; **Fl** tube straight; **Tep** short, veins pinkish.

Bayer (2007b) and Bayer (2012c) and Marx (2016b) present evidence for hybridization with *H. minima* (see there for more information).

**H. marumiana** Uitewaal (Cact. Vetpl. (Amsterdam) 9: 20, 1940). **Type:** RSA, Western Cape (*Anonymus* s.n. in *SUG* 6610 [AMD]). — **Distr:** RSA (Western Cape, Eastern Cape: Great Karoo); Nama Karoo biome.

≡ *Haworthia arachnoidea* var. *marumiana* (Uitewaal) Halda (1997).

**H. marumiana** var. **archeri** (W. F. Barker ex M. B. Bayer) M. B. Bayer (*Haworthia Revisited*, 104, ills. (pp. 104–105), 1999). **Type:** RSA, Western Cape (*Archer* s.n. [NBG]). — **Distr:** RSA (Western Cape: SW Great Karoo). **I:** Bayer (1982: Fig. 4a, as *H. archeri*).

≡ *Haworthia archeri* W. F. Barker ex M. B. Bayer (1981); **incl.** *Haworthia archeri* var. *archeri*; **incl.** *Haworthia chibita* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia fraseri* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia nudata* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *marumiana*: **Ros** small, to 6 cm Ø; **L** brownish-green.

**H. marumiana** var. **batesiana** (Uitewaal) M. B. Bayer (*Haworthia Revisited*, 105, ill. (p. 106), 1999). **Type:** RSA, Eastern Cape (*Ferguson* s.n. [AMD]). — **Distr:** RSA (Western Cape, Eastern Cape); often on cliffs. **I:** Bayer (1982: Fig. 5, as *H. batesiana*).

≡ *Haworthia batesiana* Uitewaal (1948) ≡ *Haworthia reticulata* ssp. *batesiana* (Uitewaal) Halda (1997).

[1] Differs from var. *marumiana*: **Ros** smaller, to 5 cm Ø; **L** smooth, bright green with pale reticulation.

**H. marumiana** var. **dimorpha** (M. B. Bayer) M. B. Bayer (*Haworthia Revisited*, 106, ills., 1999). **Type:** RSA, Western Cape (Bayer 2092 [NBG]). — **Distr:** RSA (Western Cape: S Great Karoo, Touws River).

≡ *Haworthia archeri* var. *dimorpha* M. B. Bayer (1981) ≡ *Haworthia dimorpha* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *marumiana*: **Ros** to 12 cm Ø; **L** to 25, curving outwards (in cultivation).

**H. marumiana** var. *marumiana* — **Distr:** RSA (Eastern Cape: Great Karoo). **I:** Bayer (1982: Fig. 23).

**Incl.** *Haworthia borealis* M. Hayashi (2006); **incl.** *Haworthia marmorata* M. Hayashi (2006) ≡ *Haworthia marumiana* var. *marmorata* (M. Hayashi) Breuer (2016); **incl.** *Haworthia tarkasia* M. Hayashi (2006); **incl.** *Haworthia euchlora* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, very proliferous, to 7 cm Ø; **L** erect, incurved, ± soft, purplish-green, opaque, with reticulate pattern, margins and keel with spines; **Inf** to 20 cm; **Fl** smallish, white.

**H. marumiana** var. *reddii* (C. L. Scott) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 34, 2012). **Type:** RSA, Eastern Cape (Scott 8968 [PRE]). — **Distr:** RSA (interior of Eastern Cape). **I:** Scott (1994a: as *H. reddii*).

≡ *Haworthia reddii* C. L. Scott (1994) ≡ *Haworthia cymbiformis* var. *reddii* (C. L. Scott) M. B. Bayer (1999) ≡ *Haworthia batesiana* var. *reddii* (C. L. Scott) Breuer (2016); **incl.** *Haworthia fatreddii* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *marumiana*: **L** subdeltoïd, surface with reticulate pattern.

**H. marumiana** var. *viridis* M. B. Bayer (Haworthia Revisited, 107, ills., 1999). **Type:** RSA, Western Cape (Bayer 3620 [NGB]). — **Distr:** RSA (Western Cape: S Karoo).

**Incl.** *Haworthia viridis* Breuer (2011) (*nom. inval.*, ICN Art. 38.1a, 40.6).

[1] Differs from var. *marumiana*: **L** light green, narrow, more erect.

**H. marxii** Gildenhuis (Aloe 44(1): 4–5, ills., 2007). **Type:** RSA, Western Cape (Marx 605 [GRA]). — **Lit:** Marx (2008b). **Distr:** RSA (Western Cape: S of Laingsburg); Succulent Karoo vegetation, summer-flowering.

[1] **Ros** to 10 cm Ø, stemless, solitary, slow-growing; **L** 15–18, dark blue-grey to purplish-black, young semi-erect, later recurved and becoming

flattish, retuse, with an acuminate tip, end-area 2 × 2 cm, with 5–11 longitudinal silvery-white lines and small scattered flecks; **Inf** to 60 cm, unbranched, with up to 23 flowers; **Fl** to 15 mm, with straight tube; **Tep** tips only slightly recurving.

**H. minima** (Aiton) Haworth (Synops. Pl. Succ., 92, 1812). **Type:** [lecto — icono]: Dillenius, Hort. Eltham., t. 16: f. 18, 1732. — **Lit:** Bayer (2010f). **Distr:** RSA (Western Cape: Swellendam to Mosselbay); mainly in Fynbos, Albany Thicket and Succulent Karoo vegetations.

≡ *Aloe margaritifera* var. *minima* Aiton (1789) ≡ *Haworthia margaritifera* var. *minima* (Aiton) Uitewaal (1947) ≡ *Haworthia pumila* ssp. *minima* (Aiton) Halda (1997) ≡ *Tulista minima* (Aiton) Boatwright & J. C. Manning (2014); **incl.** *Aloe pumila* var.  $\beta$  Linné (1753); **incl.** *Aloe pumila* var.  $\gamma$  Linné (1753); **incl.** *Aloe margaritifera* var. *major* Aiton (1789) ≡ *Haworthia major* (Aiton) Duval (1809) ≡ *Apicra margaritifera* var. *major* (Aiton) Willdenow (1811) (*incorrect name*, ICN Art. 11.4); **incl.** *Aloe margaritifera* var. *minor* Aiton (1789) ≡ *Haworthia minor* (Aiton) Duval (1809) ≡ *Apicra minor* (Aiton) Steudel (1821) (*incorrect name*, Art. 11.4) ≡ *Aloe minor* (Aiton) Roemer & Schultes fil. (1829) ≡ *Haworthia margaritifera* var. *minor* (Aiton) Uitewaal (1947); **incl.** *Aloe margaritifera* var. *media* De Candolle (1799); **incl.** *Apicra granata* Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia granata* (Willdenow) Haworth (1819) ≡ *Aloe granata* (Willdenow) Roemer & Schultes fil. (1829) ≡ *Haworthia margaritifera* var. *granata* (Willdenow) Baker (1880); **incl.** *Haworthia brevis* Haworth (1819) ≡ *Aloe brevis* (Haworth) Roemer & Schultes fil. (1829); **incl.** *Haworthia erecta* Haworth (1819) ≡ *Aloe erecta* (Haworth) Salm-Dyck (1829) ≡ *Haworthia margaritifera* var. *erecta* (Haworth) Baker (1880); **incl.** *Haworthia granata* var. *polyphylla* Haworth (1821) ≡ *Haworthia margaritifera* subvar. *polyphylla* (Haworth) Von Poellnitz (1938); **incl.** *Aloe erecta* var. *laetivirens* Salm-Dyck (1834) ≡ *Haworthia margaritifera* subvar. *laetivirens* (Salm-Dyck) A. Berger (1908); **incl.** *Aloe granata* var. *major* Salm-Dyck (1834); **incl.** *Aloe granata* var. *minor* Salm-Dyck (1834) ≡ *Haworthia margaritifera* subvar. *minor* (Salm-Dyck) A. Berger

(1908); **incl.** *Haworthia margaritifera* var. *corallina* Hort. Peacock ex Baker (1880); **incl.** *Haworthia mutabilis* Von Poellnitz (1938); **incl.** *Haworthia mertonii* Breuer (2007)  $\equiv$  *Tulista marginata* var. *mertonii* (Breuer) Breuer (2016).

The names *H. major* and *H. minor* both date from 1809 at species rank and would have nomenclatural priority; their correct application is not completely resolved, however, and before a study of their proper typification has been made, the time is not yet ripe for a final decision.

Bayer (2007b), Bayer (2012c) and Marx (2016b) present evidence for hybridization with *H. marginata*, and *H. mertonii* Breuer is probably based on such hybrid individuals. Marx (2011a) speculates that *H. uitewaaliana* could also be such a hybrid, based on the discovery of an apparently hybrid population W of Riversdale. Bayer (2010e) reports naturally occurring hybrids with *Astroloba muricata/congregata*.

**H. minima** var. **minima** — **Distr:** RSA (Western Cape). **I:** Bayer (1982: Fig. 66).

**Incl.** *Haworthia opalina* M. Hayashi (2001)  $\equiv$  *Tulista opalina* (M. Hayashi) Breuer (2016); **incl.** *Haworthia flavens* Breuer (2010) (*nom. inval.*, ICN Art. 38.1a, 40.1); **incl.** *Haworthia obrata* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[3] **Ros** stemless, slowly proliferating, to 15 cm tall; **L** to 13  $\times$  1.5 cm, nearly as thick as wide, lanceolate-deltoid, attenuate, spreading, blue-green, surfaces scabrid with raised flattened non-confluent tubercles; **Inf** sparsely branched, lax, 30–40 cm; **Fl** tube straight; **Tep** short, veins pinkish.

**H. minima** var. **poellnitziana** (Uitewaal) M. B. Bayer (Haworthia Revisited, 213, ills., 1999). **Type:** RSA, Western Cape (*Anonymus* s.n. in *Stellenbosch University Garden 7796* [AMD]). — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo). **I:** Bayer (1982: Fig. 67, as *H. poellnitziana*).

$\equiv$  *Haworthia poellnitziana* Uitewaal (1939)  $\equiv$  *Tulista minima* var. *poellnitziana* (Uitewaal) Breuer (2016).

[3] Differs from var. *minima*: **L** slender, longer, to 18 cm, grey-green; **Tep** tips yellowish.

**H. mirabilis** (Haworth) Haworth (Synops. Pl. Succ., 95, 1812). **Type:** [neo — icono]: Curtis's Bot. Mag. 33: t. 1354, 1811. — **Lit:** Bayer (2012b); Bayer (2012d); Marx (2013a). **Distr:** RSA (Western Cape); Fynbos vegetation.

$\equiv$  *Aloe mirabilis* Haworth (1804)  $\equiv$  *Apicula mirabilis* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Haworthia retusa* var. *mirabilis* (Haworth) Halda (1997).

**H. mirabilis** var. **atrofusca** (G. G. Smith) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 34, 2012). **Type:** RSA, Western Cape (*Smith* 6169 [NBG]). — **Distr:** RSA (Western Cape: Riversdale). **I:** Bayer (1982: Fig. 22b, as *H. magnifica* var.).

$\equiv$  *Haworthia atrofusca* G. G. Smith (1948)  $\equiv$  *Haworthia magnifica* var. *atrofusca* (G. G. Smith) M. B. Bayer (1977).

[1] Differs from var. *mirabilis*: **L** brownish-green, tips bluntly rounded.

**H. mirabilis** var. **badia** (Von Poellnitz) M. B. Bayer (Haworthia Revisited, 109, ills., 1999). **Type:** [lecto — icono]: Kakteenkunde 1938: 76, ill, 1938. — **Distr:** RSA (Western Cape: Napier). **I:** Bayer (1982: Fig. 25b).

$\equiv$  *Haworthia badia* Von Poellnitz (1938)  $\equiv$  *Haworthia mirabilis* ssp. *badia* (Von Poellnitz) M. B. Bayer (1976); **incl.** *Haworthia hammeri* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *mirabilis*: **Ros** robust; **L** attenuate, retuse, smooth, deep shiny brown.

**H. mirabilis** var. **beukmanii** (Von Poellnitz) M. B. Bayer (Haworthia Revisited, 110, ills., 1999). **Type** [neo]: RSA, Western Cape (*Smith* 3969 [NBG]). — **Distr:** RSA (Western Cape: N of Caledon).

$\equiv$  *Haworthia emelyae* var. *beukmanii* Von Poellnitz (1940)  $\equiv$  *Haworthia mirabilis* fa. *beukmanii* (Von Poellnitz) Pilbeam (1983)  $\equiv$  *Haworthia beukmanii* (Von Poellnitz) M. Hayashi (2000).

[1] Differs from var. *mirabilis*: **Ros** very robust, to 12 cm Ø; **L** scabrid, strongly retuse, margins with short spines.

**H. mirabilis** var. **consanguinea** M. B. Bayer (Haworthia Revisited, 111, ills., 1999). **Type**: RSA, Western Cape (*Bayer* s.n. [NMG]). — **Distr**: RSA (Western Cape: Rivieronderend Mts.); often on cliffs.

≡ *Haworthia consanguinea* (M. B. Bayer) M. Hayashi (2000) ≡ *Haworthia caespitosa* var. *consanguinea* (M. B. Bayer) Breuer (2016).

[1] Differs from var. *mirabilis*: **Ros** small, proliferous; **L** soft, turgid.

**H. mirabilis** var. **heidelbergensis** (G. G. Smith) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 34, 2012). **Type**: RSA, Western Cape (*Dekenah* 230 in *Smith* 6566 [NMG]). — **Distr**: RSA (Western Cape: Heidelberg). **I**: Bayer (1982: Fig. 18, as *H. heidelbergensis*).

≡ *Haworthia heidelbergensis* G. G. Smith (1948) ≡ *Haworthia retusa* var. *heidelbergensis* (G. G. Smith) Halda (1997).

[1] Differs from var. *mirabilis*: Generally smaller; **Ros** stemless, proliferous, to 8 cm Ø; **L** more numerous, erect to recurved, 3–5 × 0.5–1 cm.

**H. mirabilis** var. **magnifica** (Von Poellnitz) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 34, 2012). **Type**: RSA, Western Cape (*Ferguson* s.n. [BOL]). — **Distr**: RSA (Western Cape: Riversdale). **I**: Bayer (1982: Fig. 22a, as *H. magnifica*).

≡ *Haworthia magnifica* Von Poellnitz (1933) ≡ *Haworthia maraisii* var. *magnifica* (Von Poellnitz) M. B. Bayer (1976) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia retusa* var. *magnifica* (Von Poellnitz) Halda (1997); **incl.** *Haworthia magnifica* var. *magnifica*; **incl.** *Haworthia splendens* var. *hansii* M. Hayashi (2011); **incl.** *Haworthia splendens* var. *masai* M. Hayashi (2011); **incl.** *Haworthia obserata* Marx (2014) ≡ *Haworthia magnifica* var. *obserata* (Marx) Breuer (2016).

[1] Differs from var. *mirabilis*: **Ros** stemless, slowly proliferating, to 8 cm Ø.

**H. mirabilis** var. **maraisii** (Von Poellnitz) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 34, 2012). **Incorrect name**, ICN Art. 11.4. **Type**: RSA, Western Cape (*Marais* s.n. [B [lecto: unpubl. ill.]]). — **Distr**: RSA (Western Cape: Robertson).

≡ *Haworthia maraisii* Von Poellnitz (1935) ≡ *Haworthia magnifica* var. *maraisii* (Von Poellnitz) M. B. Bayer (1977); **incl.** *Haworthia maraisii* var. *pubescens* Hort. Sheilam (s.a.) (*nom. inval.*, ICN Art. 29.1, 38.1a); **incl.** *Haworthia schuldtiana* Von Poellnitz (1937) ≡ *Haworthia maraisii* var. *schuldtiana* (Von Poellnitz) Breuer (2016); **incl.** *Haworthia sublimpidula* Von Poellnitz (1937); **incl.** *Haworthia whitesloaneana* Von Poellnitz (1937) ≡ *Haworthia schuldtiana* var. *whitesloaneana* (Von Poellnitz) Von Poellnitz (1940); **incl.** *Haworthia triebneriana* var. *diversicolor* Triebner & Von Poellnitz (1938) ≡ *Haworthia diversicolor* (Triebner & Poellnitz) M. Hayashi (2010) ≡ *Haworthia notabilis* var. *diversicolor* (Triebner & Von Poellnitz) Breuer (2016); **incl.** *Haworthia schuldtiana* var. *minor* Triebner & Von Poellnitz (1940); **incl.** *Haworthia schuldtiana* var. *robertsonensis* Von Poellnitz (1940); **incl.** *Haworthia schuldtiana* var. *simplicior* Von Poellnitz (1940); **incl.** *Haworthia schuldtiana* var. *sublaevis* Von Poellnitz (1940); **incl.** *Haworthia schuldtiana* var. *subtuberculata* Von Poellnitz (1940); **incl.** *Haworthia schuldtiana* var. *unilineata* Von Poellnitz (1940); **incl.** *Haworthia angustifolia* var. *subfalcata* Von Poellnitz ex Zantner (1951) (*nom. inval.*, ICN Art. 39.1); **incl.** *Haworthia calliantha* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *mirabilis*: **Ros** stemless, slowly proliferating, 4–7 cm Ø; **L** few to many, ovate-lanceolate, to 4 × 1 cm.

Editorial note [U. Eggli]: This name is unfortunately incorrect since several prioritable names have been treated as synonyms at the time of publication.

**H. mirabilis** var. **meiringii** (M. B. Bayer) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 35, 2012). **Type**: RSA, Western Cape (*Bayer* s.n. [NMG]). — **Distr**: RSA (Western Cape: Bonnievale). **I**: Bayer (1982: Fig. 22e, as *H. magnifica* var.).



≡ *Haworthia maraisii* var. *meiringii* M. B. Bayer (1976) ≡ *Haworthia magnifica* var. *meiringii* (M. B. Bayer) M. B. Bayer (1977) ≡ *Haworthia divergens* var. *meiringii* (M. B. Bayer) M. Hayashi (2000) ≡ *Haworthia meiringii* (M. B. Bayer) Breuer (2017); **incl.** *Haworthia meiringii* M. Hayashi (2000) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] Differs from var. *mirabilis*: **L** erect, incurved, green, spiny.

**H. mirabilis** var. **mirabilis** — **Distr:** RSA (Western Cape: Bredasdorp). **I:** Bayer (1982: Fig. 25a).

**incl.** *Haworthia triebneriana* Von Poellnitz (1936) ≡ *Haworthia mirabilis* var. *triebneriana* (Von Poellnitz) M. B. Bayer (1999); **incl.** *Haworthia willowmorensis* Von Poellnitz (1937); **incl.** *Haworthia triebneriana* var. *depauperata* Von Poellnitz (1938) ≡ *Haworthia depauperata* (Poellnitz) Breuer (2010) ≡ *Haworthia mirabilis* var. *depauperata* (Von Poellnitz) Breuer (2016); **incl.** *Haworthia triebneriana* var. *multituberculata* Von Poellnitz (1938); **incl.** *Haworthia triebneriana* var. *napiensis* Triebner & Von Poellnitz (1938) ≡ *Haworthia mirabilis* fa. *napiensis* (Triebner & Von Poellnitz) Pilbeam (1983); **incl.** *Haworthia triebneriana* var. *rubrodentata* Triebner & Von Poellnitz (1938) ≡ *Haworthia mirabilis* fa. *rubrodentata* (Triebner & Von Poellnitz) Pilbeam (1983); **incl.** *Haworthia triebneriana* var. *subtuberculata* Triebner & Von Poellnitz (1938); **incl.** *Haworthia triebneriana* var. *turgida* Triebner (1938); **incl.** *Haworthia nitidula* Von Poellnitz (1939); **incl.** *Haworthia triebneriana* var. *pulchra* Von Poellnitz (1940); **incl.** *Haworthia vernalis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, proliferous, to 7 cm Ø; **L** 10–15, 3–4 × 1.5 cm, dark green, markedly retuse, tips acute, face translucent and with lines, marginal spines turning reddish in sun; **Inf** slender, to 25 cm; **Fl** narrowly elongate, bud S-shaped, **ITep** pinched at the tips.

There is no single population that can be said to conform to the type illustration and hence the name is used for the many variants that do not conform to described varieties and their origins. Bayer (2012d) notes possible hybrids with *H. retusa*.

**H. mirabilis** var. **mundula** (G. G. Smith) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 35, 2012). **Type:** RSA (Smith 5479 [NBG]). — **Distr:** RSA (Western Cape: SW of Bredasdorp).

≡ *Haworthia mundula* G. G. Smith (1946) ≡ *Haworthia mirabilis* ssp. *mundula* (G. G. Smith) M. B. Bayer (1976).

[1] Differs from var. *mirabilis*: **L** less acuminate and with more rounded convex end-area.

**H. mirabilis** var. **notabilis** (Von Poellnitz) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 35, 2012). **Incorrect name**, ICN Art. 11.4. **Type:** B [lecto: unpubl. ill.]. — **Distr:** RSA (Western Cape: Robertson). **I:** Bayer (1982: Fig. 22f, as *H. magnifica* var.).

≡ *Haworthia notabilis* Von Poellnitz (1938) ≡ *Haworthia magnifica* var. *notabilis* (Von Poellnitz) M. B. Bayer (1977) ≡ *Haworthia intermedia* var. *notabilis* (Von Poellnitz) J. Esterhuizen (2003) ≡ *Haworthia maraisii* var. *notabilis* (Von Poellnitz) M. B. Bayer (1976); **incl.** *Haworthia intermedia* Von Poellnitz (1937) ≡ *Haworthia maculata* var. *intermedia* (Von Poellnitz) M. B. Bayer (1999) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia schuldiana* var. *erecta* Triebner & Von Poellnitz (1940); **incl.** *Haworthia nitidula* var. *opaca* Von Poellnitz (1948).

[1] Differs from var. *mirabilis*: **L** erect, green, turgid.

Editorial note [U. Eggl]: The name is incorrect because the prioritable *H. schuldiana* var. *erecta* was included as synonym at the time of publication.

**H. mirabilis** var. **paradoxa** (Von Poellnitz) M. B. Bayer (Aloe 34(1–2): 6, 1997). **Type** [neo]: RSA, Western Cape (*Ferguson* s.n. [BOL]). — **Distr:** RSA (Western Cape: Riversdale). **I:** Bayer (1982: Fig. 22g, as *H. magnifica* var.); Marx (2014b: Figs. 5–7, as *H. bobii*).

≡ *Haworthia paradoxa* Von Poellnitz (1933) ≡ *Haworthia maraisii* var. *paradoxa* (Von Poellnitz) M. B. Bayer (1976) (*nom. inval.*, ICN Art. 41.5) ≡ *Haworthia magnifica* var. *paradoxa* (Von Poellnitz) M. B. Bayer (1977); **incl.** *Haworthia jakubii* Breuer (2004) ≡ *Haworthia paradoxa* var. *jakubii* (Breuer)



Breuer (2016); **incl.** *Haworthia bobii* Breuer ex M. Hayashi (2014)  $\equiv$  *Haworthia badia* var. *bobii* (M. Hayashi) Breuer (2016); **incl.** *Haworthia joleneae* M. Hayashi (2014)  $\equiv$  *Haworthia badia* var. *joleneae* (M. Hayashi) Breuer (2016).

[1] Differs from var. *mirabilis*: **L** more densely maculate with opaque light coloured dots on both sides.

A population at Infanta is notable for having densely spined leaf surfaces.

**H. mirabilis** var. **scabra** (M. B. Bayer) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 35, 2012). **Type:** RSA, Western Cape (Bayer 1700 [NBG]). — **Distr:** RSA (Western Cape: Bredasdorp to Ashton area).

$\equiv$  *Haworthia heidelbergensis* var. *scabra* M. B. Bayer (1999)  $\equiv$  *Haworthia rossouwii* var. *scabra* (M. B. Bayer) Breuer (2016); **incl.** *Haworthia scabrada* Breuer (2010).

[1] Differs from var. *mirabilis*: **Ros** to 3 cm  $\varnothing$ ; **L** very dark green, erect or suberect, slightly scabrid along margins and keel.

**H. mirabilis** var. **splendens** (S. A. Hammer & J. D. Venter) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 35, 2012). **Type:** RSA, Western Cape (Venter 93/57 [NBG]). — **Lit:** Marx (2008a: as *H. magnifica* var.); Marx (2011b: as *H. magnifica* var.). **Distr:** RSA (Western Cape: Albertinia).

$\equiv$  *Haworthia magnifica* var. *splendens* S. A. Hammer & D. J. Venter (1998)  $\equiv$  *Haworthia splendens* (S. A. Hammer & D. J. Venter) M. Hayashi (2000); **incl.** *Haworthia splendens* var. *ingoii* M. Hayashi (2011).

[1] Differs from var. *mirabilis*: **L** with shiny raised tubercles.

**H. mirabilis** var. **sublineata** (Von Poellnitz) M. B. Bayer (Haworthia Revisited, 113, ills., 1999). **Type** [neo]: RSA, Western Cape (Smith 3966 [NBG]). — **Distr:** RSA (Western Cape: Bredasdorp).

$\equiv$  *Haworthia triebneriana* var. *sublineata* Von Poellnitz (1938)  $\equiv$  *Haworthia mirabilis* fa. *sublineata* (Von Poellnitz) Pilbeam (1983)  $\equiv$  *Haworthia sublineata* (Von Poellnitz) Breuer (2010).

[1] Differs from var. *mirabilis*: **L** long and slender.

**H. mirabilis** var. **toonensis** (M. B. Bayer) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 35, 2012). **Type:** RSA, Western Cape (Smith 6797 [NBG]). — **Distr:** RSA (Western Cape: Bredasdorp Distr.).

$\equiv$  *Haworthia heidelbergensis* var. *toonensis* M. B. Bayer (1999)  $\equiv$  *Haworthia maraisii* var. *toonensis* (M. B. Bayer) M. Hayashi (2000)  $\equiv$  *Haworthia toonensis* (M. B. Bayer) Breuer (2010); **incl.** *Haworthia toonensis* M. Hayashi (2000) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] Differs from var. *mirabilis*: **L** recurved, with a distinct transparent end-area.

**H. monticola** Fourcade (Trans. Roy. Soc. South Africa 21: 78, 1937). **Type:** RSA, Western Cape (Fourcade 2498 [K]). — **Distr:** RSA (Western Cape, Eastern Cape); mainly Fynbos vegetation.

$\equiv$  *Haworthia chloracantha* var. *monticola* (Fourcade) Halda (1997).

**H. monticola** var. **asema** M. B. Bayer (Haworthia Revisited, 117, ills., 1999). **Type:** RSA, Western Cape (Venter & de Vries 12 (85/83) [NBG]). — **Distr:** RSA (Western Cape: Ladismith Distr.).

$\equiv$  *Haworthia asema* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *monticola*: **L** smoother, more turgid, generally shorter, more uniformly grey-green; flowering very much earlier.

**H. monticola** var. **monticola** — **Distr:** RSA (Western Cape, Eastern Cape: E Little Karoo). **I:** Scott (1985: 57).

**Incl.** *Haworthia divergens* M. B. Bayer (1976); **incl.** *Haworthia bronkhorstii* M. Hayashi (2001)  $\equiv$  *Haworthia monticola* var. *bronkhorstii* (M. Hayashi) Breuer (2016); **incl.** *Haworthia baviens* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia corticosa* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia glabella* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia simofuri* M. Hayashi (2010) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] **Ros** stemless, proliferous, 2–4 cm Ø; **L** 30–40, elongate-lanceolate, 2–6 cm, tips incurving, margins and keel with small spines, upper face often with pellucid spots; **Inf** slender, to 30 cm; **Fl** laxly arranged, 15–20, white.

**H. mucronata** Haworth (Suppl. Pl. Succ., 50, 1819). **Type:** K [lecto — icono, publ. Brit. Cact. Succ. J. 1: 98, 1983]. — **Lit:** Bayer (2003b); Bayer (2010g). **Distr:** RSA (Western Cape: Little Karoo); Fynbos and Succulent Karoo vegetations.

≡ *Aloe mucronata* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthia altilinea* var. *mucronata* (Haworth) Von Poellnitz (1937).

**H. mucronata** var. **habdomadis** (Von Poellnitz) M. B. Bayer (*Haworthia Revisited*, 120, *ills.*, 1999). **Type** [neo]: RSA, Western Cape (*Barker & Lewis* s.n. ex cult. NBG 2764/32 [BOL]). — **Distr:** RSA (Western Cape: Little Karoo). **I:** Bayer (1982: Fig. 17a, as *H. habdomadis*). — Fig. 8.

≡ *Haworthia habdomadis* Von Poellnitz (1938) ≡ *Haworthia inconfluens* var. *habdomadis* (Von Poellnitz) M. B. Bayer (1976) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia habdomadis* var. *habdomadis*.

[1] Differs from var. *mucronata*: **L** tips rounded, margins and keel spiny.

**H. mucronata** var. **inconfluens** (Von Poellnitz) M. B. Bayer (*Haworthia Revisited*, 121, *ills.* (p. 122), 1999). **Type:** RSA, Western Cape (*Triebner* 1031 [B [lecto: unpubl. ill.]]). — **Distr:** RSA (Western

Cape: Little Karoo). **I:** Bayer (1982: Fig. 17b, as *H. habdomadis* var.).

≡ *Haworthia altilinea* fa. *inconfluens* Von Poellnitz (1938) ≡ *Haworthia mucronata* fa. *inconfluens* (Von Poellnitz) Von Poellnitz (1940) ≡ *Haworthia inconfluens* (Von Poellnitz) M. B. Bayer (1976) ≡ *Haworthia habdomadis* var. *inconfluens* (Von Poellnitz) M. B. Bayer (1977); **incl.** *Haworthia bijliana* var. *joubertii* Von Poellnitz (1937) ≡ *Haworthia setata* subvar. *joubertii* (Von Poellnitz) Von Poellnitz (1938) ≡ *Haworthia setata* var. *joubertii* (Von Poellnitz) H. Jacobsen (1960) (*nom. inval.*, ICN Art. 41.4); **incl.** *Haworthia mucronata* var. *rooibergensis* J. Esterhuizen & Battista (1999) ≡ *Haworthia rooibergensis* (J. Esterhuizen & Battista) M. Hayashi *ex Breuer* (2017); **incl.** *Haworthia integra* var. *standeri* J. Esterhuizen (2000) ≡ *Haworthia standeri* (J. Esterhuizen) M. Hayashi (2010); **incl.** *Haworthia mucronata* var. *calitzdorpensis* Breuer (2003) ≡ *Haworthia calitzdorpensis* (Breuer) M. Hayashi (2010) ≡ *Haworthia arachnoidea* var. *calitzdorpensis* (Breuer) Breuer (2016); **incl.** *Haworthia ernstii* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7); **incl.** *Haworthia crystallina* M. Hayashi (2006) ≡ *Haworthia inconfluens* var. *crystallina* (M. Hayashi) Breuer (2016); **incl.** *Haworthia allomadis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia calitzensis* M. Hayashi (2010) (*nom. inval.*, ICN Art. 61.1); **incl.** *Haworthia horrida* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia kotei* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia erii* M. Hayashi *ex Breuer* (2017) (*nom. inval.*, ICN Art. 36.2, 40.1) ≡ *Haworthia rooibergensis* var. *erii* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 36.2, 40.1).

[1] Differs from var. *mucronata*: **L** pale green, often without **Sp**.

**H. mucronata** var. **morrissiae** (Von Poellnitz) Von Poellnitz (*Repert. Spec. Nov. Regni Veg.* 49 (1–4): 29, 1940). **Type:** B [lecto: unpubl. ill.]. — **Distr:** RSA (Western Cape: Little Karoo). **I:** Bayer (1982: Fig. 17c, as *H. habdomadis* var.).

≡ *Haworthia altilinea* var. *morrissiae* Von Poellnitz (1938) ≡ *Haworthia inconfluens* var. *morrissiae* (Von Poellnitz) M. B. Bayer (1976) ≡ *Haworthia habdomadis* var. *morrissiae* (Von



**Fig. 8** *Haworthia mucronata* var. *habdomadis*. (Copy-right: E. J. Van Jaarsveld)



**Fig. 9** *Haworthia mucronata* var. *mucronata*. (Copy-right: E. J. Van Jaarsveld)

Poellnitz) M. B. Bayer (1977); **incl.** *Haworthia sakaii* M. Hayashi (2000).

[1] Differs from var. *mucronata*: **L** bright to emerald-green with brownish tips.

**H. mucronata** var. *mucronata* — **Distr:** RSA (Western Cape: Little Karoo). **I:** Bayer (1982: Fig. 41a, as *H. unicolor*). — Fig. 9.

**Incl.** *Haworthia limpida* Haworth (1819)  $\equiv$  *Aloe limpida* (Haworth) Roemer & Schultes fil. (1829)  $\equiv$  *Haworthia altilinea* var. *limpida* (Haworth) Von Poellnitz (1937)  $\equiv$  *Haworthia mucronata* var. *limpida* (Haworth) Von Poellnitz (1940); **incl.** *Haworthia integra* Von Poellnitz (1933)  $\equiv$  *Haworthia reticulata* var. *integra* (Von Poellnitz) Halda (1997); **incl.** *Haworthia unicolor* Von Poellnitz (1937); **incl.** *Haworthia altilinea* fa. *typica* Von Poellnitz (1938) (*nom. inval.*, ICN Art. 24.3)  $\equiv$  *Haworthia mucronata* fa. *typica* (Von Poellnitz) Von Poellnitz (1940) (*nom. inval.*, ICN Art. 24.3); **incl.** *Haworthia mclarenii* Von Poellnitz (1939)  $\equiv$  *Haworthia chloracantha* var. *mclarenii* (Von Poellnitz) Halda (1997); **incl.** *Haworthia tradouwensis* Breuer (2003)  $\equiv$  *Haworthia cangoensis* var. *tradouwensis* (Breuer) Breuer (2016) (*nom. inval.*, ICN Art. 35.1); **incl.** *Haworthia armata* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia confluens* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia montagua* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, proliferous, 6–12 cm  $\varnothing$ ; **L** 30–45, soft, incurved, broadly ovate-lanceolate,

slightly pellucid, with translucent margins and keel, both often spiny; **Inf** robust, to 40 cm; **Fl** numerous, closely arranged, broad and flat across the base of the tube, white with green venation.

Here belongs *H. aristata* in the sense of Scott (1980) and Scott (1985).

**H. mucronata** var. *rycroftiana* (M. B. Bayer) M. B. Bayer (*Haworthia Revisited*, 124, ills., 1999). **Type:** RSA, Western Cape (Bayer 1701 [NBG]). — **Distr:** RSA (Western Cape: Little Karoo). **I:** Bayer (1982: Fig. 34, as *H. rycroftiana*).  $\equiv$  *Haworthia rycroftiana* M. B. Bayer (1981). [1] Differs from var. *mucronata*: **Ros** compact; **L** shorter, broader and more turgid.

**H. mutica** Haworth (Revis. Pl. Succ., 55, 1821). **Type:** K [lecto — icono, publ. *Excelsa* 8: 50, 1978]. — **Distr:** RSA (Western Cape); Fynbos vegetation. **I:** Bayer (1982: Fig. 26).

$\equiv$  *Aloe mutica* (Haworth) Roemer & Schultes fil. (1829)  $\equiv$  *Haworthia retusa* var. *mutica* (Haworth) Baker (1896); **incl.** *Haworthia otzenii* G. G. Smith (1945).

[1] **Ros** stemless, solitary, 6–8 cm  $\varnothing$ ; **L** 12–15, 6  $\times$  1.5 cm, retuse, brownish-green, in habitat developing a purplish cloudiness, barely pellucid with several longitudinal lines, tip blunt; **Inf** to 20 cm; **Fl** white with brownish veins.

Plants described as *H. groenewaldii* should probably be regarded as a variety of *H. mutica*.

**H. nigra** (Haworth) Baker (J. Linn. Soc., Bot. 18(109): 203, 1880). **Type:** RSA, Western Cape? (Bowie s.n. [[lecto — icono]: K [drawing]]). — **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape), Fynbos, Albany Thicket and Nama Karoo vegetations.

$\equiv$  *Apicra nigra* Haworth (1825) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Aloe nigra* (Haworth) Roemer & Schultes fil. (1829)  $\equiv$  *Haworthia venosa* ssp. *nigra* (Haworth) Halda (1997)  $\equiv$  *Haworthia viscosa* ssp. *nigra* (Haworth) Halda (1998)  $\equiv$  *Haworthiopsis nigra* (Haworth) G. D. Rowley (2013).

**H. nigra** var. *diversifolia* (Triebner & Von Poellnitz) Uitewaal (*Succulenta* 1948: 51, 1948).

**Type** [neo]: RSA, Eastern Cape (*Bruyns* s.n. in *Karoo Garden* 435/75 [NBG]). — **Distr**: RSA (Western Cape, Northern Cape, Eastern Cape). **I**: Scott (1985: 30, as *H. nigra*); Gildenhuis (2017: 51–52, as *Haworthiopsis*).

≡ *Haworthia diversifolia* Von Poellnitz (1937) ≡ *Haworthia schmidtiana* var. *diversifolia* (Triebner & Von Poellnitz) Von Poellnitz (1938) ≡ *Haworthiopsis nigra* var. *diversifolia* (Von Poellnitz) G. D. Rowley (2013); **incl.** *Haworthia schmidtiana* fa. *nana* Von Poellnitz (1938) ≡ *Haworthia nigra* fa. *nana* (Von Poellnitz) Uitewaal (1948).

[2] Differs from var. *nigra*: **L** more tightly appressed to the stem, greyish-green, tubercles pale and confluent in transverse bands.

**H. nigra** var. **elongata** (Von Poellnitz) Uitewaal (Succulenta 1948: 51, 1948). **Type** [neo]: RSA, Eastern Cape (*Van Jaarsveld & Marthinus* 7913 [NBG]). — **Distr**: RSA (Eastern Cape). **I**: Gildenhuis (2017: 52, as *Haworthiopsis*).

≡ *Haworthia schmidtiana* var. *elongata* Von Poellnitz (1938) ≡ *Haworthiopsis nigra* var. *elongata* (Von Poellnitz) G. D. Rowley (2013).

[2] Differs from var. *nigra*: **Ros** elongated, stems leafy.

**H. nigra** var. **nigra** — **Distr**: RSA (Eastern Cape: Karoo). **I**: Bayer (1982: Fig. 55); Gildenhuis (2017: 49–50, as *Haworthiopsis*).

**Incl.** *Haworthia schmidtiana* Von Poellnitz (1929) ≡ *Haworthia nigra* var. *schmidtiana* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia schmidtiana* var. *angustata* Von Poellnitz (1937) ≡ *Haworthia nigra* var. *angustata* (Von Poellnitz) Uitewaal (1948) ≡ *Haworthia nigra* fa. *angustata* (Von Poellnitz) Pilbeam (1983); **incl.** *Haworthia schmidtiana* var. *suberecta* Von Poellnitz (1937) ≡ *Haworthia nigra* var. *suberecta* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia schmidtiana* var. *pusilla* Von Poellnitz (1938) ≡ *Haworthia nigra* var. *pusilla* (Von Poellnitz) Uitewaal (1948); **incl.** *Haworthia ryneveldii* Von Poellnitz (1939); **incl.** *Haworthia eonigra* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[2] **Ros** usually caulescent, slowly proliferating or often stoloniferous, to 5 cm tall or

occasionally taller; **L** to 3 × 1.5 cm, ovate-deltoid, erect or recurved-spreading, blackish to grey-green, opaque, surfaces scabrid with distinct raised non-confluent concolorous tubercles; **Inf** simple, lax, to 40 cm; **Fl** erect, tube obcapitate, **ITep** revolute.

**H. nortieri** G. G. Smith (J. South Afr. Bot. 12: 13, 1946). **Type**: RSA, Western Cape (*Smith* 1676a [NBG]). — **Lit**: Bayer (2004b); Marx (2009b). **Distr**: RSA (Northern Cape, Western Cape); mainly Fynbos and Succulent Karoo vegetations.

≡ *Haworthia mucronata* var. *nortieri* (G. G. Smith) Halda (1997).

**H. nortieri** var. **albispina** (M. Hayashi) M. B. Bayer (*Haworthia Update* Vol. 7, Part 4, 35, 2012). **Type**: RSA, Western Cape (*Hayashi* 02-48 [Res. Inst. Evol. Biol., Tokyo [TUAT]]). — **Distr**: RSA (Western Cape: E of Laingsburg).

≡ *Haworthia albispina* M. Hayashi (2002) ≡ *Haworthia pehlemanniae* var. *albispina* (M. Hayashi) Breuer (2016).

[1] Differs from var. *nortieri*: **L** with prominent white spines.

**H. nortieri** var. **devriesii** (Breuer) M. B. Bayer (*Haworthia Update* Vol. 7, Part 4, 36, 2012). **Type**: RSA, Western Cape (*de Vries* 643 in *Breuer* 6930 [Res. Inst. Evol. Biol. Tokyo [TUAT]]). — **Distr**: RSA (Western Cape: N of Prince Albert).

≡ *Haworthia devriesii* Breuer (2003).

[1] Differs from var. *nortieri*: **Ros** solitary, sunken into the soil.

**H. nortieri** var. **globosiflora** (G. G. Smith) M. B. Bayer (*Haworthia Handb.*, 119, 1976). **Type**: RSA, Western Cape (*Smith* 7198 [NBG]). — **Distr**: RSA (Western Cape: N Ceres Karoo). **I**: Bayer (1982: Fig. 27b).

≡ *Haworthia globosiflora* G. G. Smith (1950).

[1] Differs from var. *nortieri*: **Ros** compact; **L** ovate, with translucent dots; **Fl** ovoid to globose.

**H. nortieri** var. **nortieri** — **Distr**: RSA (Northern Cape, N Western Cape: Namaqualand). **I**: Bayer (1982: Fig. 27a).



**Incl.** *Haworthia nortieri* var. *giftbergensis* G. G. Smith (1950)  $\equiv$  *Haworthia giftbergensis* (G. G. Smith) M. Hayashi (2007); **incl.** *Haworthia nortieri* var. *montana* G. G. Smith (1950); **incl.** *Haworthia agnis* Battista (2002)  $\equiv$  *Haworthia nortieri* var. *agnis* (Battista) Breuer (2016); **incl.** *Haworthia lateritia* M. Hayashi (2004); **incl.** *Haworthia montana* M. Hayashi (2005) (*nom. inval.*, ICN Art. 40.7)  $\equiv$  *Haworthia nortieri* var. *montana* (M. Hayashi) Breuer (2016) (*nom. inval.*, ICN Art. 40.7).

[1] **Ros** stemless, proliferous, 3–5 cm  $\varnothing$ ; **L** 25–45, soft, suberect, 6  $\times$  0.75 cm, ovate-lanceolate to obovate, pale to purplish-green, with translucent spots, margins and keel with small spines; **Inf** slender, to 30 cm; **Fl** 15–20, greyish-white, throat yellowish.

**H. nortieri** var. **pehlemanniae** (C. L. Scott) M. B. Bayer (*Haworthia Revisited*, 130, *ills.*, 1999). **Type:** RSA, Western Cape (*Scott* 7450 [PRE]). — **Distr:** RSA (Western Cape: Laingsburg).  $\equiv$  *Haworthia pehlemanniae* C. L. Scott (1982)  $\equiv$  *Haworthia arachnoidea* var. *pehlemanniae* (C. L. Scott) Halda (1997).

[1] Differs from var. *nortieri*: **L** greyish-green, unspotted.

**H. outeniquensis** M. B. Bayer (*Haworthia Revisited*, 130–131, *ills.*, 1999). **Type:** RSA, Western Cape (*Venter & al.* 94/61 [NBG]). — **Distr:** RSA (Western Cape: Oudtshoorn Distr.); Fynbos vegetation.

**Incl.** *Haworthia heroldia* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, 4–6 cm  $\varnothing$ , proliferous; **L** erect to suberect, to 6  $\times$  0.6–1 cm, 2–3 mm thick, incurving tips with a 2 mm long terminal awn, surfaces with pellucid anastomosing dots, yellowish-green, upper face convex with 4–5 prominent rows of conspicuous pellucid dots, lower face convex with 3–6 rows of pellucid dots, with a sharper keel with spines to 1 mm, margins similarly spined; **Inf** with 7–15 flowers; **Ped** 4–6 mm; **Per** white and yellowish-green, 15 mm.

**H. parksiana** Von Poellnitz (*Repert. Spec. Nov. Regni Veg.* 41: 205–206, 1937). **Type:**

RSA, Western Cape (*Helms* s.n. in *Parks* 636/32 [B [lecto: *ill. publ. Desert Pl. Life* 10: 48, 1938]]). — **Distr:** RSA (Western Cape: Great Brak); Fynbos vegetation. **I:** Bayer (1982: Fig. 28).

[1] **Ros** stemless, proliferous, 3–4 cm  $\varnothing$ ; **L** 25–35, triangular, sublanceolate, 1.5–3 cm, blackish-green, sharply recurved, minutely tubercled, tip barely pointed; **Inf** slender, to 20 cm; **Fl** few, narrow, whitish with dull greenish venation.

**H. pubescens** M. B. Bayer (*J. South Afr. Bot.* 38: 129–130, *ills.* (pp. 126–127), 1973). **Type:** RSA, Western Cape (*Bayer* s.n. in *Karoo Garden* 112/70 [NBG]). — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo). **I:** Bayer (1982: Fig. 29).

[1] **Ros** stemless, rarely proliferating, to 4 cm  $\varnothing$ ; **L** 20–35, ovate-lanceolate, 5  $\times$  0.8 cm, shortly incurved, opaque grey-green, covered with minute spines; **Inf** to 20 cm; **Fl** 10–15, white with pinkish venation, upper **Tep** tips flaring.

**H. pulchella** M. B. Bayer (*J. South Afr. Bot.* 39: 232, 1973). **Type:** RSA, Western Cape (*Bayer* 162 in *Karoo Garden* 43/71 [NBG]). — **Distr:** RSA (Western Cape); mainly Succulent Karoo vegetation.

$\equiv$  *Haworthia chloracantha* var. *pulchella* (M. B. Bayer) Halda (1997).

**H. pulchella** var. **globifera** M. B. Bayer (*Haworthia Revisited*, 136, *ill.*, 1999). **Type:** RSA, Western Cape (*Bruyns* 7338 [BOL]). — **Distr:** RSA (Western Cape: Anysberg).

$\equiv$  *Haworthia globifera* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *pulchella*: **Ros** glabrous, slightly caulescent, forming clusters.

**H. pulchella** var. **pulchella** — **Distr:** RSA (Western Cape: Touws Rivier). **I:** Bayer (1982: Fig. 30).

[1] **Ros** stemless, occasionally proliferous, to 5 cm  $\varnothing$ ; **L** 30–45, narrowly triangular, incurved, coriaceous, dark to emerald-green, with block-patterned reticulation, margins and keel with pronounced whitish spines; **Inf** slender, to 30 cm; **Fl** 15–20, white.





**Fig. 10** *Haworthia pungens*. (Copyright: E. J. Van Jaarsveld)

**H. pungens** M. B. Bayer (*Haworthia* Revisited, 188–189, ills., 1999). **Type:** RSA, Eastern Cape (*Bruyns* 7090 [BOL]). — **Distr:** RSA (Eastern Cape: Willowmore); mainly Fynbos vegetation. **I:** Gildenhuis (2017: 48, as *Haworthiopsis*). – Fig. 10.

≡ *Tulista pungens* (M. B. Bayer) G. D. Rowley (2013) ≡ *Haworthiopsis pungens* (M. B. Bayer) Boatwright & J. C. Manning (2014).

[2] **Ros** to 6 cm Ø, caulescent, proliferating; **L** many, usually in 5 (rarely 3) rows, to 5 × 1.8 cm, spreading, smooth, rigid, sharp-pointed, green in the shade, darkening and reddening in the sun; **Inf** simple, to 30 cm; **Fl** with straight tube; **ITep** revolute.

Similar to *H. viscosa* and superficially reminiscent of the genus *Astroloba*.

**H. pygmaea** Von Poellnitz (Repert. Spec. Nov. Regni Veg. 27: 132, 1929). **Type** [neo]: RSA, Western Cape (*Fourcade* 4759 [BOL]). — **Distr:** RSA (Western Cape); mainly Fynbos vegetation.

**H. pygmaea** var. **acuminata** (M. B. Bayer) M. B. Bayer (*Haworthia* Update Vol. 7, Part 4, 36, 2012). **Type:** RSA (*Bayer* s.n. [NBG †?]). — **Distr:** RSA (Western Cape: Albertinia). **I:** Bayer (1982: Fig. 33b, as *H. retusa* var.).

≡ *Haworthia retusa* fa. *acuminata* M. B. Bayer (1976) ≡ *Haworthia retusa* var. *acuminata* (M. B. Bayer) M. B. Bayer (1982) ≡ *Haworthia magnifica* var. *acuminata* (M. B. Bayer) M. B. Bayer (1997) ≡

*Haworthia acuminata* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *pygmaea*: **L** with long acuminate truncate end-area.

**H. pygmaea** var. **argenteo-maculosa** (G. G. Smith) M. B. Bayer (*Aloe* 34(1–2): 6, 1997). **Type:** RSA, Western Cape (*Emett* s.n. [NBG 68037, PRE]). — **Distr:** RSA (Western Cape: Albertinia). **I:** Bayer (1976: 68, as *H. dekenahii* var.).

≡ *Haworthia dekenahii* var. *argenteo-maculosa* G. G. Smith (1945) ≡ *Haworthia retusa* fa. *argenteo-maculosa* (G. G. Smith) M. B. Bayer (1976); **incl.** *Haworthia silviae* M. Hayashi (2000).

[1] Differs from var. *pygmaea*: **L** almost smooth, conspicuously white-spotted.

**H. pygmaea** var. **dekenahii** (G. G. Smith) M. B. Bayer (*Haworthia* Update Vol. 7, Part 4, 36, 2012). **Type:** RSA, Western Cape (*Smith* 5489 [NBG, PRE]). — **Distr:** RSA (Western Cape: Albertinia). **I:** Bayer (1982: Fig. 33c, as *H. retusa* var.).

≡ *Haworthia dekenahii* G. G. Smith (1944) ≡ *Haworthia retusa* var. *dekenahii* (G. G. Smith) M. B. Bayer (1982) ≡ *Haworthia magnifica* var. *dekenahii* (G. G. Smith) M. B. Bayer (1997); **incl.** *Haworthia enigma* M. Hayashi (2002) ≡ *Haworthia atrofusca* var. *enigma* (M. Hayashi) Breuer (2016); **incl.** *Haworthia magnifica* var. *pseudomutica* Breuer (2002) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] Differs from var. *pygmaea*: **L** with raised tubercles and silvery flecks, tips bluntly rounded.

**H. pygmaea** var. **fusca** (Breuer) M. B. Bayer (*Haworthia* Update Vol. 7, Part 4, 36, 2012). **Type:** RSA, Western Cape (*Breuer* 8971 [GRA]). — **Distr:** RSA (Western Cape: W of Albertinia).

≡ *Haworthia fusca* Breuer (2004) ≡ *Haworthia retusa* var. *fusca* (Breuer) Breuer (2016).

[1] Differs from var. *pygmaea*: **Ros** more compact; **L** broader and shorter.

**H. pygmaea** var. **pygmaea** — **Distr:** RSA (Western Cape: Mossel Bay). **I:** Bayer (1982: Fig. 31).

**Incl.** *Haworthia pygmaea* fa. *crystallina* Pilbeam (1983); **incl.** *Haworthia pygmaea* fa. *major* Pilbeam (1983) (*nom. inval.*, ICN Art. 40.1); **incl.** *Haworthia asperata* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, slowly proliferating, 6–10 cm Ø; **L** 12–15, 6 × 1.8 cm, retuse, round-tipped, surface pellucid with obscure raised tubercles, sometimes intensely papillose; **Inf** robust, to 30 cm; **Fl** 15–20, white with greenish veins.

**H. pygmaea** var. **vincentii** (Breuer) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 36, 2012). **Type:** RSA, Western Cape (*de Vries* 71 in *Breuer* 5424 [GRA]). — **Lit:** *Vries* (2010). **Distr:** RSA (Western Cape: E of Albertinia); Fynbos vegetation. **I:** Hayashi (2002: Fig. 2, as *H. esterhuizenii*); Marx (2014b: Figs. 26–30, as *H. esterhuizenii* and *H. vincentii*).

≡ *Haworthia vincentii* Breuer (2004); **incl.** *Haworthia esterhuizenii* M. Hayashi (2002) ≡ *Haworthia pygmaea* var. *esterhuizenii* (M. Hayashi) Breuer (2016); **incl.** *Haworthia albertinensis* Breuer (2002) (*nom. inval.*, ICN Art. 39.1, 40.1).

[1] Differs from var. *pygmaea*: **Ros** smaller; **L** more strongly patterned.

**H. reinwardtii** (Salm-Dyck) Haworth (Revis. Pl. Succ., 53, 1821). **Type:** [neo — icono]: Salm-Dyck, Monogr. Gen. Aloes & Mesembr. 1: Aloe t. 12 (Sect. 6: 16), 1836. — **Distr:** RSA (Eastern Cape); Albany Thicket and Savanna vegetations.

≡ *Aloe reinwardtii* Salm-Dyck (1821) ≡ *Haworthiopsis reinwardtii* (Salm-Dyck) G. D. Rowley (2013).

**H. reinwardtii** fa. **chalumnensis** (G. G. Smith) M. B. Bayer (Haworthia Handb., 106, 1976). **Type:** RSA, Eastern Cape (*Smith* 513 [NBG, PRE]). — **Distr:** RSA (Eastern Cape: Chalumna). **I:** Bayer (1982: Fig. 57b); Gildenhuis (2017: 31, as *Haworthiopsis*).

≡ *Haworthia reinwardtii* var. *chalumnensis* G. G. Smith (1943) ≡ *Haworthiopsis reinwardtii* fa. *chalumnensis* (G. G. Smith) Gildenhuis & Klopper (2016).

[2] Differs from var. *reinwardtii*: **L** elongate, incurved, conspicuously tuberculate.

**H. reinwardtii** fa. **kaffirdriftensis** (G. G. Smith) M. B. Bayer (Haworthia Handb., 126, 1976). **Type:** RSA, Eastern Cape (*Smith* 3364 [NBG, PRE]). — **Distr:** RSA (Eastern Cape: Fish River). **I:** Bayer (1982: Fig. 57c); Gildenhuis (2017: 32, as *Haworthiopsis*).

≡ *Haworthia reinwardtii* var. *kaffirdriftensis* G. G. Smith (1943) ≡ *Haworthiopsis reinwardtii* fa. *kaffirdriftensis* (G. G. Smith) Gildenhuis & Klopper (2016).

[2] Differs from var. *reinwardtii*: Outer side of **L** with tubercles in longitudinal rows.

**H. reinwardtii** fa. **olivacea** (G. G. Smith) M. B. Bayer (Haworthia Handb., 142, 1976). **Type:** RSA, Eastern Cape (*Smith* 5260 [NBG, PRE]). — **Distr:** RSA (Eastern Cape: Fish River). **I:** Bayer (1976: 66); Gildenhuis (2017: 33–34, as *Haworthiopsis*).

≡ *Haworthia reinwardtii* var. *olivacea* G. G. Smith (1944) ≡ *Haworthia olivacea* (G. G. Smith) Breuer (2010) ≡ *Haworthiopsis reinwardtii* fa. *olivacea* (G. G. Smith) Gildenhuis & Klopper (2016) ≡ *Haworthiopsis reinwardtii* var. *olivacea* (G. G. Smith) Breuer (2016).

[2] Differs from var. *reinwardtii*: **L** olive-green, relatively smooth, tubercles rounder and sparser.

**H. reinwardtii** fa. **zebrina** (G. G. Smith) M. B. Bayer (Nation. Cact. Succ. J. 32(1): 18, 1977). **Type:** RSA, Eastern Cape (*Smith* 5258 [NBG, PRE]). — **Distr:** RSA (Eastern Cape: Fish River). **I:** Bayer (1976: 65).

≡ *Haworthia reinwardtii* var. *zebrina* G. G. Smith (1944).

[2] Differs from var. *reinwardtii*: Outside of **L** with tubercles conspicuous in prominent transverse white bands.

Gildenhuis (2017: 33–34) does no longer accept fa. *zebrina*, which he interpretes merely as selected clones of fa. *olivacea*, probably to be recognized at the horticultural level.

**H. reinwardtii** var. **brevicula** G. G. Smith (J. South Afr. Bot. 10: 11, 1944). **Type:** RSA, Eastern Cape (*Smith* 3138 [NBG, PRE]). — **Distr:** RSA (Eastern Cape: Grahamstown). **I:** Bayer



**Fig. 11** *Haworthia reinwardtii* var. *reinwardtii*. (Copy-right: E. J. Van Jaarsveld)

(1982: Fig. 57f); Gildenhuis (2017: 34–35, as *Haworthiopsis*).

≡ *Haworthia reinwardtii* fa. *brevicula* (G. G. Smith) Pilbeam (1975) (*nom. inval.*, ICN Art. 41.5) ≡ *Haworthia brevicula* (G. G. Smith) Breuer (2010) ≡ *Haworthiopsis reinwardtii* var. *brevicula* (G. G. Smith) G. D. Rowley (2013); **incl.** *Haworthia reinwardtii* var. *diminuta* G. G. Smith (1948) ≡ *Haworthia reinwardtii* fa. *diminuta* (G. G. Smith) Pilbeam (1975) (*nom. inval.*, ICN Art. 41.5).

[2] Differs from var. *reinwardtii*: **Ros** small, to 10 cm tall and 4 cm Ø.

**H. reinwardtii** var. **reinwardtii** — **Distr:** RSA (Eastern Cape). **I:** Bayer (1982: Fig. 57a); Gildenhuis (2017: 29–30, as *Haworthiopsis*). — Fig. 11.

**Incl.** *Haworthia reinwardtii* var. *major* hort. ex Baker (1880); **incl.** *Haworthia reinwardtii* var. *archibaldiae* Von Poellnitz (1937); **incl.** *Haworthia reinwardtii* var. *pulchra* Von Poellnitz (1937); **incl.** *Haworthia reinwardtii* var. *peddiensis* G. G. Smith (1943); **incl.** *Haworthia reinwardtii* var. *triebneri* Resende (1943); **incl.** *Haworthia reinwardtii* var. *valida* G. G. Smith (1943); **incl.** *Haworthia reinwardtii* var. *haworthii* Resende (1943) (*nom. illeg.*, ICN Art. 52.1, 26.1); **incl.** *Haworthia reinwardtii* var. *grandicula* G. G. Smith (1944).

[2] **Ros** to 10 cm Ø, caulescent, to 20 cm tall, proliferating; **L** numerous, to 7 × 2 cm, ratio stem diameter : leaf width = 1:1.2, **L** erectly spreading or incurved, scabrid, brownish-green, usually

with flattened scale-like tubercles; **Inf** simple or occasionally compound, to 30 cm; **Fl** 15–20, tube obcapitate, curved, **ITep** revolute.

**H. reticulata** (Haworth) Haworth (Synops. Pl. Succ., 94, 1812). **Type:** [neo — icono]: Curtis's Bot. Mag. 32: t. 1314, 1810. — **Distr:** RSA (Western Cape); Succulent Karoo vegetation.

≡ *Aloe reticulata* Haworth (1804) ≡ *Aloe arachnoidea* var. *reticulata* (Haworth) Ker Gawler (1811) ≡ *Apicra reticulata* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4).

**H. reticulata** var. **attenuata** M. B. Bayer (*Haworthia Revisited*, 140, ills., 1999). **Type:** RSA, Western Cape (*Smith* 3979 [NBG]). — **Distr:** RSA (Western Cape: Bonnievale).

[1] Differs from var. *reticulata*: **L** longer, more slender.

**H. reticulata** var. **hurlingii** (Von Poellnitz) M. B. Bayer (*New Haworthia Handb.*, 52, 1982). **Type:** RSA, Western Cape (*Hurling* s.n. [B [lecto: ill., publ. Desert Pl. Life 10: 125, 1938]]). — **Distr:** RSA (Western Cape: W of Bonnievale). **I:** Bayer (1982: Fig. 32b).

≡ *Haworthia hurlingii* Von Poellnitz (1937).

[1] Differs from var. *reticulata*: **Ros** small, to 3 cm Ø; **L** obtuse.

**H. reticulata** var. **reticulata** — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo). **I:** Bayer (1982: Fig. 32a).

**Incl.** *Aloe pumilio* Jacquin (1804) ≡ *Apicra pumilio* (Jacquin) Willdenow (1811) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia hurlingii* var. *ambigua* Triebner & Von Poellnitz (1938); **incl.** *Haworthia reticulata* var. *acuminata* Von Poellnitz (1938); **incl.** *Haworthia guttata* Uitewaal (1947); **incl.** *Haworthia oxygona* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** proliferous, sometimes with a short stem, to 8 cm Ø; **L** 25–40, lanceolate-acuminate, 6 × 1 cm, firmly suberect, incurved, yellowish-green, opaque with reticulate to mottled patterning, reddening in the sun, margins and keel frequently with short spines; **Inf** to 25 cm; **Fl** 20–30, large, white to pinkish, buds arcuate with flattened tips.

**H. reticulata** var. **subregularis** (Baker) Pilbeam (Haworthia and Astroloba Coll. Guide, 116, 1983). **Type:** [lecto — icono]: Refug. Bot. 4: t. 232, 1871. — **Distr:** RSA (Western Cape: Worcester).

≡ *Haworthia subregularis* Baker (1871); **incl.** *Haworthia haageana* Von Poellnitz (1930); **incl.** *Haworthia haageana* var. *subreticulata* Von Poellnitz (1937).

[1] Differs from var. *reticulata*: **Ros** >10 cm Ø; **L** more suberect to spreading.

**H. retusa** (Linné) Duval (Pl. Succ. Horto Alencon., 7, 1809). **Type:** [lecto — icono]: Commelin, Horti Med. Amstelod. 2: 11, t. 6, 1701. — **Distr:** RSA (Western Cape); Fynbos vegetation.

≡ *Aloe retusa* Linné (1753) ≡ *Catevala retusa* (Linné) Medikus (1786) ≡ *Apicra retusa* (Linné) Willdenow (1811) (*incorrect name*, ICN Art. 11.4).

**H. retusa** var. **longibracteata** (G. G. Smith) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 36, 2012). **Type:** RSA, Western Cape (*Dekenah* 18 in *Smith* 5378 [NBG, PRE]). — **Distr:** RSA (Western Cape). **I:** Scott (1985: 127, as *H. longibracteata*).

≡ *Haworthia longibracteata* G. G. Smith (1945) ≡ *Haworthia retusa* fa. *longibracteata* (G. G. Smith) Pilbeam (1983) ≡ *Haworthia turgida* var. *longibracteata* (G. G. Smith) M. B. Bayer (1999).

[1] Differs from var. *retusa*: **L** erect to suberect, ovate-lanceolate.

**H. retusa** var. **nigra** (M. B. Bayer) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 36, 2012). **Type:** RSA, Western Cape (*Smith* 5753 [NBG]). — **Lit:** Bayer (2004a); Bayer (2004c); Bayer (2005); all as *H. mutica* var. **Distr:** RSA (Western Cape: Heidelberg area).

≡ *Haworthia mutica* var. *nigra* M. B. Bayer (1999) ≡ *Haworthia silviae* var. *nigra* (M. B. Bayer) M. Hayashi (2000); **incl.** *Haworthia chromutica* M. Hayashi (2000) (*nom. inval.*, ICN Art. 39.1, 40.1); **incl.** *Haworthia quimutica* Breuer (2011) (*nom. inval.*, ICN Art. 38.1a).

[1] Differs from var. *retusa*: **Ros** more profliferous; **L** greener and more translucent.

**H. retusa** var. **retusa** — **Distr:** RSA (Western Cape: Riversdale). **I:** Bayer (1982: Fig. 33a).

**Incl.** *Haworthia fouchei* Von Poellnitz (1940) ≡ *Haworthia retusa* fa. *fouchei* (Von Poellnitz) Pilbeam (1983) ≡ *Haworthia retusa* var. *fouchei* (Von Poellnitz) Breuer (2016); **incl.** *Haworthia retusa* var. *densiflora* G. G. Smith (1946); **incl.** *Haworthia retusa* var. *multilineata* G. G. Smith (1946) ≡ *Haworthia retusa* fa. *multilineata* (G. G. Smith) Pilbeam (1983) ≡ *Haworthia multilineata* (G. G. Smith) C. L. Scott (1985); **incl.** *Haworthia retusa* var. *solitaria* G. G. Smith (1946) ≡ *Haworthia solitaria* (G. G. Smith) C. L. Scott (1973); **incl.** *Haworthia geraldii* C. L. Scott (1965) ≡ *Haworthia retusa* fa. *geraldii* (C. L. Scott) Pilbeam (1983) (*nom. inval.*, ICN Art. 41.5); **incl.** *Haworthia retusa* var. *quimutica* Hayashi (2001); **incl.** *Haworthia subretusa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, rarely slowly proliferating, to 12 cm Ø; **L** 10–15, turgid, rigid, with pronouncedly retuse end-areas, 8 × 2 cm, brownish or green and rarely with purplish hue, variously lined and windowed, surface and usually also margins and keel without spines or tubercles, tips pointed; **Inf** robust, to 30 cm; **Fl** 20–30, closely spaced, white with greenish-brown veins.

Possible hybridization with *H. mirabilis* is mentioned by Bayer (2012d).

**H. retusa** var. **suberecta** (Von Poellnitz) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 36, 2012). **Type** [neo]: RSA, Western Cape (*Bayer* s.n. in *Karoo Garden* 631/69 [NBG]). — **Distr:** RSA (Western Cape). **I:** Scott (1985: 126, as *H. dekenahii*).

≡ *Haworthia turgida* var. *suberecta* Von Poellnitz (1938) ≡ *Haworthia turgida* fa. *suberecta* (Von Poellnitz) Pilbeam (1983) ≡ *Haworthia suberecta* (Poellnitz) Breuer (2010); **incl.** *Haworthia turgida* var. *subtuberculata* Von Poellnitz (1938); **incl.** *Haworthia turgida* var. *pallidifolia* G. G. Smith (1946) ≡ *Haworthia turgida* fa. *pallidifolia* (G. G. Smith) Pilbeam (1983) ≡ *Haworthia pallidifolia* (G. G. Smith) M. Hayashi (2010) ≡ *Haworthia suberecta* var.



*pallidifolia* (G. G. Smith) Breuer (2016); **incl.** *Haworthia pseudo* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia reflexa* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia rodinii* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] Differs from var. *retusa*: **L** strongly mottled, tips slightly truncate and rounded.

**H. retusa** var. **turgida** (Haworth) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 36, 2012). **Type** [neo]: RSA, Western Cape (*Bayer* 2420 [NBG 132378]). — **Distr**: RSA (Western Cape). **I**: Bayer (1982: Fig. 40, as *H. turgida*).

≡ *Haworthia turgida* Haworth (1819) ≡ *Aloe turgida* (Haworth) Roemer & Schultes fil. (1829); **incl.** *Haworthia laetevirens* Haworth (1819) ≡ *Aloe laetevirens* (Haworth) Link (1822); **incl.** *Haworthia caespitosa* Von Poellnitz (1937) ≡ *Haworthia turgida* fa. *caespitosa* (Von Poellnitz) Pilbeam (1983); **incl.** *Haworthia caespitosa* fa. *subplana* Von Poellnitz (1938); **incl.** *Haworthia caespitosa* fa. *subproliferans* Von Poellnitz (1938).

[1] Differs from var. *turgida*: **Ros** partially stemless, proliferous, 5–10 cm Ø; **L** 20–40, ovate-lanceolate, 4 × 1.2 cm, turgid, often as thick as broad, recurved or slightly retuse, margins and keel lightly spined.

**H. rossouwii** Von Poellnitz (Kakteenkunde 1938: 75, ill., 1938). **Type**: RSA, Western Cape (*Rossouw* s.n. in *Triebner* 1059 [B [lecto, ill. later publ. l.c. p. 75]]). — **Lit**: Bayer (2001). **Distr**: RSA (Western Cape: Bredasdorp to Heidelberg); mainly in Fynbos vegetation.

**H. rossouwii** var. **calcarea** (M. B. Bayer) M. B. Bayer (*Aloe* 38(1–2): 36, 2001). **Type**: RSA, Western Cape (*Burgers* 1648 [NBG]). — **Distr**: RSA (Western Cape: Bredasdorp Distr.). **I**: Bayer (2001).

≡ *Haworthia mirabilis* var. *calcarea* M. B. Bayer (1999) ≡ *Haworthia calcarea* (M. B. Bayer) M. Hayashi (2000) ≡ *Haworthia mundula* var. *calcarea* (M. B. Bayer) Breuer (2016).

[1] Differs from var. *rossouwii*: **Ros** with fewer leaves; **L** short, erect, with short retuse end-area.

**H. rossouwii** var. **elizeae** (Breuer) M. B. Bayer (Haworthia Update Vol. 2, 154, 2006). **Nom. inval.**, ICN Art. 41.5. **Type**: RSA, Western Cape (*de Vries* 563 in *Breuer* 6936 [Res. Inst. Evol. Biol. Tokyo]). — **Distr**: RSA (Western Cape: W of Swellendam).

≡ *Haworthia elizeae* Breuer (2003) (*nom. inval.*, ICN Art. 41.5); **incl.** *Haworthia esterhuizenii* Breuer (2002) (*nom. inval.*, ICN Art. 41.5).

[1] Differs from var. *rossouwii*: **Ros** smaller, more globose.

Unfortunately, there is no valid name available for this taxon.

**H. rossouwii** var. **minor** (M. B. Bayer) M. B. Bayer (Haworthia Update Vol. 7, Part 4, 36–37, 2012). **Type**: RSA, Western Cape (*Bayer* s.n. in *Karoo Garden* 36/70 [NBG]). — **Distr**: RSA (Western Cape: Bredasdorp Distr.).

≡ *Haworthia heidelbergensis* var. *minor* M. B. Bayer (1999); **incl.** *Haworthia rooivleiensis* Breuer (2010).

[1] Differs from var. *rossouwii*: **Ros** much smaller, to 3 cm Ø; **L** light yellowish-green, well-spined.

**H. rossouwii** var. **petrophila** (M. B. Bayer) M. B. Bayer (*Aloe* 38(1–2): 36, 2001). **Type**: RSA, Western Cape (*Burgers* 2158 [NBG]). — **Distr**: RSA (Western Cape: Bromberg, Stormsvlei).

≡ *Haworthia variegata* var. *petrophila* M. B. Bayer (1999) ≡ *Haworthia petrophila* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *rossouwii*: **Ros** very proliferous; **L** slender, shorter and incurved, strongly spined.

**H. rossouwii** var. **rossouwii** — **Distr**: RSA (Western Cape: SW of Heidelberg to Bredasdorp); mainly in Fynbos vegetation. **I**: Bayer (1982: Fig. 36, as *H. serrata*).

**Incl.** *Haworthia serrata* M. B. Bayer (1973) ≡ *Haworthia chloracantha* var. *serrata* (M. B. Bayer) Halda (1997) ≡ *Haworthia rossouwii* var. *serrata* (M. B. Bayer) Breuer (2016).

[1] **Ros** stemless, rarely proliferating, to 7 cm Ø; **L** 20–30, narrow, 6 × 1 cm, acuminate, bright



yellowish-green with translucent lines above, margins and keel spiny; **Inf** robust, to 40 cm; **Fl** 20–30, white with green venation.

**H. scabra** Haworth (Suppl. Pl. Succ., 58, 1819). **Type:** K [lecto — icono]: publ. Cact. Succ. J. (US) 52: 274, 1980. — **Distr:** RSA (Western Cape, Eastern Cape); mainly in Fynbos and Succulent Karoo vegetation.

≡ *Aloe scabra* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthiopsis scabra* (Haworth) G. D. Rowley (2013).

**H. scabra** var. **lateganiae** (Von Poellnitz) M. B. Bayer (Haworthia Revisited, 195, *ills.*, 1999). **Type:** B [lecto — icono]: photograph publ. Desert Pl. Life 9: 103, 1937. — **Distr:** RSA (Western Cape: Little Karoo, E of Oudtshoorn). **I:** Bayer (1982: Fig. 60b, as *H. starkiana* var.); Gildenhuis (2017: 56, as *Haworthiopsis*).

≡ *Haworthia lateganiae* Von Poellnitz (1937) ≡ *Haworthia starkiana* var. *lateganiae* (Von Poellnitz) M. B. Bayer (1976) ≡ *Haworthiopsis scabra* var. *lateganiae* (Von Poellnitz) G. D. Rowley (2013).

[2] Differs from var. *scabra*: **L** long and slender, smooth and shiny, dark green.

**H. scabra** var. **morrisiae** (Von Poellnitz) M. B. Bayer (Haworthia Handb., 137, 1976). **Type:** B [lecto — icono]: *ill.*, publ. Kakteenkunde 1937: 132. — **Distr:** RSA (Western Cape: Little Karoo, Schoemanspoort). **I:** Bayer (1982: Fig. 58b); Gildenhuis (2017: 57, as *Haworthiopsis*).

≡ *Haworthia morrisiae* Von Poellnitz (1937) ≡ *Haworthiopsis scabra* var. *morrisiae* (Von Poellnitz) G. D. Rowley (2013).

[2] Differs from var. *scabra*: **L** surfaces minutely scabrid, tubercles small and confluent.

**H. scabra** var. **scabra** — **Distr:** RSA (Eastern Cape: Baviaanskloof). **I:** Bayer (1982: Fig. 58a); Gildenhuis (2017: 53–55, as *Haworthiopsis*).

**Incl.** *Haworthia tuberculata* Von Poellnitz (1931) ≡ *Haworthia scabra* var. *tuberculata* (Von Poellnitz) Halda (1997); **incl.** *Haworthia tuberculata* var. *acuminata* Von Poellnitz (1938); **incl.** *Haworthia tuberculata* var. *subexpansa* Von

Poellnitz (1938); **incl.** *Haworthia tuberculata* var. *sublaevis* Von Poellnitz (1938); **incl.** *Haworthia tuberculata* var. *angustata* Von Poellnitz (1940); **incl.** *Haworthia scabra* var. *johanii* M. Hayashi (2001) ≡ *Haworthia johanii* (M. Hayashi) Breuer (2010) ≡ *Haworthiopsis scabra* var. *johanii* (M. Hayashi) Breuer (2016); **incl.** *Haworthia plettens* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[2] **Ros** stemless, slowly proliferating, to 16 cm tall, 6 cm Ø; **L** 12–25, to 1.6 × 2.2 cm, triangular-lanceolate, attenuate, almost as thick as wide, dull green covered with dust, incurved, surfaces scabrid or smooth, with or without distinct raised non-confluent concolorous tubercles; **Inf** sparsely branched, lax, to 48 cm; **Fl** 15–20, tube obcapitate, curved; **ITep** revolute.

**H. scabra** var. **starkiana** (Von Poellnitz) M. B. Bayer (Haworthia Revisited, 197, *ills.*, 1999). **Type:** RSA, Western Cape (*Taylor* s.n. [B [lecto — icono]: unpubl. photograph]). — **Distr:** RSA (Western Cape: Little Karoo, Schoemanspoort). **I:** Bayer (1982: Fig. 60a, as *H. starkiana*); Gildenhuis (2017: 58–59, as *Haworthiopsis*).

≡ *Haworthia starkiana* Von Poellnitz (1933) ≡ *Haworthia starkiana* var. *starkiana* (1976) ≡ *Haworthia scabra* ssp. *starkiana* (Von Poellnitz) Halda (1997) ≡ *Haworthiopsis scabra* var. *starkiana* (Von Poellnitz) G. D. Rowley (2013); **incl.** *Haworthia taylorii* W. F. Barker *ms.* (s.a.) (*nom. inval.*, ICN Art. 29.1); **incl.** *Haworthia smitii* Von Poellnitz (1938) ≡ *Haworthia pumila* var. *smitii* (Von Poellnitz) Halda (1997) ≡ *Haworthiopsis scabra* var. *smitii* (Von Poellnitz) Gildenhuis & Klopper (2016).

[2] Differs from var. *scabra*: **Ros** larger, forming clumps; **L** smooth, shiny, without tubercles, yellowish-green.

Gildenhuis (2017: 58) also accepts var. *smitii*, which he terms a “very distinct taxon”.

**H. semiviva** (Von Poellnitz) M. B. Bayer (Haworthia Handb., 153, 1976). **Type:** B [lecto — icono]: photograph publ. Succulenta 22: 25, 1940. — **Distr:** RSA (Northern Cape, Western Cape); Nama Karoo vegetation. **I:** Bayer (1982: Fig. 35).

≡ *Haworthia bolusii* var. *semiviva* Von Poellnitz (1938) ≡ *Haworthia arachnoidea* var. *semiviva* (Von Poellnitz) Halda (1997); **incl.** *Haworthia sphaeroidea* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia victoria* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** stemless, rarely proliferating, 5–6 cm Ø; **L** 30–40, broadly ovate, 6 × 1.5 cm, thin, incurved, pale green, translucent and usually drying up from the tips; **Inf** 20–30 cm; **Fl** 30–35, white with green venation, broad and flat across the upper base of the tube.

**H. sordida** Haworth (Revis. Pl. Succ., 51, 1821). **Type:** [neo — icono]: Salm-Dyck, Monogr. Gen. Aloes & Mesembr. 7: Aloe t. 1 (Sect. 7: 2), 1863. — **Distr:** RSA (Eastern Cape); mainly Albany Thicket vegetation.

≡ *Aloe sordida* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthia scabra* ssp. *sordida* (Haworth) Halda (1997) ≡ *Haworthia scabra* var. *sordida* (Haworth) Halda (1997) ≡ *Haworthiopsis sordida* (Haworth) G. D. Rowley (2013).

**H. sordida** var. **lavrani** C. L. Scott (Cact. Succ. J. (US) 53(3): 124–126, ill., 1981). **Type:** RSA, Eastern Cape (*Hechter* s.n. [PRE 61124]). — **Distr:** RSA (Eastern Cape: Little Karoo). **I:** Scott (1985: 8); Gildenhuis (2017: 67, as *Haworthiopsis*).

≡ *Haworthia scabra* var. *lavrani* (C. L. Scott) Halda (1997) ≡ *Haworthia lavrani* (C. L. Scott) Breuer (2010) ≡ *Haworthiopsis sordida* var. *lavrani* (C. L. Scott) G. D. Rowley (2013).

[2] Differs from var. *sordida*: **Ros** smaller, to 5 cm Ø; **L** shorter, recurved.

**H. sordida** var. **sordida** — **Distr:** RSA (Eastern Cape: E Little Karoo). **I:** Bayer (1982: Fig. 59); Gildenhuis (2017: 64–66, as *Haworthiopsis*).

**Incl.** *Haworthia agavoides* Zantner & Von Poellnitz (1938) ≡ *Haworthia sordida* var. *agavoides* (Zantner & Von Poellnitz) G. G. Smith (1950) ≡ *Haworthiopsis sordida* var. *agavoides* (Zantner & Von Poellnitz) Breuer (2016).

[2] **Ros** stemless, rarely proliferating, to 15 cm tall, 8 cm Ø; **L** 6–15, to 15 × 2 cm, lanceolate-deltoid, attenuate, erect, dark grey to blackish-green, surfaces scabrid with indistinct slightly raised non-confluent tubercles, margins obtuse; **Inf** sparsely branched, lax, to 40 cm; **Fl** tube straight; **ITep** revolute.

**H. springbokvlakensis** C. L. Scott (J. South Afr. Bot. 36: 287–288, 1970). **Type:** RSA, Eastern Cape (*Scott* 245 [PRE]). — **Distr:** RSA (Eastern Cape: E Little Karoo); Albany Thicket vegetation. **I:** Bayer (1982: Fig. 37).

≡ *Haworthia retusa* var. *springbokvlakensis* (C. L. Scott) Halda (1997); **incl.** *Haworthia groenewaldii* Breuer (2011).

[1] **Ros** stemless, solitary, to 10 cm Ø; **L** 8–12, turgid, 6 × 1.5 cm, very rounded and retuse with translucent end-area and several short longitudinal lines, smooth; **Inf** 20–25 cm; **Fl** white with brownish venation.

**H. ×tauteae** Archibald *pro sp.* (Flow. Pl. Afr. 25: t. 992 + text, 1946). **Type:** RSA, Western Cape (*Taute* s.n. [[lecto — icono]: l.c. t. 992]).

≡ *Haworthiopsis ×tauteae* (Archibald) Gildenhuis & Klopper (2016).

This is the naturally occurring hybrid *H. viscosa* × *H. scabra*. — [U. Eggli]

**H. tessellata** Haworth (Philos. Mag. J. 64: 300, 1824). **Type:** K [lecto — icono]: ill. publ. in Cact. Succ. J. (US): 50: 75, 1978. — **Distr:** S Namibia, RSA (Northern Cape, Free State); Nama Karoo and Succulent Karoo vegetation. **I:** Bayer (1982: Fig. 61c, as *H. venosa* ssp.); Hildyard (2016b); Gildenhuis (2017: 44–45, as *Haworthiopsis*). — Fig. 12.

≡ *Aloe tessellata* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthia venosa* ssp. *tessellata* (Haworth) M. B. Bayer (1982) ≡ *Haworthia venosa* var. *tessellata* (Haworth) Halda (1997) ≡ *Haworthiopsis tessellata* (Haworth) Boatwright & J. C. Manning (2014); **incl.** *Haworthia parva* Haworth (1824) ≡ *Aloe parva* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthia tessellata* var. *parva* (Haworth) Baker (1880); **incl.** *Haworthia tessellata* var. *inflexa* Baker (1880); **incl.** *Haworthia*



**Fig. 12** *Haworthia tessellata*. (Copyright: U. Eggli)

*engleri* Dinter (1914)  $\equiv$  *Haworthia tessellata* var. *engleri* (Dinter) Von Poellnitz (1938); **incl.** *Haworthia pseudotessellata* Von Poellnitz (1929); **incl.** *Haworthia tessellata* var. *tuberculata* Von Poellnitz (1936); **incl.** *Haworthia minutissima* Von Poellnitz (1939)  $\equiv$  *Haworthia tessellata* var. *minutissima* (Von Poellnitz) Viveiros (1949); **incl.** *Haworthia tessellata* var. *elongata* van Woerden (1940); **incl.** *Haworthia tessellata* fa. *brevior* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* fa. *longior* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* var. *coriacea* Resende & Von Poellnitz (1942)  $\equiv$  *Haworthia coriacea* (Resende & Von Poellnitz) Breuer (2010); **incl.** *Haworthia tessellata* var. *luisieri* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* var. *obesa* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* var. *palhinhia* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* var. *simplex* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* var. *stepheniana* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* var. *velutina* Resende & Von Poellnitz (1942); **incl.** *Haworthia tessellata* fa. *major* J. R. Brown (1947); **incl.** *Haworthia crousii* M. Hayashi (2001)  $\equiv$  *Haworthiopsis tessellata* var. *crousii* (M. Hayashi) Gildenhuis & Klopper (2016); **incl.** *Haworthia crausii* M. Hayashi (2001) (*nom. inval.*, ICN Art. 61.1)  $\equiv$  *Haworthiopsis tessellata* var. *crausii* (M. Hayashi) Gildenhuis & Klopper (2016) (*nom. inval.*, Art. 61.1); **incl.** *Haworthia helensis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a); **incl.** *Haworthia mediata* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[2] Description as for *H. venosa* but **Ros** stemless; **L** 8–10, subdeltoïd, variously patterned.

Gildenhuis (2017: 45) also accepts *H. crousii* at varietal level (under *Haworthiopsis*), which differs by being more robust and less proliferous than var. *tessellata*.

**H. transiens** (Von Poellnitz) M. Hayashi (*Haworthia* Study 3: 13, 2000). **Type:** B [lecto — icono]: unpubl. photograph. — **Distr:** RSA (Eastern Cape: Baviaanskloof, Langkloof); Fynbos and Albany Thicket vegetations. **I:** Bayer (1982: Fig. 11d, as *H. cymbiformis* var.).

$\equiv$  *Haworthia planifolia* var. *transiens* Von Poellnitz (1938)  $\equiv$  *Haworthia cymbiformis* var. *transiens* (Von Poellnitz) M. B. Bayer (1976); **incl.** *Haworthia cymbiformis* var. *brevifolia* Triebner & Von Poellnitz (1938); **incl.** *Haworthia cymbiformis* var. *multifolia* Triebner (1938)  $\equiv$  *Haworthia cymbiformis* fa. *multifolia* (Triebner) Pilbeam (1983); **incl.** *Haworthia cymbiformis* var. *translucens* Triebner & Von Poellnitz (1938); **incl.** *Haworthia diaphana* M. Hayashi (2006); **incl.** *Haworthia klipensis* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[1] **Ros** similar to *H. cymbiformis* and to *H. cooperi* var. *picturata*; **L** obtuse, surface reticulate with translucent areas between the veins.

**H. truncata** Schönland (Trans. Roy. Soc. South Africa 1: 391, 1910). **Type:** RSA, Western Cape (*Britten* s.n. [K]). — **Distr:** RSA (Western Cape: Little Karoo); Succulent Karoo vegetation.

Mak (2003) presents a synopsis of hybrids involving this species as one parent.

**H. truncata** var. **maughanii** (Von Poellnitz) B. Fearn (Nation. Cact. Succ. J. 21(1): 28–29, 1966). **Type** [neo]: RSA, Western Cape (*Malherbe* s.n. in NBG 307/40 [NBG 68307]). — **Distr:** RSA (Western Cape: Little Karoo, Calitzdorp). **I:** Bayer (1982: Fig. 24, as *H. maughanii*).

$\equiv$  *Haworthia maughanii* Von Poellnitz (1933).

[1] Differs from var. *turgida*: **L** multifarious, round in cross-section.



**Fig. 13** *Haworthia truncata* var. *truncata*. (Copyright: E. J. Van Jaarsveld)

**H. truncata** var. *truncata* — **Distr:** RSA (Western Cape: C Little Karoo). **I:** Bayer (1982: Fig. 39). — **Fig.** 13.

**Incl.** *Haworthia truncata* fa. *crassa* Von Poellnitz (1938); **incl.** *Haworthia truncata* fa. *normalis* Von Poellnitz (1938); **incl.** *Haworthia truncata* fa. *tenuis* Von Poellnitz (1938)  $\equiv$  *Haworthia truncata* var. *tenuis* (Von Poellnitz) M. B. Bayer (1976); **incl.** *Haworthia truncata* var. *minor* Breuer (2003); **incl.** *Haworthia papillaris* Breuer (2010).

[1] **Ros** stemless, slowly proliferating; **L** distichous, 10–12, abruptly truncate with flat to slightly corrugated and subpellucid end-areas, 1.2–4 cm wide, 0.3–1 cm thick, dark grey-green, scabrid with minute tubercles; **Inf** to 20 cm; **Fl** 20–30, white with brownish veins.

**H. variegata** L. Bolus (J. Bot. 67: 137, 1929). **Type:** RSA, Western Cape (*Ferguson* s.n. [BOL]). — **Distr:** RSA (Western Cape); Fynbos vegetation.  $\equiv$  *Haworthia chloracantha* ssp. *variegata* (L. Bolus) Halda (1997)  $\equiv$  *Haworthia chloracantha* var. *variegata* (L. Bolus) Halda (1997).

[1] **Ros** stemless, proliferous, to 4 cm  $\varnothing$ ; **L** 30–40, erect, slender lanceolate, dark green, variegated, margins and keel spined; **Inf** slender, to 35 cm, lax; **Fl** 15–20, greenish-white with brownish venation.

**H. variegata** var. *hemicypta* M. B. Bayer (*Haworthia Revisited*, 158, ills., 1999). **Type:** RSA, Western Cape (*Burgers* 2582 [NBG]). — **Distr:** RSA (Western Cape: Bredasdorp).

$\equiv$  *Haworthia hemicypta* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *variegata*: Plants moderately variegated to plain; **L** long and slender, tending to arch out and then curve inwards.

**H. variegata** var. *modesta* M. B. Bayer (*Haworthia Revisited*, 159, ills., 1999). **Type:** RSA, Western Cape (*Bayer* 2551 [NBG]). — **Distr:** RSA (Western Cape: Bredasdorp).

$\equiv$  *Haworthia modesta* (M. B. Bayer) M. Hayashi (2000).

[1] Differs from var. *variegata*: **L** broader and shorter and with less conspicuous spination.

**H. variegata** var. *variegata* — **Distr:** RSA (Western Cape: Riversdale).

[1] Plants strongly variegated.

**H. venosa** (Lamarck) Haworth (*Revis. Pl. Succ.*, 51, 1821). **Type:** [lecto — icono]: Commelin, *Praeludia Bot.* t. 29, 1703. — **Distr:** RSA (Northern Cape, Western Cape: lower Breede and Gouritz river valleys); Fynbos and Albany Thicket vegetations. **I:** Bayer (1982: Fig. 61a); Gildenhuis (2017: 46, as *Haworthiopsis*).

$\equiv$  *Aloe venosa* Lamarck (1783)  $\equiv$  *Haworthiopsis venosa* (Lamarck) G. D. Rowley (2013); **incl.** *Aloe recurva* Haworth (1804)  $\equiv$  *Apicra recurva* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4)  $\equiv$  *Haworthia recurva* (Haworth) Haworth (1812)  $\equiv$  *Haworthia venosa* ssp. *recurva* (Haworth) M. B. Bayer (1976); **incl.** *Aloe tricolor* Haworth (1804)  $\equiv$  *Apicra tricolor* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4); **incl.** *Haworthia distincta* N. E. Brown (1876); **incl.** *Haworthia venosa* var. *oertendahlii* Hjelmquist (1943); **incl.** *Haworthia irimiae* Breuer (2010) (*nom. inval.*, ICN Art. 36.1b, 38.1a).

[2] **Ros** usually stemless, slowly proliferating with offsets or stolons, to 3 cm tall and 5 cm  $\varnothing$ ; **L** 12–20, to 10  $\times$  1.5 cm, ovate-deltoid, spreading to recurved, upper surface smooth, reticulate, lower surface usually slightly scabrid; **Inf** sparsely branched, lax, to 35 cm; **Fl** 15–20, tube obcapitate; **ITep** revolute.





**Fig. 14** *Haworthia viscosa*. (Copyright: E. J. Van Jaarsveld)

**H. viscosa** (Linné) Haworth (Synops. Pl. Succ., 90, 1812). **Type:** [lecto — icono]: Commelin, Praeludia Bot., 82, t. 31, 1703. — **Distr:** RSA (Western Cape, Eastern Cape: Little Karoo); Succulent Karoo and Albany Thicket vegetations. **I:** Bayer (1982: Fig. 62); Gildenhuis (2017: 60–61, as *Haworthiopsis*). – Fig. 14.

≡ *Aloe viscosa* Linné (1753) ≡ *Apicra viscosa* (Linné) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthiopsis viscosa* (Linné) G. D. Rowley (2013) ≡ *Tulista viscosa* (Linné) G. D. Rowley (2013) (*nom. inval.*, ICN Art. 36.2); **incl.** *Aloe triangularis* Medikus (1784); **incl.** *Aloe* × *tortuosa* Haworth *pro sp.* (1804) ≡ *Apicra tortuosa* (Haworth) Willdenow (1811) (*incorrect name*, ICN Art. 11.4) ≡ *Haworthia tortuosa* (Haworth) Haworth (1812) ≡ *Haworthiopsis* × *tortuosa* (Haworth) Gildenhuis & Klopper (2016); **incl.** *Aloe pseudotortuosa* Salm-Dyck (1817) ≡ *Haworthia pseudotortuosa* (Salm-Dyck) Haworth (1819) ≡ *Haworthia viscosa* var. *pseudotortuosa* (Salm-Dyck) Baker (1880) ≡ *Haworthia viscosa* fa. *pseudotortuosa* (Salm-Dyck) Pilbeam (1983) (*nom. inval.*, ICN Art. 41.5); **incl.** *Haworthia asperiuscula* Haworth (1819) ≡ *Aloe asperiuscula* (Haworth) Salm-Dyck (1840) ≡ *Haworthia viscosa* fa. *asperiuscula* (Haworth) Pilbeam (1983) (*nom. inval.*, ICN Art. 41.5) ≡ *Haworthiopsis viscosa* var. *asperiuscula* (Haworth) Breuer (2016); **incl.** *Haworthia concinna* Haworth (1819) ≡ *Aloe concinna* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Haworthia viscosa* var. *concinna*

(Haworth) Baker (1880); **incl.** *Haworthia cordifolia* Haworth (1819) ≡ *Aloe cordifolia* (Haworth) Roemer & Schultes *fil.* (1829); **incl.** *Haworthia indurata* Haworth (1821) ≡ *Aloe indurata* (Haworth) Roemer & Schultes *fil.* (1829) ≡ *Aloe viscosa* var. *indurata* (Haworth) Salm-Dyck (1836) ≡ *Haworthia viscosa* var. *indurata* (Haworth) Baker (1880); **incl.** *Haworthia viscosa* var. *major* Haworth (1821) ≡ *Aloe viscosa* var. *major* (Haworth) Roemer & Schultes *fil.* (1829); **incl.** *Haworthia viscosa* var. *minor* Haworth (1821) ≡ *Aloe viscosa* var. *minor* (Haworth) Roemer & Schultes *fil.* (1829); **incl.** *Haworthia viscosa* var. *parvifolia* Haworth (1821) ≡ *Aloe viscosa* var. *parvifolia* (Haworth) Roemer & Schultes *fil.* (1829); **incl.** *Haworthia torquata* Haworth (1827) ≡ *Aloe torquata* (Haworth) Salm-Dyck (1836) ≡ *Haworthia viscosa* var. *torquata* (Haworth) Baker (1880) ≡ *Haworthia viscosa* fa. *torquata* (Haworth) Pilbeam (1983) (*nom. inval.*, ICN Art. 41.5); **incl.** *Aloe subtortuosa* Roemer & Schultes *fil.* (1829); **incl.** *Haworthia viscosa* var. *caespitosa* Von Poellnitz (1938); **incl.** *Haworthia viscosa* var. *subobtusa* Von Poellnitz (1938) ≡ *Haworthia viscosa* fa. *subobtusa* (Von Poellnitz) Pilbeam (1983) (*nom. inval.*, ICN Art. 41.5); **incl.** *Haworthia beanii* G. G. Smith (1944) ≡ *Haworthia viscosa* fa. *beanii* (G. G. Smith) Pilbeam (1983) ≡ *Haworthiopsis viscosa* var. *beanii* (G. G. Smith) Breuer (2016); **incl.** *Haworthia beanii* var. *minor* G. G. Smith (1944); **incl.** *Haworthia asperiuscula* var. *subintegra* G. G. Smith (1945); **incl.** *Haworthia viscosa* var. *cougaensis* G. G. Smith (1945); **incl.** *Haworthia viscosa* var. *viridissima* G. G. Smith (1945); **incl.** *Haworthia asperiuscula* var. *patagiata* G. G. Smith (1946); **incl.** *Haworthia viscosa* var. *quaggaensis* G. G. Smith (1948); **incl.** *Haworthia viscosa* ssp. *dereki-clarki* Halda (1998); **incl.** *Haworthia viscosa* var. *variabilis* Breuer (2003) ≡ *Haworthia variabilis* (Breuer) Breuer (2010) ≡ *Haworthiopsis variabilis* (Breuer) Zonneveld (2014) ≡ *Haworthiopsis viscosa* var. *variabilis* (Breuer) Gildenhuis & Klopper (2016).

[2] **Ros** caulescent, proliferous, to 8 cm Ø, to 30 cm tall; **L** 20–60, to 5 × 1.5 cm, deltoid,



closely arranged in 3 rows, spreading, surfaces scabrid, tips spreading, pungent; **Inf** sparsely branched, lax, 15–20 cm; **Fl** 8–15, tube obcapitate, curved; **ITep** revolute.

Gildenhuis (2017: 62, with ills.) also accepts var. *variabilis* as “one of the many known variations” of *H. viscosa*.

**H. vlokii** M. B. Bayer (Haworthia Revisited, 160–161, ills., 1999). **Type:** RSA, Western Cape (*Vlok* s.n. in *Venter* 91/2 [NBG]). — **Distr:** RSA (Western Cape: Little Karoo, Swartberg Mts.); Fynbos vegetation.

[1] **Ros** acaulescent, 4–5 cm Ø, proliferous; **L** spreading to suberect, surface opaque, with inconspicuous whiter dots towards the tips, margins and keel with short spines; **Inf** simple, 30–45 cm; **Fl** white and brownish-pink.

**H. wittebergensis** W. F. Barker (J. South Afr. Bot. 8: 245, 1942). **Type:** RSA, Western Cape (*Pieterse* s.n. [NBG 68214]). — **Distr:** RSA (Western Cape: Laingsburg: Witteberg Mts.); mainly Fynbos vegetation. **I:** Bayer (1982: Fig. 43). — Fig. 15.

[1] **Ros** stemless, slowly proliferating, to 3 cm Ø; **L** 20–30, long and slender, 15 × 0.8 cm, attenuate, conspicuously amplexicaul, grey-green with white spines on margins and keel, coriaceous; **Inf** slender, to 30 cm, lax; **Fl** 15–20, laxly arranged, white with green venation.

**H. woolleyi** Von Poellnitz (Repert. Spec. Nov. Regni Veg. 42: 269–270, 1937). **Type:** B [lecto, ill.



**Fig. 15** *Haworthia wittebergensis*. (Copyright: E. J. Van Jaarsveld)

publ. Cact. J. (Croydon) 7: 3, 1938]. — **Distr:** RSA (Eastern Cape: E Little Karoo: Steytlerville); Albany Thicket vegetation. **I:** Bayer (1982: Fig. 63); Gildenhuis (2017: 47, as *Haworthiopsis*).

≡ *Haworthia venosa* ssp. *woolleyi* (Von Poellnitz) Halda (1997) ≡ *Haworthiopsis woolleyi* (Von Poellnitz) G. D. Rowley (2013) ≡ *Haworthiopsis venosa* var. *woolleyi* (Von Poellnitz) Breuer (2016).

[1] Description as for *H. tessellata* but **Ros** stemless; **L** 20–25, slender, attenuate.

**H. zantneriana** Von Poellnitz (Cact. J. (Croydon) 5: 35, in clavi, 1935). **Type:** B [lecto, ill. publ. Desert Pl. Life 9: 90, 1937]. — **Distr:** RSA (Eastern Cape); Albany Thicket vegetation. **I:** Bayer (1982: Fig. 45).

≡ *Haworthia chloracantha* var. *zantneriana* (Von Poellnitz) Halda (1997).

[1] **Ros** stemless, proliferous, 5–6 cm Ø; **L** 20–40, lanceolate, acuminate, 6 × 1.2 cm, attenuate, soft, glabrous, spreading, pale green, usually with pellucid white longitudinal marks; **Inf** slender, to 25 cm; **Fl** sparsely arranged, 20–30, white with green venation.

**H. zantneriana** var. *minor* M. B. Bayer (Haworthia Revisited, 164, ills., 1999). **Type:** RSA, Eastern Cape (*Bayer* 1702 [NBG]). — **Distr:** RSA (Eastern Cape: Willowmore, S Karoo). ≡ *Haworthia inspida* Breuer (2010).

[1] Differs from var. *zantneriana*: **Ros** small, to 5 cm Ø; **L** unmarked.

**H. zantneriana** var. *zantneriana* — **Distr:** RSA (Eastern Cape: Willowmore, Steytlerville).

[1] Plants to 8 cm tall; **L** with markings.

## References

- Battista, L. (2009) Il genere *Haworthia*. Piante Grasse 29 (Suppl.): 1–52, ills. map.
- Bayer, M. B. (1976) *Haworthia* handbook. A guide to the species, with identification keys and illustrations. Kirstenbosch (ZA): National Botanic Gardens of South Africa.
- Bayer, M. B. (1982) The new *Haworthia* handbook. A revised guide to the literature of the genus, with discussion of the species, identification keys and colour

- illustrations. Kirstenbosch (ZA): National Botanic Gardens of South Africa.
- Bayer, M. B. (1999) *Haworthia* revisited. A revision of the genus. Hatfield (ZA): Umdaus Press.
- Bayer, M. B. (2001) *Haworthia rossouwii* V.Poelln. and the demise of *H. serrata* Bayer. *Aloe* 38(1-2): 31–36, ills.
- Bayer, M. B. (2002a) *Haworthia* update. Essays on *Haworthia* — Volume 1. Hatfield (ZA): Umdaus Press.
- Bayer, M. B. (2002b) An odd population of *H.[aworthia] arachnoidea* var. *nigricans*. *Aloe* 38(3-4): 76–79, ills.
- Bayer, M. B. (2003a) Where to *Haworthia limifolia*? *Aloe* 40(2): 41–51, ills., map.
- Bayer, M. B. (2003b) Some of the interplay of *Haworthia arachnoidea* and *H. mucronata*. *Haworthiad* 17(3): 94–99, ills., map.
- Bayer, M. B. (2004a) Still on about *H.[aworthia] mutica* var. *nigra*. *Haworthiad* 18(1): 21–33, ills., map.
- Bayer, M. B. (2004b) *Haworthia arachnoidea* and *H. nortieri*. *Haworthiad* 18(2): 44–51, ills.
- Bayer, M. B. (2004c) Continuing the saga of *Haworthia mutica* var. *nigra*. *Haworthiad* 18(2): 52–57, ills.
- Bayer, M. B. (2005) Completing the saga of *H. mutica* var. *nigra*? *Haworthiad* 19(1): 7–13, ills.
- Bayer, M. B. (2006) *Haworthia* update. Essays on *Haworthia*. Volume 2. St. Michaels on Wyre (GB): Alsterworthia International / Harry Mays.
- Bayer, M. B. (2007a) *Haworthia* update. Essays on *Haworthia*. Volume 3. Part 1 / Part 2. St. Michaels on Wyre (GB): Alsterworthia International / Harry Mays.
- Bayer, M. B. (2007b) Comments on *Haworthia mertonii* I. Breuer. *Alsterworthia Int.* 7(3): 25–27, ills.
- Bayer, M. B. (2008) *Haworthia* update. Essays on *Haworthia*. Volume 4. St. Michaels on Wyre (GB): Alsterworthia International / Harry Mays.
- Bayer, M. B. (2009) *Haworthia* update. Essays on *Haworthia*, volume 5. Part 1 / Part 2. St. Michaels on Wyre (GB): Alsterworthia International / Harry Mays.
- Bayer, M. B. (2010a) *Haworthia* update. Essays on *Haworthia*. Volume 6. St. Michaels on Wyre (GB): Alsterworthia International / Harry Mays.
- Bayer, M. B. (2010b) Variants of *Haworthia aristata* at Kaboega. *Haworthiad* 24(1): 20–23, ills.
- Bayer, M. B. (2010c) Klip River plants in cultivation. *Haworthiad* 24(2): 36–37, ills.
- Bayer, M. B. (2010d) A case of mistaken identity. *Haworthiad* 24(2): 40–41, ill.
- Bayer, M. B. (2010e) *Haworthia minima* 'opalina'. *Haworthiad* 24(3): 64–65, ills.
- Bayer, M. B. (2010f) *Haworthia kingiana* and *H. minima* variants. *Haworthiad* 24(3): 68–74, ills.
- Bayer, M. B. (2010g) Comments on *Haworthiad* 24 No. 2, 2010. *Haworthiad* 24(3): 79–86, ills.
- Bayer, M. B. (2012a) *Haworthia* update. Essays on *Haworthia*, Volume 7 (part 1 / 2 / 3 / 4). St. Michaels on Wyre (GB): Alsterworthia International / Harry Mays.
- Bayer, M. B. (2012b) *Haworthia* update. Essays on *Haworthia*, Volume 8. St. Michaels on Wyre (GB): Alsterworthia International / Harry Mays.
- Bayer, M. B. (2012c) New finds in *Haworthia*. *Cact. Succ. J. (US)* 84(1): 41–50, ills., map. <https://doi.org/10.2985/0007-9367-84.1.41>
- Bayer, M. B. (2012d) Just what do we do with names for *Haworthia*? *CactusWorld* 30(4): 211–214, ills.
- Bayer, M. B. (2013a) Plants in my collection 11: *Haworthia decipiens*. *Haworthiad* 27(2): 42–43, ills.
- Bayer, M. B. (2013b) The *Haworthia* pollinator. *Alsterworthia Int.* 13(1): 30, ills.
- Bayer, M. B. (2013c) Another *Haworthia* pollinator. *Alsterworthia Int.* 13(1): 31, ills.
- Bayer, M. B. & Dold, T. (2003) Ecotypes in *Haworthia*. *Aloe* 40(1): 10–15, ills., maps.
- Bayer, M. B. & Manning, J. C. (2012a) A rationalization of names in *Haworthia*. A list of species with new combinations and new synonyms. *Alsterworthia Int.* 12(1): 7–17.
- Bayer, M. B. & Manning, J. C. (2012b) The *Haworthia* nomenclator: A list of accepted species with some guidelines for infraspecific names. Redditch (GB): Haworthia Society.
- Biko'o, A. A. [ & al. 2011], Plessis, D. G. C. du & Myburgh, W. J. (2011) Population size, structure and habitat features of *Haworthia koelmaniorum* var. *mcmurtryi*, an endemic plant from Mpumalanga Province, South Africa. *Koedoe* 53(1): 1–8, ill., map. <https://doi.org/10.4102/koedoe.v53i1.1025>
- Bosch, P. J. A. (2004) The geological, pedological and climatological influence on variety generation in *Haworthia koelmaniorum* var. *koelmaniorum* and *H. koelmaniorum* var. *mcmurtryi*. *Aloe* 41(2-3): 56–60, ills., map.
- Breuer, I. (1998a) The world of *Haworthias*. Volume 1. Bibliography and annotated index. Niederzier / Homburg (DE): Ingo Breuer / Arbeitskreis für Mammillarienfunde.
- Breuer, I. (1998b) Die Gattung *Haworthia* im Überblick. *Schumannia* 2: 3–74, ills., maps.
- Breuer, I. (2010) The genus *Haworthia*. Book 1. St. Michaels on Wyre (GB): Alsterworthia International.
- Breuer, I. (2011) The genus *Haworthia*. Book 2, part 1 / part 2. St. Michaels on Wyre (GB): Alsterworthia International.
- Breuer, I. & Metzger, D. (1997) Types of names accepted in *Haworthia* (*Aloaceae*). *Taxon* 46(1): 3–14. <https://doi.org/10.2307/1224286>
- Coopoosamy, R. M. & Naidoo, K. K. (2011) Screening of traditional utilized *Haworthia limifolia* for antibacterial and antifungal properties. *J. Med. Pl. Res.* 5(1): 109–113.
- Craib, C. (2007) The autoecology and status of *Haworthia koelmaniorum* variety *mcmurtryi*. *Aloe* 44(1): 22–27, ills.
- Daru, B. H. [ & al. 2013], Manning, J. C., Boatwright, J. S., Maurin, O., Mclean, N., Schaefer, H., Kuzmina, M. & Bank, M. van der (2013) Molecular and morphological analysis of subfamily *Aloioideae* (*Asphodelaceae*) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62(1): 62–76, ills. <http://www.jstor.org/stable/24389313>
- Gildenhuis, S. D. (2017) *Haworthiopsis* — an illustrated taxonomy. *Aloe* 53(1): 2–78, ills., map.
- Gildenhuis, S. D. & Klopper, R. R. (2016) A synoptic review and new infrageneric classification for the genus *Haworthiopsis* (*Xanthorrhoeaceae: Asphodeloideae*).

- Phytotaxa 265(1): 1–26, map, key. <https://doi.org/10.11646/phytotaxa.265.1.1>
- Grenier, F. (2013) *Haworthia* taxonomy: A practical approach. *Aloe* 50(3): 110–115, ills.
- Guillot, D. & Laguna Lumberas, E. (2012) Algunas especies y formas horticolas escapadas de cultivo o pertenecientes a cultivos abandonados presentes en la Comunidad Valenciana (citas y aspectos históricos). *Bouteloua* 9: 47–55, ills.
- Hayashi, M. (2002) Some new species of [*Haworthia*] section *Retusae*. *Haworthia Study* 7: 14, ills.
- Hayashi, M. (2008) A system for *Haworthia*. *Haworthia Study* 19: 10–15.
- Hayashi, M. (2013) Total list of *Haworthia* cultivars. *Haworthia* cultivar names published in Japan since 1905. *Haworthia Study* 28: [i]–[vi], 1–271 pp., ills.
- Hildyard, B. (2016a) Variegates. *Haworthiad* 30(1): 15–20, ills.
- Hildyard, B. (2016b) *Haworthia tessellata* Haw. (*Haworthiopsis tessellata*). *Haworthiad* 30(3): 73–80, map, ills.
- Jacobsen, H. (1960) A handbook of succulent plants. London (GB): Blandford Press.
- Jarvis, C. (2007) Order out of chaos. Linnean plant names and their types. London (GB): The Linnean Society of London / Natural History Museum, London.
- Mak, H. C. K. (2003) *Haworthia truncata* hybrids — a preliminary survey (part 1) / part 2. *Haworthiad* 17(2): 63–74, (3): 103–114, ills.
- Manning, J. C. (2013) *Haworthia margaritifera* / *pumila*. *Alsterworthia Int.* 13(1): 6, ill.
- Manning, J. C. [ & al. 2014a], Boatwright, J. S., Daru, B. H., Maurin, O. & Bank, M. van der (2014) A molecular phylogeny and generic classification of *Asphodelaceae* subfamily *Aloioideae*: A final resolution of the prickly issue of polyphyly in the Alooids. *Syst. Bot.* 39(1): 55–74, key. <https://doi.org/10.1600/036364414X678044>
- Marx, G. (2008a) *Haworthia magnifica* var. *splendens* revisited. *Aloe* 44(3): 70–74, ills.
- Marx, G. (2008b) *Haworthia marxii* S. D. Gildenhuys — an update. *Haworthiad* 22(3): 74–80, ills.
- Marx, G. (2009a) *Haworthia emelyae*, the ‘Klein Karoo Kliprosie’. *Aloe* 46(4): 76–95, ills., map.
- Marx, G. (2009b) A few notes on *Haworthia devriesii* Breuer. *Alsterworthia Int.* 9(1): 10–12, ills.
- Marx, G. (2011a) *Haworthias uitewaaliana* von Poellnitz. *Aloe* 48(2): 28–29, ills.
- Marx, G. (2011b) *Haworthia splendens*: Undeniably magnificent, conceivably mirabiloid, but a rarity in need of protection. *Haworthiad* 25(1): 3–9, ills.
- Marx, G. (2013a) *Haworthia mirabilis* (Haw.) Haw. — a medley of mystery and misinterpretation. *Aloe* 50(3): 98–109, ills.
- Marx, G. (2013b) *Haworthia* pollination and pollinators. *Haworthiad* 27(3): 59–62, ills.
- Marx, G. (2014a) Two new populations of *Haworthia emelyae*. *Aloe* 51(1): 20–24, ills.
- Marx, G. (2014b) *Haworthias* — nature’s naughty cultivars. A dated update regarding a few fascinating and vindicable retusoids. *Cact. Succ. J. (US)* 86(4): 136–148, ills. <https://doi.org/10.2985/015.086.0401>
- Marx, G. (2016a) *Haworthia correctae* Poelln. corrected. *Aloe* 52(1): 18–23, ills.
- Marx, G. (2016b) The quick brown fox jumps over the lazy dog. *Haworthiad* 30(2): 31–37, ills.
- Mays, H. (2013) Hybrids & cultivars of the succulent *Asphodelaceae* [sic!]. Volume 2. *Haworthia*. St. Michaels on Wyre (GB): Harry Mays.
- Molteno, S. & Smith, G. F. (2017) Notes on morphological variation in, and the biogeography of, *Tulista kingiana* Gideon F. Sm. & Molteno [sic!] (*Asphodelaceae: Aloioideae*) from the south-central Western Cape Province of South Africa. *Bradleya* 35: 46–57, ills., map. <https://doi.org/10.25223/brad.n35.2017.a5>
- North, G. B. [ & al. 2008], Brinton, E. K. & Garrett, T. Y. (2008) Contractile roots in succulent monocots: Convergence, divergence and adaptation to limited rainfall. *Pl. Cell Environm.* 31: 1179–1189, ills. <https://doi.org/10.1111/j.1365-3040.2008.01832.x>
- Ramdhani, S. [ & al. 2009], Bayer, M. B., Cowling, R. M. & Barker, N. P. (2009) Molecular phylogenetic studies in *Haworthia* Duval (*Asphodelaceae*). *Alsterworthia Int.* 9(3): 13–17, ills.
- Ramdhani, S. [ & al. 2011], Barker, N. P. & Cowling, R. M. (2011) Revisiting monophyly in *Haworthia* Duval (*Asphodelaceae*): Incongruence, hybridization and contemporary speciation. *Taxon* 60(4): 1001–1014. <https://www.jstor.org/stable/41317322>
- Rowley, G. D. (2013a) Generic concepts in the *Aloioideae* — part 3. The phylogenetic story. *Alsterworthia Int. Spec. Issue* 10: 3–6.
- Schulz, R. (2009) *Haworthia* for the collector. San Bruno (US): Schulz Publishing.
- Scott, C. L. (1977) The identity of *Haworthia arachnoidea* (L.) Duval. *Cact. Succ. J. (US)* 49(5): 205–208.
- Scott, C. L. (1980) *Haworthia aristata* Haw. *Nation. Cact. Succ. J.* 35(1): 11–13.
- Scott, C. L. (1985) The genus *Haworthia* (*Liliaceae*), a taxonomic revision. Johannesburg (ZA): Aloe Books.
- Scott, C. L. (1994a) A new species of *Haworthia*, *H. reddii*. *Cact. Succ. J. (US)* 66(4): 182–183, ill.
- Scott, C. L. (1994b) A new species of *Haworthia* (*Asphodelaceae*) — *H. pringlei*. *Bradleya* 12: 103–104. <https://doi.org/10.25223/brad.n12.1994.a7>
- Scott, C. L. (1996) A new species of *Haworthia* (*Asphodelaceae*) — *H. venusta*. *Bradleya* 14: 87–88, ills. <https://doi.org/10.25223/brad.n14.1996.a12>
- Scott, M. (2011) General notes on the phenotypes and morphological features of *Haworthia maxima* (Haw.) Duval. *Aloe* 48(2): 42–45, ills.
- Smith, G. F. [ & al. 2002], Wyk, B-E. van, Steyn, E. M. A. & Breuer, I. (2002) Infrageneric classification of *Haworthia* (*Aloaceae*): Perspectives from nectar sugar analysis. *Syst. & Geogr. Pl.* 71(2): 391–397. [www.jstor.org/stable/3668687](http://www.jstor.org/stable/3668687)
- Treutlein, J. [ & al. 2003b], Smith, G. F., Wyk, B-E. van & Wink, M. (2003) Evidence for the polyphyly of *Haworthia* (*Asphodelaceae* subfamily *Aloioideae*;

- Asparagales*) inferred from nucleotide sequences of *rbcL*, *matK*, ITS1 and genomic fingerprinting with ISSR-PCR. *Pl. Biol. (Stuttgart)* 5(5): 513–521. <https://doi.org/10.1055/s-2003-44793>
- Vosa, C. G. (2005) On the classification of some species of the genus *Haworthia*, subgenus *Haworthia* (*Asphodelaceae*). *Caryologia* 57(4): 395–399, ills. <https://doi.org/10.1080/00087114.2004.10589422>
- Vries, V de. (2010) *Haworthia vincentii* — east of Albertinia. *Haworthiad* 24(2): 38–39, ills.
- Zietsman, P. C. & Smith, G. F. (2010) Notes on African plants. *Asphodelaceae*. Occurrence of *Haworthia bolusii* var. *blackbeardiana* in the Free State, South Africa. *Bothalia* 40(1): 58, ill. <http://hdl.handle.net/2263/16110>
- Zonneveld, B. J. M. (2015) Nuclear genome sizes of 343 accessions of wild collected *Haworthia* and *Astroloba* (*Asphodelaceae*, *Aloioideae*), compared with the genome sizes of *Chortolirion*, *Gasteria* and 83 *Aloe* species. *Pl. Syst. Evol.* 301(3): 931–953. <https://doi.org/10.1007/s00606-014-1127-4>
- Scott, C. L. (1995) A new species of *Haworthia* (*Asphodelaceae*) - *H. joeyae*. *Bradleya* 13: 80–81, ills. <https://doi.org/10.25223/brad.n13.1995.a>





## Kniphofia ASPHODELACEAE

G. F. Smith and E. Figueiredo

**Kniphofia** Moench (Methodus, 631, 1794). **Type:** *Kniphofia alooides* Moench [*nom. illeg.*,  $\equiv$  *Kniphofia uvaria* (Linné) Oken]. — *Asphodeloideae* — **Lit:** Baker (1896: 275, Flora Capensis); Berger (1908: 31–32, synopsis); Codd (1968: revision RSA); Marais (1973: revision tropical Africa); Kativu (1996: 28, revision Flora Zambesiaca area). **Distr:** Mostly continental Africa but extending with 1 species each to Madagascar and the Arabian Peninsula (Yemen), esp. widespread in S Africa in all countries except Namibia and Botswana. **Etym:** For Johann Jeremias (Hieronymus) Kniphof (1704–1765), German physician, naturalist and botanist.

**Incl.** *Notosceptrum* Benth (1883). **Type:** *Kniphofia benguellensis* Baker [see Codd, Taxon 34: 510, 1985 on the typification].

Herbaceous perennials, tufted or solitary from a thick, simple or branched rhizome, rarely somewhat caulescent, up to 2 (–4) m high; **L** soft (mesophytic), rarely succulent (*K. typhoides*), rosulate, rarely distichous, linear, long-tapered to the apex,

V-shaped in cross section, usually carinate, margins smooth or minutely serrulate; **Inf** a terminal, dense to lax, many-flowered, subspicate, simple or very rarely branched raceme; **Bra** scarious, persistent, longer than the short pedicels; **Ped** inconspicuously articulated; **Fl** spreading or pendulous; **Per** deciduous, tube campanulate to cylindrical, lobes short, white, yellow, brownish or various shades of red; **St** as long as or longer than the perianth at anthesis; **Ov** sessile, with many axile ovules; **Sty** filiform, usually finally exerted; **Sti** capitate, minute; **Fr** a capsule, globose to ovoid, often triquetrous, chartaceous when dry; **Se** somewhat flattened, acutely 3-angled or winged; endosperm fleshy. — **Cytology:**  $x = 6$ .

In one of the first comprehensive treatments of *Kniphofia*, Berger (1908) recognised 67 species and some varieties. He upheld the small genus *Notosceptrum* based on floral characters, but Codd (1967) merged it with *Kniphofia*. For *Kniphofia* in South Africa, Codd (1968) recognised 45 species and some subspecies, while Marais (1973) treated 22 tropical African species. Kativu (1996) and Kativu (2001: 26–33) included eight species for the Flora Zambesiaca area, while Whitehouse (2002) recorded eight species of *Kniphofia* from the Flora of Tropical East Africa region. In the most recently published regional treatment of the genus, Codd (2005) documented 48 species and 6 subspecies from southern Africa (Swaziland, Lesotho and South Africa). In total, *Kniphofia* consists of about 70 species with a predominantly African distribution, single outliers occurring on

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**Fig. 1** *Kniphofia typhoides*. (Copyright: G. Fritz)



Madagascar and in Yemen. In terms of number of species, the genus is best represented in southern Africa. Ramdhani & al. (2006) and Ramdhani & al. (2009) discussed the phylogeny of *Kniphofia*.

The genus essentially consists of herbaceous perennials that prefer moist habitats, where they often occur in vast numbers in dense colonies. Several species of *Kniphofia*, commonly and in the gardening trade known as red-hot poker, are of considerable horticultural value in parts of the mild-temperate Northern Hemisphere where, for example in the United Kingdom, numerous very attractive hybrids are offered for sale. Some of the species and cultivars have value as cut flowers, again more so in Europe than in its native Africa.

Succulence has evolved in a single South African species of the genus:

**K. typhoides** Codd (Flow. Pl. Afr. 36(3–4): t. 1424 + text, 1964). **Type:** RSA, KwaZulu-Natal (*K. Saunders* s.n. in *Medley Wood* 3895 [K]). —

**Distr:** RSA (KwaZulu-Natal, Mpumalanga, Gauteng, North-West, Free State); almost invariably found in heavy black clay soils in usually moist depressions, watercourses and seepage areas. — Fig. 1.

≡ *Notosceptrum natalense* Baker (1896).

Plants with one to several stems from a short, thick rhizome; **L** ± distichous, glaucous, 35–65 × 0.8–2 cm, shallowly channelled above, keeled below, often spirally twisted, succulent, margins smooth; **Inf** peduncle 40–70 cm; raceme cylindrical, very dense, 15–30 × 1.5–2.5 cm, rounded at the apex; buds erect, dark brown; **Fl** ascending to spreading, distinctly sugar-scented; **Bra** obovate or subrotund to ovate, 4–6 mm, rounded at the apex, margin entire to minutely denticulate; **Ped** up to 0.5 mm; **Per** subcampanulate or shortly cylindrical, 4.5–6.5 mm long, brown to purplish-brown, lobes ovate to rounded, 1.5 mm, not spreading; **St** exerted by 3–4 mm at anthesis; **Fr** ovoid, 5–6 mm.

Smith & al. (1997) were the first to point out that *K. typhoides* is a typical leaf succulent. In its natural habitat it flowers from late summer to early autumn (February to March).

## References

- Baker, J. G. (1896) *Liliaceae*. In: Thiselton-Dyer, W. T. (ed.): *Flora Capensis*; 6(2): 253–384. London (GB): L. Reeve & Co. <http://biodiversitylibrary.org/page/712288>
- Berger, A. (1908) *Liliaceae* — *Asphodeloideae* — *Aloineae*. In: Engler, A. (ed.): *Das Pflanzenreich* IV.38 (Heft 33). Leipzig (DE): Wilhelm Engelmann. <http://www.biodiversitylibrary.org/bibliography/72397#/>
- Codd, L. E. (1967) The status of the genus *Notosceptrum* Benth. (*Liliaceae*). *Bot. Not.* 120: 41–45.
- Codd, L. E. (1968) The South African species of *Kniphofia*. *Bothalia* 9(3–4): 363–513. <https://doi.org/10.4102/abc.v9i3/4.1790>
- Codd, L. E. (2005) *Kniphofia*. In: Germishuizen, G. & Mombberg, B. A. (eds.): *Flora of southern Africa*, 5(1: Fasc. 2): *Asphodelaceae* (first part). Pretoria (ZA): South African National Biodiversity Institute.
- Kativu, S. (1996) *Asphodelaceae* of the Flora Zambesiaca area. *Kirkia* 16: 27–53.
- Kativu, S. (2001) *Asphodelaceae*. In: Pope, G. V. (ed.): *Flora Zambesiaca*; 12(3): 25–48, keys. Richmond (GB): Royal Botanic Gardens Kew.
- Marais, W. (1973) A revision of the tropical species of *Kniphofia* (*Liliaceae*). *Kew Bull.* 28: 465–483. <https://doi.org/10.2307/4108891>
- Ramdhani, S., Barker, N. P. & Baijnath, H. (2006) Phylogenetics of the genus *Kniphofia* Moench (*Asphodelaceae*). In: Ghazanfar, S. A. & Beentje, H. J. (eds.): *Taxonomy and Ecology of African Plants: their conservation and sustainable use* (Proceedings of the 17th AETFAT Congress); pp. 559–573. Richmond (GB): Royal Botanic Gardens, Kew.
- Ramdhani, S., Barker, N. P. & Baijnath, H. (2009) Rampant non-monophyly of species in *Kniphofia* Moench (*Asphodelaceae*) suggests a recent Afrotropical radiation. *Taxon* 58: 1141–1152. <https://www.jstor.org/stable/27757008>
- Smith, G. F. [ & al. 1997], Jaarsveld, E. J. van, Arnold, T. H., Steffens, F. E., Dixon, R. D. & Retief, J. A. (eds.) (1997) *List of Southern African succulent plants*. Pretoria (ZA): Umdaus Press.
- Whitehouse, C. M. (2002) *Asphodelaceae*. In: Beentje, H. J. (ed.): *Flora of Tropical East Africa*. (Rotterdam (NL)/Brookfield (US): A. A. Balkema.





## × *Maysara* ASPHODELACEAE

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× **Maysara** D. M. Cumming (Haworthiad 13(3): 115, 1999). — *Aloioideae* — **Lit:** Cumming (1999). **Etym:** For Harry Mays (fl. 1999), English succulent plant enthusiast and at the time editor of the journal “Haworthiad”; plus the suffix ‘-ara’, indicating plurigeneric hybrids.

**Incl.** × *Rowleyara* D. M. Cumming (1999) (*nom. illeg.*, Art. 53.1).

= *Astroloba* × *Gasteria* × *Haworthia*. The only known combination has not been named formally.

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### References

Cumming, D. M. (1999) New nothogenera proposed for four trigeneric hybrids within *Aloaceae*. *Haworthiad* 13(1): 20–21.

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## × *Poellneria* ASPHODELACEAE

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× *Poellneria* G. D. Rowley (Nation. Cact. Succ. J. 28(1): 7, 1973). — *Aloioideae*

= *Poellnitzia* × *Gasteria*. No formally named taxa are known, and Rowley (1982: 49) lists a single combination with an unidentified *Gasteria* as the other parent.

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### References

Rowley, G. D. (1982) Intergeneric hybrids in succulents. Nation. Cact. Succ. J. 37(1): 2–6, (2): 45–49, (3): 76–80, (4): 119, ills.

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## Poellnitzia ASPHODELACEAE

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**Poellnitzia** Uitewaal (Succulenta 22: 61, 1940). **Type:** *Apicra rubriflora* L. Bolus. — **Alooiidae** — **Lit:** Smith (1994: taxonomic history); Smith (1995: monograph). **Distr:** RSA (Western Cape: Worcester-Robertson Karoo). **Etym:** For Joseph Karl L. A. Von Poellnitz (1896–1945), German agriculturist and botanist in Thüringen, strongly interested in succulent plant systematics.

Herbaceous perennials, caulescent, proliferous, stems to 25 cm,  $\pm 1$  cm  $\varnothing$ ; **Ros** of 4-ranked leaves in spiralling rows; **L** thick, hard, squarrose-imbricate, dark green,  $2\text{--}4 \times \pm 2$  cm broad near the base, to 5 mm thick, margin minutely scabrid, apex pungent-acuminate; **Inf** racemose, simple, born horizontally, to 50 cm, sterile part bracteate, with secund erect flowers; **Ped** short, erect, persistent; **Tep** orange to red with dark green tips, basally united into a narrow elongate tube  $\pm 20$  mm long and 3 mm  $\varnothing$  with the upper  $\frac{1}{3}$  slightly decurved, free parts of the tepals closely adhering, apically spoon-shaped, connivent; **St** 6, inserted in the perianth tube,  $\pm 18$  mm; **Fil** light green; **Anth** yellow, dorsifixed, dehiscing longitudinally, introrse; **Ov** superior, green, sessile, 6–7 mm, 3 mm  $\varnothing$ ; **Sty** white, straight,

capitate, 12 mm; **Fr** 3-locular capsules, cylindrical, apically retuse, dehiscing loculicidally,  $\pm 16$  mm, 3–4 mm  $\varnothing$ ; **Se** angled, dark brown to black, shortly winged,  $\pm 4$  mm. — **Cytology:**  $2n = 14$  (Smith 1991).

On vegetative morphological grounds, this monotypic genus shows affinities with some representatives of *Aloe*, *Astroloba* and *Haworthia*, and the molecular phylogeny studies of Daru & al. (2013) and Manning & al. (2014a) indeed place *Poellnitzia* as sister to *Astroloba* species. However, the flower morphology is unique in the family in that the dark green free portions of the tepals are connivent with the very tips scarcely separated. Cumming (2006) found that *Poellnitzia* does not produce hybrids with *Astroloba*, *Haworthia* or *Aloe*, and in crosses with *Gasteria*, seed only forms on *Gasteria*, but never on *Poellnitzia*. Cumming (2006) therefore suggests that *Poellnitzia* is best treated as a monotypic genus. However, further investigations of *Poellnitzia* and its relatives may place it in one of the other *Alooiidae* genera. In this regard, Manning & Smith (2000) suggested the placement of *Poellnitzia* in *Astroloba*, as the tepals are imbricate as in species of *Astroloba*, and the flower characters represent a bird-pollination syndrome. *P. rubriflora* is restricted to the Worcester-Robertson Karoo centre of endemism in South Africa (Wyk & Smith 2001).

**P. rubriflora** (L. Bolus) Uitewaal (Succulenta 22: 61, 1940). **Type:** RSA, Western Cape (Smith

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**Fig. 1** *Poellnitzia rubriflora*. (Copyright: U. Eggli)



**Fig. 2** *Poellnitzia rubriflora*. (Copyright: U. Eggli)

s.n. [BOL 45213]). — **Distr:** RSA (Western Cape: Worcester-Robertson Karoo: Robertson, Bonnievale and McGregor districts); predominantly winter rainfall areas, karroid shrublands, 400–800 m. **I:** Smith (1994: 74); Smith & al. (1995). – Figs. 1 and 2.

≡ *Apicra rubriflora* L. Bolus (1920) ≡ *Haworthia rubriflora* (L. Bolus) Parr (1971) ≡ *Aloe rubriflora* (L. Bolus) G. D. Rowley (1981) ≡ *Astroloba rubriflora* (L. Bolus) G. F. Smith & J. C. Manning (2000) (*incorrect name*, ICN Art. 11.4) ≡ *Tulista rubriflora* (L. Bolus) G. D. Rowley (2013); **incl.** *Apicra jacobsoniana* Von Poellnitz (1939) ≡ *Poellnitzia rubriflora* var. *jacobsoniana* (Von Poellnitz) Uitewaal (1955) ≡ *Haworthia rubriflora* var. *jacobsoniana* (Von Poellnitz) Parr (1972) (*nom. inval.*, ICN Art. 41.5).

Description as for the genus.

## References

- Cumming, D. M. (2006) *Poellnitzia* Uitewaal: Inferred relationships from limited hybridization. *Alsterworthia Int.* 6(1): 13–16.
- Daru, B. H. [& al. 2013], Manning, J. C., Boatwright, J. S., Maurin, O., Mclean, N., Schaefer, H., Kuzmina, M. & Bank, M. van der (2003) Molecular and morphological analysis of subfamily *Aloioideae* (*Asphodelaceae*) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62(1): 62–76, ills. <http://www.jstor.org/stable/24389313>.
- Manning, J. C. & Smith, G. F. (2000) The genus *Poellnitzia* included in *Astroloba*. *Bothalia* 30(1): 53. <http://www.abcjournal.org/index.php/ABC/article/view/540>.
- Manning, J. C. [& al. 2014a], Boatwright, J. S., Daru, B. H., Maurin, O. & Bank, M. van der (2014) A molecular phylogeny and generic classification of *Asphodelaceae* subfamily *Aloioideae*: A final resolution of the prickly issue of polyphyly in the Alooids. *Syst. Bot.* 39(1): 55–74, key. <https://doi.org/10.1600/036364414X678044>.
- Smith, G. F. (1991) The chromosomes of *Chortolirion* and *Poellnitzia* (*Asphodelaceae: Aloioideae*). *Bothalia* 21(2): 171–175, ills. <http://abcjournal.org/index.php/ABC/article/view/884>.
- Smith, G. F. (1994) Taxonomic history of *Poellnitzia* Uitewaal, a unispesific genus of *Aloioideae* (*Asphodelaceae*). *Haseltonia* 2: 74–78, ills.
- Smith, G. F. (1995) FSA contributions 3: *Asphodelaceae/Aloaceae*, 1028000 *Poellnitzia*. *Bothalia* 25(1): 35–36, ill., map. <http://abcjournal.org/index.php/ABC/article/view/709>.
- Smith, G. F., Wyk, B-E. van & Condy, G. (1995) *Poellnitzia rubriflora*. *Flow. Pl. Afr.* 54: 94–98, t. 2119, map.
- Wyk, A. E. (B.) van & Smith, G. F. (2001) Regions of floristic endemism in Southern Africa. A review with emphasis on succulents. Hatfield (ZA): Umduas Press.



## Trachyandra ASPHODELACEAE

E. Van Jaarsveld

**Trachyandra** Kunth (Enum. Pl. 4: 573, 1843).  
**Type:** *Anthericum hispidum* Linné. —  
*Asphodeloideae* — **Lit:** Obermeyer (1962: revision RSA). **Distr:** S Africa (esp. SW RSA) extending to tropical Africa (Somalia, Ethiopia, Yemen), 1 species in Madagascar. **Etym:** Gr. ‘trachys’, rough; and Gr. ‘aner, andros’, male; for the rough filaments.

**Incl.** *Lepicaulon* Rafinesque (1837) (*nomen rejiciendum*, Art. 56.1). **Type:** *Anthericum squameum* Linné *fil.*

**Incl.** *Obsitila* Rafinesque (1837) (*nomen rejiciendum*, Art. 56.1). **Type:** *Anthericum hispidum* Linné [lectotype, designated by Merrill, Ind. Raf., 92, 1949 (ICBN 2006: 283)].

**Incl.** *Dilanthes* Salisbury (1866). **Type:** *Dilanthes revoluta* Salisbury [typification by inference, only element included].

**Incl.** *Liriothamnus* Schlechter (1924). **Type:** *Anthericum involucreatum* Baker.

Plants variable, perennial, glabrous to glandular-pubescent rosulate leaf succulents, acaulescent, geophytic or shrubby to 2 m tall; **R**stock a tuberous caudex or as erect rhizome; **R** fusiform to fibrous, terete; stem erect, woody and covered with leaf

bases; **L** dimorphic or uniform, lamina flat or triangular in cross-section to terete, often linear-lorate, rarely canaliculate, straight or undulating; **Inf** racemose, occasionally paniculate, peduncle terete, bracteose; **Fl** solitary, spreading to pendulous; **Per** rotate, often becoming recurved; **Tep** 6 in 2 whorls, white to mauve, **OTep** narrower than **ITep**; **St** 6, adnate to the tepal bases; **Fil** scabrid; **Anth** dorsifixed, introrse; **Ov** globose, superior, 3-locular; **Sty** terete; **Sti** capitate; **Fr** loculicidal globose capsules, drooping; **Se** dark grey to black, smooth to papillate, becoming glutinous.

A genus of  $\pm 65$  species (Whitehouse 2002), most of which are geophytes with some claim to succulence. *Trachyandra* has a wide distribution in S Africa but shows a concentration of species in the winter rainfall regions of RSA. They are seldom cultivated but are easy and should be kept dry during the summer months. *T. adamsonii* is the largest in the genus, and has a shrub-like growth form superficially resembling climbing species of *Aloe* such as *A. ciliaris*. Most if not all species exhibit considerable succulence. Some species show distinct basal caudices, esp. those of Sect. *Liriothamnus*, while those of the other sections are usually without a caudex. Only a limited number of species is in cultivation, and for this reason, only a small selection is covered below by way of example.

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The genus is divided into 3 sections according to Obermeyer (1962: 717):

- [1] Sect. *Liriothamnus* (Schlechter) Obermeyer 1962: Plants glabrous; outer **L** not reduced to scales; **Inf** mostly simple.
- [2] Sect. *Trachyandra*: Plants glabrous; outer **L** reduced to scales; **Inf** mostly branched.
- [3] Sect. *Glandulifera* Obermeyer 1962: Plants glandular-pubescent.

**T. adamsonii** (Compton) Obermeyer (Bothalia 7 (4): 720, 1962). **Type:** RSA, Western Cape (*Compton* s.n. in NBG 318/22 [NBG]). — **Distr:** RSA (Northern Cape, Western Cape); dry Olifants Sandstone Fynbos and Succulent Karoo vegetations, on quartzitic sandstones.

≡ *Liriothamnus adamsonii* Compton (1931).

[1] Erect, sparingly branched, woody, rosulate shrubs to 2 m; caudex depressed, globose above and tapering into the stem, flat below with grey bark; **R** succulent, terete, 5 mm Ø; **Br** 1–2 cm Ø, grey with peeling leaf remains, becoming smooth at the base; **L** glaucous, 16–30 × 1.5–3.5 cm, striate, crowded at the stem tips, linear-lanceolate, flat, lower face slightly keeled, upper face basally channelled, margin denticulate, apex acuminate; **Inf** ascending, racemose, to 50 cm, with a pair of side branches at the base; **Bra** triangular to ovate-acuminate, 2–10 × 1–3 mm; **Ped** erect, 6–11 mm; **Fl** white with yellow eye at the tepal bases, to 30 mm Ø; **OTep** 11 × 2.5 mm, linear-lanceolate; **ITep** 10 × 3.5 mm; **St** 8 mm; **Ov** oblong, 2 mm; **Fr** erect, ovoid, 12 mm; **Se** grey, oblong, 3 mm.

**T. aridimontana** J. C. Manning (South Afr. J. Bot. 56(1): 1–5, ills., 1990). **Type:** RSA, Northern Cape (*Oliver & al.* 478 [PRE]). — **Distr:** RSA (Northern Cape: Richtersveld); Rosyntjieberg Succulent Shrubland and Succulent Karoo vegetations.

[1] Erect sparingly branched rosulate deciduous succulent herbs to 35 cm; caudex depressed, globose above and tapering into the stem, flat below with grey bark; **R** succulent, terete, 3 mm Ø; **Br** 0.4–1.5 cm Ø, bark grey; **L** glaucous, crowded at the stem tips, 3–6, linear-lanceolate, 3–12 × 0.3–0.7 cm Ø, subterete but

dorsiventrally flattened, lower face convex, upper face flat to canaliculate, margin denticulate, apex mucronate; **Inf** ascending, racemose, to 22 cm; **Bra** ovate to lanceolate-acuminate, to 8 mm; **Ped** patent, 1–5 mm; **Fl** white, 15–20 mm Ø; **OTep** linear, 11–13 × 2–3.5 mm; **ITep** ovate, 11–13 × 3–5.5 mm; **St** 8–9 mm; **Ov** ovoid, 1.5 mm; **Sty** 7–8 mm; **Fr** erect, narrowly ovoid, 8–12 × 4 mm; **Se** black, oblong, 3 × 1.5 mm.

**T. ciliata** (Linné *fil.*) Kunth (Enum. Pl. 4: 585, 1843). **Type:** RSA, “Cape Prov.” (*Thunberg* s.n. [UPS]). — **Distr:** Namibia, RSA (Northern Cape, Western Cape, Eastern Cape); Sandstone Fynbos and Renosterveld vegetations. – Fig. 1.

≡ *Anthericum ciliatum* Linné *fil.* (1781) ≡ *Bulbine ciliata* (Linné *fil.*) Link (1821); **incl.** *Anthericum longifolium* Jacquin (1786) ≡ *Phalangium longifolium* (Jacquin) Poiret (1804) ≡ *Trachyandra longifolia* (Jacquin) Kunth (1843); **incl.** *Anthericum canaliculatum* Aiton (1789) ≡ *Phalangium canaliculatum* (Aiton) Poiret (1804) ≡ *Bulbine canaliculata* (Aiton) Sprengel (1825) ≡ *Trachyandra canaliculata* (Aiton) Kunth (1843); **incl.** *Anthericum vespertinum* Jacquin (1804) ≡ *Phalangium vespertinum* (Jacquin) Poiret (1804) ≡ *Trachyandra vespertina* (Jacquin) Kunth (1843); **incl.** *Anthericum blepharophoron* Roemer & Schultes (1829) ≡ *Trachyandra blepharophora* (Roemer & Schultes) Kunth (1843); **incl.** *Trachyandra bracteosa* Kunth (1843); **incl.** *Anthericum recurvatum* Dinter (1931); **incl.**



**Fig. 1** *Trachyandra ciliata*. (Copyright: E. Van Jaarsveld)

*Anthericum hamatum* Von Poellnitz (1942); **incl.** *Anthericum maculatum* Von Poellnitz (1942); **incl.** *Anthericum pilosiflorum* Von Poellnitz (1942); **incl.** *Anthericum pilosiflorum* var. *subpappillosum* Von Poellnitz (1942); **incl.** *Anthericum spongiosum* Von Poellnitz (1942).

[2] Acaulescent fast-growing geophytes, rosulate, caudex absent; **R** fleshy, terete, spreading; **L** linear, to 1 m, to 2.5 cm  $\varnothing$ , upper face flat, lower face distinctly keeled, softly succulent, margins ciliate; **Inf** racemose, ascending-spreading, to 50 cm, with a pair of side branches at the base; peduncle pubescent, becoming glabrous; **Bra** to 10 mm, cymbiform, auriculate, younger bracts imbricate, subulate; **Fl** white, translucent, 20 mm  $\varnothing$ , **Tep** recurved; **OTep** linear, 10  $\times$  2 mm; **ITep** ovate, 10  $\times$  3 mm; **St** 8–9 mm; **Ov** globose, 1.5 mm; **Sty** 7–8 mm; **Fr** globose, to 14 mm  $\varnothing$ ; **Se** black, rough.

**T. falcata** (Linné *fil.*) Kunth (Enum. Pl. 4: 486, 1843). **Type:** RSA, “Cape Prov.” (*Thunberg* s.n. [UPS]). — **Distr:** S Namibia, RSA (Northern Cape, Western Cape); Succulent Karoo vegetation, sandy areas, winter- to spring-flowering.

$\equiv$  *Anthericum falcatum* Linné *fil.* (1782)  $\equiv$  *Bulbine falcata* (Linné *fil.*) Schultes *fil.* (1829); **incl.** *Chlorophytum drepanophyllum* Baker (1897)  $\equiv$  *Anthericum drepanophyllum* (Baker) Schlechter (1907); **incl.** *Anthericum weissianum* Dinter (1931).

[2] Ascending, evergreen, from a reduced rhizome, to 60 cm tall; **R** numerous, spreading, swollen during spring; shoots incl. leaves and peduncle base surrounded by membranous scales; **L** up to 4, distichous, 30  $\times$  2–3 cm, flat, semi-succulent, falcately curved, glabrous or shortly pubescent, margins minutely ciliate; **Inf** ascending sparingly branched racemes (or rarely unbranched) longer than the leaves, 30–50 cm, peduncle  $\pm$  of the same length as the flowering part, hairy at first becoming glabrous; lower **Bra** amplexicaul, short, forming a wide ascending collar around the axis, apiculate; fertile **Bra** widely ovate, subulate, membranous, white with a brown patch near the tip, closely imbricate in bud; **Ped** 10–15 mm; **Fl** white to pale mauve; **Tep** 12 mm; **Fil** scabrid; **Ov** with 8–10 ovules; **Fr**

turbinate, 10–12 mm, apiculate; **Se** grey with raised hyaline margins.

Well known as “veldkool”; the young soft inflorescences are eaten in the same way as asparagus and the species is an important food plant of the Khoi.

**T. involucrata** (Baker) Obermeyer (Bothalia 7 (4): 721, 1962). **Type:** RSA, Northern Cape (*Drège* 2681 [K, L, PRE [photo]]). — **Distr:** RSA (Northern Cape); Succulent Karoo, rocks.

$\equiv$  *Anthericum involucratum* Baker (1876)  $\equiv$  *Liriothamnus involucratus* (Baker) Schlechter (1924).

[1] Erect sparingly branched rosulate deciduous succulent gnarled shrublets to 60 cm; caudex depressed, globose above and tapering into the stem, flat below with grey bark; **R** succulent, terete, 3 mm  $\varnothing$ ; **Br** 5–15 mm  $\varnothing$ , bark grey; **L** glaucous, crowded at the stem tips, 3–6, linear-lanceolate, 17  $\times$  0.6 cm  $\varnothing$ , subterete, canaliculate, denticulate at the base, apex mucronate; **Inf** ascending, racemose, to 26 cm; **Bra** ovate to lanceolate-acuminate, to 7 mm, clasping; **Ped** recurved in fruit, 5–10 mm; **Fl** white, 15–20 mm  $\varnothing$ ; **OTep** linear, 10–14  $\times$  2–2.5 mm; **ITep** ovate, 10–14  $\times$  3–4 mm; **St** 8–9 mm; **Ov** oblong to globose, 1.5 mm; **Sty** 7–10 mm; **Fr** erect, narrowly ovoid, 10–19  $\times$  2–3 mm; **Se** black, ovoid, 3  $\times$  1.5 mm.

**T. tabularis** (Baker) Obermeyer (Bothalia 7 (4): 730, 1962). **Type:** RSA, Western Cape (*Bolus* 4726 [K, BOL]). — **Distr:** RSA (Western Cape: mainly Table Mountain); Fynbos, sandstone cliffs, 500–1000 m, summer-flowering.

$\equiv$  *Anthericum tabulare* Baker (1897); **incl.** *Anthericum glabrum* Adamson (1941); **incl.** *Anthericum palustre* Adamson (1941).

[2] First solitary, then dividing to form dense clusters; rhizome herbaceous, subterranean, wiry, to 30 cm; **R** yellow; outer **L** reduced to whitish-translucent papery scales; **L** 1–8, succulent, bright green and reddish at the base, pendent, terete in young plants, becoming flat in mature plants, 75  $\times$  0.25–0.7 cm, surface smooth, faintly striate, slightly translucent, margin entire to obscurely denticulate; **Inf** solitary or loose panicles up to

5-branched, peduncle arcuate, to 50 cm, curved upwards; **Ped** 5–7 mm; **Fl** white, sweetly scented,  $\pm 30$  mm  $\varnothing$  at anthesis; **Tep** 14 mm, with reddish-brown midribs; **OTep** oblanceolate; **ITep** linear to oblanceolate; **Fr** globose, 5 mm  $\varnothing$ ; **Se** black, angular, 2.5–3 mm  $\varnothing$ .

**T. tortilis** (Baker) Obermeyer (Bothalia 7(4): 745, 1962). **Type:** RSA, Western Cape (*Schlechter* 4846 [Z, PRE]). — **Lit:** Jaarsveld (1991); Boatwright & Manning (2010). **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo, rocks.

≡ *Anthericum tortile* Baker (1904); **incl.** *Anthericum salteri* Leighton (1938); **incl.** *Anthericum oocarpum* Schlechter ex Von Poellnitz (1942).

[2] Acaulescent geophytes to 15 cm tall with a subterranean tuber crowned with broad scale leaves; **R** swollen, fused to the elongate tuber, spreading, terete; **L** 3–6, linear, glaucous, widely spreading, transversely and plicately folded, 6–10  $\times$  0.2 cm, glabrous or sparingly pubescent, flat, margin entire; **Inf** lax ascending divaricate panicles to 9.5 cm, with up to 5 pairs of side

branches; peduncle pubescent becoming glabrous, basally arcuate; **Bra** to 3 mm, ovate-lanceolate, cymbiform, auriculate; **Ped** to 5 mm; **Fl** white to pale pink, 15 mm  $\varnothing$ ; all **Tep** linear-obovate, 5  $\times$  2 mm; **St** 2–3 mm; **Ov** globose, 0.75 mm  $\varnothing$ ; **Sty** 2–3 mm; **Fr** linear-ovoid, 7 mm; **Se** ridged.

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## References

- Boatwright, J. S. & Manning, J. C. (2010) Notes on the genus *Trachyandra* (*Asphodelaceae: Asphodeloideae*) 1: A review of the *T. thyrsoidea* group (section *Trachyandra*), including three new species from the Northern Cape. *South Afr. J. Bot.* 76(3): 499–510, ill., map, key. <https://doi.org/10.4102/abc.v40i1.183>.
- Jaarsveld, E. J. van (1991) The subfamily *Asphodeloideae* with specific reference to *Trachyandra tortilis*. *Cact. Succ. J. (US)* 63(4): 196–199, ill.
- Obermeyer, A. A. (1962) A revision of the South African species of *Anthericum*, *Chlorophytum* and *Trachyandra*. *Bothalia* 7(4): 669–767, keys, ill. <https://doi.org/10.4102/abc.v7i4.1679>.
- Whitehouse, C. M. (2002) *Asphodelaceae*. In: Beentje, H. J. (ed.): *Flora of Tropical East Africa*. Rotterdam (NL) / Brookfield (US): A. A. Balkema.

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**Part VII**

**The Family Bromeliaceae**







## Bromeliaceae

U. Eggli and E. J. Gouda

**Including** *Tillandsiaceae* Wilbreed.

Perennial small to large herbs or rarely somewhat shrubby, terrestrial or often epiphytic with caulescent or sessile small to large **Ros**; **L** spiral (rarely distichous), simple, entire or serrate, basally often broadened and  $\pm$  sheathing, often leathery or succulent, usually covered with peltate, shortly stalked, whitish, multicellular scales; **Inf** terminal (and rosettes often monocarpic), seemingly lateral (*Hechtia* p.p.) or more rarely lateral (*Dyckia*), pedunculate or sessile, simple or compound panicles, racemes, spikes or congested heads; **Bra** often brightly coloured; **Fl** bisexual or rarely unisexual and plants monoecious (*Cryptanthus* p.p., *Dyckia* p.p.) or dioecious (*Catopsis*, *Hechtia*), regular or almost so; **Per** a perigone, with 3 outer **Tep** (referred to as sepals, usually smaller and green, rarely petaloid) and 3 inner free or basally united **Tep** (referred to as petals), sometimes with a basal-lateral appendage (termed scale or nectary scale) or longitudinal callosities (termed lateral folds in some literature); **St** 6 in 2 series; **Fil** united to each other or to the tepals, or free; **Ov** of 3 carpels,

superior to inferior, with septal nectaries and axile placentation, with 2 to many ovules per locule; **Fr** longitudinally dehiscent 3-parted capsules, or fleshy berries, rarely the individual fruits of an inflorescence united into a fleshy collective fruit (*Ananas*); **Se** various, often winged or plumose, embryo small with copious endosperm.

**Order:** Poales

**Important Literature:** Smith & Downs (1974: Fl. Neotropica, *Pitcairnioideae*); Smith & Downs (1977: dto., *Tillandsioideae*); Smith & Downs (1979: dto., *Bromelioideae*); Böhme (1988: nectary and ovary anatomy); Rauh (1990: synopsis cult. taxa); Baensch (1994: synopsis cult. taxa); Smith & Till (1998: family synopsis); Benzing (2000: ecology); Butcher (2000: updated key to genera); Crayn & al. (2004: CAM origin); Barfuss & al. (2005: phylogeny *Tillandsioideae*); Givnish & al. (2007: phylogeny); Horres & al. (2007: systematics *Bromelioideae*); Schulte & Zizka (2008: phylogeny *Bromelioideae*); Givnish & al. (2011: phylogeny & biogeography); Gouda & al. (2012+: digital encyclopedia); Silvestro & al. (2014: evolution *Bromelioideae*); Givnish & al. (2014: radiation & evolution); Aguilar-Rodríguez & al. (2014: synopsis bat pollination); Gitai & al. (2014: cytology); Evans & al. (2015: phylogeny *Bromelioideae*); Roguenant & al. (2016: ill. synopsis); Palma-Silva & al. (2016: perspectives on evolution); Schütz & al. (2016: phylogeny *Pitcairnioideae*); Barfuss & al. (2016: phylogeny/classification *Tillandsioideae*);

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Males (2016: ecophysiology); Brown (2017: history of classification); Males & Griffiths (2017: functional types); Gouda & al. (cont.updated).

**Distribution:** Tropical and subtropical America (Florida to C Argentina), one species (*Pitcairnia feliciana*, not succulent) in tropical W Africa.

This large family —  $\pm 58$  genera and  $\pm 3140$  species (Givnish & al. 2014) to 75 genera and 3590 species (Gouda & Butcher 2016+: accessed 19 March 2019) — is well-known in cultivation, where its species are colloquially referred to as bromeliads. Numerous species are cultivated as house and foliage plants, and a multitude of hybrids and cultivars is generally available in the horticultural trade. Species of *Tillandsia* (“air plants”) are esp. popular among specialized collectors, and numerous hobby clubs and societies exist worldwide. *Ananas* (“pineapple”) is an important fruit crop, and several species have in the past been valued for their strong fibres (e.g. species of *Aechmea*, *Bromelia*, *Neoglaziovia*) (see Bennett (2000) for a complete list of known uses).

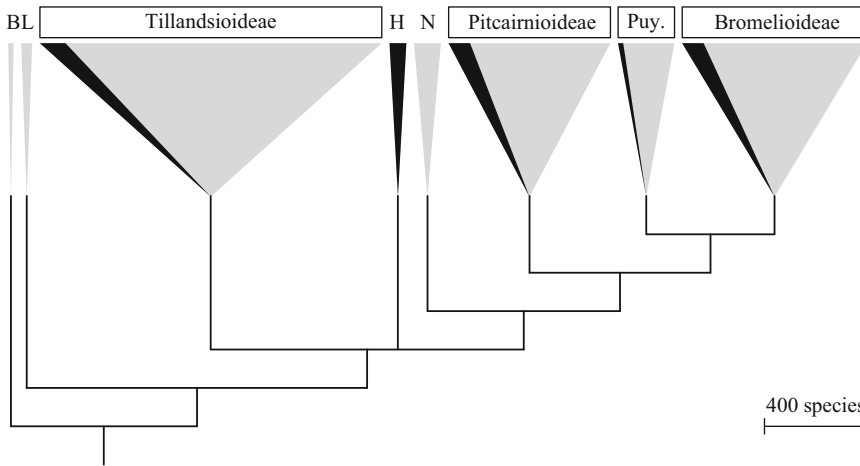
**Classification and History:** The circumscription of the family is unambiguous, and all recent studies have confirmed its monophyly. *Bromeliaceae* are part of a basal grade within Poales, and its closest relationship is with the small South American family *Rapataceae* (16 genera, 90 species; no succulents).

In traditional classifications (e.g. Smith & Downs (1974), Smith & Downs (1977) and Smith & Downs (1979)), three subfamilies (*Bromelioideae*, *Pitcairnioideae*, *Tillandsioideae*) were recognized. Recent molecular investigations do not support such a classification, and esp. the *Pitcairnioideae* in their traditional circumscription are widely paraphyletic (Givnish & al. 2007). Today, eight named clades are recognized at the rank of subfamily (Givnish & al. 2011) (Fig. 1). Palma-Silva & al. (2016) provide a summary of recent evolutionary and phylogenetic studies at different levels of the family, and also discuss biogeography and speciation in the light of current knowledge.

According to the analysis of Givnish & al. (2011), the origin of the family is on the Guayana Shield and can be dated to  $\pm 100$  mybp, while Bouchenack-Khelladi & al. (2014) place the origin of the family around 80 mybp. The modern lineages only started to differentiate much later beginning around 19 mybp, and the diversification intensified considerably after about 15.4 mybp, concurrent with major geological events in South America, esp. the rising of the Andes. Many genera have a comparatively recent origin, as witnessed by a calculated age of only  $\pm 2$  mybp for the speciose genus *Dyckia*. Diversification rates can be linked to the evolution of several characteristics (e.g. epiphytism, impounding tank rosettes, ornithophily) and are strongly coupled to life in fertile, moist, montane habitats (Givnish & al. 2014). Silvestro & al. (2014) showed that diversification rates in *Bromelioideae* are correlated both with the evolution of CAM photosynthesis (enhancing speciation rate) and the formation of tank rosettes (diminishing extinction rate).

**Terminology:** Scharf & Gouda (2008) present a detailed discussion of the erroneous terminology frequently used in the past for describing features of the inflorescence, and esp. the different ways of branching. Inflorescences of bromeliads can be unbranched spikes (flowers sessile) or racemes (flowers pedicellate), or are branched and are then correctly termed panicles. In traditional literature, such as the Smith & Down volumes, the terms ‘pinnate’, ‘bipinnate’, ‘tripinnate’, etc. are incorrectly used to describe inflorescence branching, but these terms refer to compound leaves, rather than to different branching orders of branched inflorescences. In addition, the peduncle of the inflorescence (i.e. the basal, usually bract-bearing part of several internodes without flowers) is often incorrectly referred to as ‘scape’ (whose correct application describes the base of an inflorescence that consists of a single internode and is thus without bracts, as e.g. in many *Amaryllidaceae* or *Hyacinthaceae*).

In addition to the problematical terminology used for inflorescence descriptions, that used for the parts of the perianth is also to some degree in dispute: Bromeliads, like other monocotyledons,



**Fig. 1** Summary phylogeny of *Bromeliaceae* (3140 species total, data from Givnish & al. (2014) and Stevens (2001+), accessed Aug 2016). B, *Brocchinioideae*; H,

*Hechtioideae*; L, *Lindmanioideae*; N, *Navioideae*; Puy, *Puyoideae*. (Copyright: U. Eggli)

have a perigone, and its elements would, according to a strict terminology, have to be referred to as tepals. Because frequently only the inner whorl is petaloid, the use of the terms sepals and petals has become established by tradition throughout bromeliad literature, and this is also the usage followed here.

A further complication is caused by the position of the ovary, which is inferior in *Bromelioideae* but partly half-inferior in the traditional *Pitcairnioideae* and *Tillandsioideae* (Böhme 1988, Bernardello & al. 1991), or superior in *Dyckia* (Fagundes & Mariath 2010, Santos-Silva & al. 2015). In the case of *Tillandsioideae*, the ovary appears to be superior macroscopically, but both Böhme (1988) and Bernardello & al. (1991) showed that the ovary is partially sunken into a receptacle. Accordingly, the often used term ‘pedicel’ cannot be used in descriptions of *Tillandsia*.

**Ecology:** Ecological specializations are numerous. Especially epiphytic taxa are often densely covered in greyish-white scales which absorb water from the atmosphere (“atmospheric epiphytes”). The large tank bromeliads from humid climates harbour an often unique microfauna (frogs, insects etc.) and -flora (specialized *Utricularia* species) in their water-filled rosettes. A limited number of bromeliads, such as

*Brocchinia* growing on nutrient-poor soils, have for long been suspected to be partly carnivorous (Benzing 2000: 217–223).

Benzing (2000: 112) refined earlier concepts first formulated by Pittendrigh (1948), and differentiates between five different ecophysiological types, based on the presence/absence of tanks (= impounding rosettes = phytothelmata), the role of roots, the place of water and nutrient uptake, and photosynthetic pathways:

- Type I: Terrestrial, without tanks, water and nutrient uptake via roots, with C3 or CAM
- Type II: Terrestrial, with weakly developed tanks, water and nutrient uptake via roots and absorptive trichomes on the leaf bases, with CAM
- Type III: Terrestrial (usually saxicolous) or epiphytic, with well-developed tanks, roots for mechanical support, water and nutrient uptake through absorptive scales on the leaf bases, mostly with CAM
- Type IV: Usually epiphytic, with well-developed tanks, roots for mechanical support, water and nutrient uptake through absorptive scales on the leaf bases, mostly with C3
- Type V: Epiphytic or more rarely terrestrial and then mostly saxicolous, roots for mechanical support or absent, water and nutrient uptake through absorptive scales over the entire shoots

and leaves, with CAM — this group conforms to the so-called “atmospheric bromeliads”

According to Males & Griffiths (2017) these types conform to different functional types, with close congruence of physiological parameters (such as degree of succulence, or photosynthetic pathway) with the climatic niches they inhabit. These authors also stress that different combinations of drought avoidance (by developing water storage tissues) and drought tolerance (by allowing lower tissue water potentials) are found in species of the family.

Heteroblasty, i.e. an abrupt change in leaf shape during the development of young plants into adult plants, is known from several species (Meisner & Zotz 2012, Meisner & al. 2013), and is probably associated with the transition to the tank-forming habit of adult plants.

Reyes-García & Griffiths (2009) stress that there are gradual switches from roots that function as absorptive organs to roots as anchor organs only, and that this grade is inversely parallel to an increasing presence of trichomes as absorptive structures.

CAM photosynthesis is common in several clades (Horres & Zizka 1995), but Loeschen & al. (1993) did not find a correlation between the presence of CAM and the degree of succulence. Overall, about 45% of all bromeliads show some degree of CAM (Silvera & al. 2010) (see Matiz & al. (2013) and Crayn & al. (2015) for lists of taxa and references). CAM evolved at least five times independently from the supposedly ancestral C3 condition (Crayn & al. 2015) and is more predominant in terrestrial taxa (e.g. *Deuterocohnia*, *Dyckia*, *Encholirium*, where all species exhibit CAM). According to Quezada & Gianoli (2011) and Silvestro & al. (2014), the evolution of CAM is an evolutionary key innovation, and clades where CAM has evolved are generally more speciose than sister clades without CAM.

Pierce & al. (2001) hypothesize that the peculiar foliar trichomes so common in the family were of hydrophobic nature ancestrally and served to repel water esp. from the abaxial leaf faces.

Benzing (2000) ascribes a general function of deterring predators and pathogens to the bromeliad trichomes. In *Tillandsioideae*, the scales have developed into complicated multicellular organs that serve in water uptake, and probably also for photoprotection (Pierce 2007), although the increase in light reflection is generally small (Pierce & al. 2001). The ontogeny of the absorptive trichomes has been studied in detail by Papini & al. (2010): The scales consist of a stem or axis that is connected to the internal leaf tissue (mesophyll parenchyma), and a shield that consists of several cells. The shield cells die when the trichome is fully developed and intercellular channels appear which connect the shield cells amongst them, and to the central stem. When plants with such trichomes become wet, a water film develops under the trichome shields, and is then passively absorbed by the shield cells.

**Succulence:** Many bromeliads are slightly to distinctly leaf-succulent, and some have somewhat succulent stems. There is a transition from mesic to coriaceous and to distinctly succulent leaves, although even relatively mesic forms such as *Catopsis floribunda* or *Vriesea incurvata* or many *Pitcairnia* species have minimal amounts of water storage tissue (Benzing 2000: 65). In the case of the more succulent species, the degree of succulence is comparable to that of many undisputed leaf succulents from the *Crassulaceae* (Horres & Zizka 1995). The succulent tissue, which can make up to 85% of the total leaf cross-sectional area, is parenchymatous mesophyll, and is usually devoid of chlorophyll; epidermis and hypodermis are not contributing significantly to succulence (Metzler 1924, Loeschen & al. 1993, Horres & Zizka 1995). Some authors interpret the succulent tissues as representing a hypodermis (e.g. Pereira & al. (2011) for four species of *Bromelioideae*, Gomes-da-Silva & al. (2012) for species of the *Vriesea corcovadensis* group), but the hypodermis proper consists of one to five layers of sclerified cells (Monteiro & al. 2011, for *Bromelia* spp., although these authors also explicitly refer to a “water storage hypodermis” in the abstract). There is an abrupt change between the water-storage tissue and the chlorenchyma in most taxa. The architecture, however, can be variable even within a genus,



and Monteiro & al. (2011) report an abrupt change for most species of *Bromelia*, but a gradual change in *B. auriculata*, *B. morreniana*, *B. scarlatina* and *B. tubulosa*.

The water-storage tissue is usually predominantly located on the adaxial face of the leaves, but conditions vary and are of limited diagnostic value (e.g. both adaxial and abaxial in *Dyckia* and *Encholirium*, but adaxial only in most species of *Pitcairnia*, see Santos-Silva & al. (2013)), and can also be variable within a genus (e.g. abaxial in *Bromelia morreniana*, and present on both faces in *B. tubulosa* or *B. scarlatina* (Monteiro & al. 2011)). Horres & Zizka (1995: 53–55) tabulate the presence of water-storage tissue on both leaf faces for species of many additional genera. When the water-storage tissue is clearly demarcated from the chlorophyllous tissue, cells are often  $\pm$  isodiametric, but can also be narrow and elongate resembling a palisade parenchyma. Intercellular spaces are generally absent in the water storage tissue. The leaves of *Guzmania lingulata* consist of a rather uniform large-celled parenchymatic tissue, of which all cells except those of the uppermost one to two layers contain about equal and low amounts of chlorophyll (Vieira da Silva & al. 2011: Fig. 10). Under drought conditions, water is preferentially drawn from the water storage tissue (e.g. Freschi & al. (2010) for *Guzmania monostachia*), resulting in increasingly undulate cell walls concomitant with the loss of volume (e.g. Vieira da Silva & al. (2011: Fig. 15) for *Guzmania lingulata*). Pereira & al. (2011) describe reversible cell-shrinkage on the base of the concertina-pattern observable in anticlinal walls (their Fig. 26, with scant evidence, however). Collapsible cells are also reported from species of *Bromelia* by Benzing (2000: 32, Fig. 2.13b), and for *Alcantarea* by Versieux & al. (2010), but these plants do not appear to be truly succulent, although the water-storage tissue can be quite well-developed in species from inselberg habitats (Versieux & al. 2010, Versieux & al. 2012).

Succulence is very much a matter of degree in the family, and can be quite cryptic—even *Tillandsia usneoides* shows considerable succulence, although no specialized succulent tissue is

present (Horres & Zizka 1995). Interestingly, the degree of succulence is, at least in some cases, not linked to environmental conditions, and Flores (1975) found the leaves of *Aechmea mexicana* (a moist-forest epiphyte) to have more pronounced water storage tissue than those of *Hechtia glomerata* (terrestrial in arid zones). Moreover, the extent of water storage tissues is under environmental control at least in some taxa, but contrary to expectations, water storage is more pronounced (but still insignificant) in shade plants of *Billbergia elegans* and *Neoregelia mucugensis* than in plants growing in open conditions (Rodrigues Pereira & al. 2013).

*Alcantarea glaziouana* from the steep granite inselbergs in the Rio de Janeiro area shows a remarkable shift in life strategy because young plants have normal rosettes of very succulent leaves, and the large impounding tank rosettes are only present in adult plants, when leaf succulence disappears (Reinert & Meirelles 1993: as *Vriesea geniculata*, Versieux & al. 2010).

Some species of *Puya* and *Tillandsia* form a conspicuous bulbous base. For *Tillandsia*, Rauh (1990) distinguishes “true bulbs” (e.g. *T. argentea*), with tightly packed leaf sheaths, from “pseudobulbs” (e.g. *T. caput-medusae*), where the leaf sheaths are thin and not succulent, and are separated from each other by a space of free air, which is often inhabited by ants. None of these two forms represents a monophyletic clade, however (Chew & al. 2010).

Succulence has evolved independently in five of the eight currently recognized subfamilies. The succulent or predominantly succulent genera *Hechtia* (*Hechtioideae*), *Deuterocohnia*, *Dyckia*, *Encholirium* (*Pitcairnioideae*) and *Puya* (*Puyoideae*) show a remarkable degree of “concerted convergence” in six anatomical and physiological leaf characters that are all associated with an occurrence at (semi-) arid sites (Givnish & al. 2007).

Apart from the genera with a full or partial treatment in this handbook, some degree of succulence is also present in at least some species of the genera shortly discussed in the list below. According to present knowledge, the water storage tissues are less well-developed in these

cases, and the claim to succulence (according to the definition of Eggli & Nyffeler (2009)) remains to be tested:

**Ananas (Bromelioideae):** A genus of three species (Butcher & Gouda 2014), of which *A. ananassoides* (“pineapple”, still usually known as *A. comosus*) is the most well-known. *A. ananassoides* has a well defined water-storage tissue with collapsible cell walls under drought conditions, while the chlorenchyma tissue does not shrink (Sideris & Krauss 1955 cited from Benzing (2000)). A distinct water-storage tissue, making up  $\pm 50\%$  of the leaf cross-section, has been illustrated by Vieira da Silva & al. (2011: Fig. 1), showing a distinctly large-celled palisade-like hydrenchyma and a small-celled chlorenchyma. About 30% water-storage volume is reported for *A. lucidus* (Krahl & al. 2013).

**Brocchinia (Brocchinioideae):** A genus of 20 species. Horres & Zizka (1995) report a water-storage tissue of 48% cross-sectional leaf area for *B. uaipanensis* (as *Ayensua uaipanensis*). The plants appear quite succulent (see Oliva-Estevé & Steyermark (1987: 307) for an illustration), but in view of its habitat (rocks on tepuis in an overall humid climate), the taxon does not appear to be truly succulent (E. Gouda, pers. obs.).

**Bromelia (Bromelioideae):** A genus of  $\pm 70$  species. The majority have distinctly coriaceous leaves and can withstand considerable aridity. Benzing (2000: 32, Fig. 2.13b) illustrates collapsible water-storage cells for *B. balansae*. For other species, minimal volumes of water-storage tissues are reported (*B. antiacantha*: almost nil, Pereira & al. (2011); *B. pinguin*: 16%, Horres & Zizka (1995)).

**Catopsis (Tillandsioideae):** A genus of 18 species. Water-storage tissue makes up  $\pm 50\%$  of the cross-sectional leaf area for *C. delicatula*, *C. juncifolia* and *C. morreniana* (Horres & Zizka 1995), but these plants are mesophytic with overall very thin leaves. Palací &

al. (2004) found that adaxial water-storage tissue is present throughout the genus and is generally more developed in semi-mesophytic species compared with the mesophytic species.

**Disteganthus (Bromelioideae):** A genus of five species (Aguirre-Santoro & Michelangeli 2015). The leaves of some species are described as succulent, but they are merely  $\pm$  markedly coriaceous, similar to those of many species of *Bromelia*. *Disteganthus* species usually grow in at least partial shade and thus are not specially adapted to cope with water shortage.

**Guzmania (Tillandsioideae):** A genus of  $\pm 220$  species. For *G. lingulata*, Vieira da Silva & al. (2011) illustrate a uniform tissue throughout the leaf with large cells with primarily water-storage function, and few chloroplasts, but this species is mesophytic and has thin leaves (E. Gouda, pers. obs.). Freschi & al. (2010) found that there is a clear partitioning of functions (water storage vs. photosynthesis) within the leaves of *G. monostachia* from the base to the tip. Versieux & Medeiros (2018) found small amounts of water storage parenchyma both in adaxial as well as abaxial position for several allegedly mesophytic *Guzmania* species.

**Navia (Navioideae):** A genus of 95 species. A number of species from arid sites (dry rocks, xerophytic savanna, dry cliffs) are described as having distinctly thickly coriaceous leaves by Robinson (1969) and Horres & Zizka (1995) report 67% water-storage cross-sectional leaf area for *N. splendens*. Illustrations (e.g. Oliva-Estevé & Steyermark (1987: 332–355)) suggest that some might be truly succulent, but more research is necessary to evaluate whether this is really the case.

**Pitcairnia (Pitcairnioideae):** A genus of  $\pm 408$  species (incl. *Pepinia*). Horres & Zizka (1995) report a water-storage cross-sectional leaf area of  $\pm 50\%$  for *P. andreana* and *P. burle-marxii*. In addition, *P. balsaminea*, *P. cristalinensis* and *P. encholirioides* appear

to be somewhat succulent (Santos-Silva & al. 2013), as well as the recently described *P. volker-schaedlichii*.

**Portea** (*Bromelioideae*): A genus of 8 species. Horres & al. (2007) report fairly well-developed water-storage for *P. leptantha*.

**Quesnelia** (*Bromelioideae*): A genus of 22 species. The water-storage tissue makes up 25 to >33% of the cross-sectional leaf area according to Mantovani & al. (2012). For *Q. strobilispica*, 40% water-storage volume is reported by Pereira & al. (2011).

**Vriesea** (*Tillandsioideae*): A genus of  $\pm 225$  species. Horres & Zizka (1995) report a water-storage tissue making up 50% of the cross-sectional leaf area for *V. espinosae* (later transferred to *Tillandsia*), but the species appears to be at most xerophytic, rather than truly succulent (E. Gouda, pers. obs.).

**Bromeliads and malaria:** Species with impounding rosettes are a malaria (and probably also dengue, zika, Mocellin & al. (2009)) vector, esp. in urban areas close to forests or rock outcrops that are inhabited by such species (e.g. the large-growing *Alcantarea* species in SE Brazil), and that are also breeding places for mosquitoes. This continuously encourages tree cutting and heavy herbicide use to eliminate the offending bromeliads in parts of Amazonian Brazil (Reitz 1983), but also in SE Brazil and Colombia. Bromeliads and their relationship with malaria were first intensely studied during World War II in Trinidad, where native species like *Aechmea aquilega* support *Anopheles bellator* that transmit malaria (Downs & Pittendrigh 1946, Pittendrigh 1948). *Anopheles bellator* is a small forest mosquito that breeds in water-filled bromeliad tanks. It has a disjunctive distribution and is a primary human malaria vector species (“bromeliad malaria”) in Trinidad and the coastal Atlantic forest of S Brazil (Gadelha 1994, Carvalho-Pinto

**Key to subfamilies and genera with succulents.** NB: A complete key to all genera of the family, updated from the keys in the three Smith & Downs-volumes, has been published by Butcher (2000)

1a	<b>Fr</b> indehiscent berries dispersed by animals (usually birds)	<i>Bromelioideae</i> (see separate key below)
1b	<b>Fr</b> usually capsular and dehiscent, or rarely indehiscent ( <i>Pitcairnia</i> p.p.) but then not berries, <b>Se</b> dispersed by wind	2
2a	<b>Se</b> with a plumose appendage	<i>Tillandsioideae</i> (only <i>Tillandsia</i> p.p. with succulents)
2b	<b>Se</b> winged, with a single hair-like appendage at both ends, or naked	3
3a	<b>Fl</b> unisexual and plants dioecious (only N to C America)	<i>Hechtioideae</i> (only genus: <i>Hechtia</i> )
3b	<b>Fl</b> hermaphrodite or rarely unisexual and plants then monoecious or polygamodioecious, or dioecious and then from the Brazilian Shield	4
4a	<b>Pet</b> blades showy, tightly spiralled after anthesis, broad and distinct from the claw	<i>Puyoideae</i> (only genus: <i>Puya</i> )
4b	<b>Pet</b> blades showy or not, remaining free after anthesis or if slightly coiled then not clawed	5
5a	<b>Pet</b> large and conspicuous, or if minute then <b>Sep</b> imbricate and <b>Anth</b> basifixed, linear	<i>Pitcairnioideae</i> (see separate key below)
5b	<b>Pet</b> minute and <b>Sep</b> cochlear (= abaxial sepal margins overlapping both axial ones), or <b>Pet</b> and <b>Bra</b> various and <b>Sep</b> twisted-convolute (= each sepal overlapping another with the margin at one side) or cochlear	6
6a	<b>Sep</b> twisted-convolute, <b>Pet</b> mostly many times longer than the sepals	<i>Lindmanioideae</i> (no succulents)
6b	<b>Sep</b> cochlear and <b>Pet</b> minute	7
7a	<b>L</b> entire, star-like cells in the chlorenchyma abundant	<i>Brocchioideae</i> (no succulents)
7b	<b>L</b> margins toothed, star-like cells in the chlorenchyma absent	<i>Navioideae</i> (no succulents)

**Key to genera of subfamily Bromelioideae with succulents**

<b>1a</b>	<b>Fl</b> laxly arranged in simple or compound <b>Inf</b> , axes wholly visible	2
<b>1b</b>	<b>Fl</b> in dense spikes, racemes, or in dense compound and often prominently bracteate <b>Inf</b>	11
<b>2a</b>	<b>Inf</b> simple	3
<b>2b</b>	<b>Inf</b> compound	8
<b>3a</b>	<b>Fl</b> pedicellate; <b>Sep</b> with soft and usually obtuse apices	4
<b>3b</b>	<b>Fl</b> sessile	6
<b>4a</b>	<b>Per</b> slightly zygomorphic; <b>Sep</b> 15–35 mm; <b>Pet</b> 33–65 mm; pollen mostly sulcate (C America to Argentina and Uruguay)	<i>Billbergia</i>
<b>4b</b>	<b>Per</b> actinomorphic; <b>Sep</b> 6–9 mm; <b>Pet</b> 13–20 mm	5
<b>5a</b>	Ovules obtuse; pollen sulcate; <b>L</b> attenuate, $\pm$ as thick as wide (NE Brazil)	<i>Neoglaziovia</i>
<b>5b</b>	Ovules long-caudate; pollen porate; <b>L</b> flat and apiculate (C-E Brazil)	<i>Aechmea</i> ( <i>A. racinae</i> )
<b>6a</b>	<b>Sep</b> mucronate or pungent (N & S America)	<i>Aechmea</i> p.p.
<b>6b</b>	<b>Sep</b> unarmed	7
<b>7a</b>	Ovules long-caudate; <b>Sep</b> mostly <10 mm; <b>Pet</b> <30 mm (S America)	<i>Aechmea</i> p.p.
<b>7b</b>	Ovules unappendaged; <b>Sep</b> 13–30 mm; <b>Pet</b> 35–56 mm	<i>Billbergia</i> + marginally succulent taxa of <i>Quesnelia</i>
<b>8a</b>	<b>Fil</b> connate and forming a tube to which the fleshy petals are joined along their centres but with their margins free; <b>Sep</b> mostly free or nearly so, 6–30 mm; <b>Pet</b> 15–35 mm; <b>L</b> very laxly and coarsely spinose-serrate (N & S America)	Marginally succulent <i>Bromelia</i> p.p.
<b>8b</b>	<b>Fil</b> not connate	9
<b>9a</b>	<b>Pet</b> not appendaged	<i>Aechmea</i> p.p.
<b>9b</b>	<b>Pet</b> appendaged	10
<b>10a</b>	<b>Sep</b> mucronate or pungent	<i>Aechmea</i> + marginally succulent taxa of <i>Portea</i>
<b>10b</b>	<b>Sep</b> unarmed or soft-apiculate	<i>Billbergia</i> + marginally succulent taxa of <i>Quesnelia</i>
<b>11a</b>	<b>Inf</b> simple; <b>Fl</b> solitary in the axil of each bract	12
<b>11b</b>	<b>Inf</b> compound or sometimes pseudo-simple with fascicles of two or more flowers concealed by the outermost bracts	19
<b>12a</b>	Peduncle short or absent; <b>Inf</b> sunken into the centre of the rosette or pseudo-lateral	13
<b>12b</b>	Peduncle well-developed and evident	15
<b>13a</b>	<b>Sep</b> $\pm$ half-connate, rounded, long-mucronate (SE Brazil, Paraguay, Uruguay, Argentina)	<i>Aechmea</i> p.p.
<b>13b</b>	<b>Sep</b> free or short-connate	14
<b>14a</b>	<b>Sep</b> obtuse, carinate; <b>Pet</b> free, appendaged; pollen entire (Chile)	<i>Fascicularia</i> + marginally succulent taxa of <i>Greigia</i>
<b>14b</b>	<b>Sep</b> acute to attenuate, pungent, mucronate	<i>Ochagavia</i>
<b>15a</b>	<b>Inf</b> lateral or pseudo-lateral, spicate or racemose	16
<b>15b</b>	<b>Inf</b> obviously terminal	17
<b>16a</b>	Peduncle naked; <b>Fl</b> sessile; <b>Pet</b> appendaged (S Brazil, Paraguay, Argentina)	<i>Acanthostachys</i>
<b>16b</b>	Peduncle bracteate; <b>Pet</b> appendages reduced or lacking	<i>Aechmea</i> p.p.
<b>17a</b>	<b>Sep</b> mucronate or pungent (N & S America)	<i>Aechmea</i> p.p.
<b>17b</b>	<b>Sep</b> soft and unarmed	18
<b>18a</b>	Ovules long-caudate; <b>Sep</b> 6–12 mm (E Brazil but <i>A. bromeliifolia</i> to C America)	<i>Aechmea</i> p.p. + marginally succulent taxa of <i>Ananas</i>
<b>18b</b>	Ovules unappendaged; <b>Sep</b> 8–20 mm (E Brazil)	<i>Billbergia</i> + marginally succulent taxa of <i>Quesnelia</i>

(continued)

**Key to genera of subfamily Bromelioideae with succulents** (continued)

<b>19a</b>	<b>Fl</b> in terete strobili, little if at all hidden by the outer bracts, <b>Inf</b> obviously compound	<i>Aechmea</i> p.p.
<b>19b</b>	<b>Fl</b> in ± flattened spikes, or in fascicles; <b>Inf</b> often pseudo-simple with two or more flowers concealed beneath large outer bracts	20
<b>20a</b>	<b>Fl</b> pedicellate	Marginally succulent taxa of <i>Bromelia</i>
<b>20b</b>	<b>Fl</b> sessile or subsessile	21
<b>21a</b>	Peduncle very short or none; <b>Inf</b> sunken in the centre of the rosette or pseudo-lateral	22
<b>21b</b>	Peduncle well-developed; <b>Inf</b> raised above the leaf sheaths; pollen porate	24
<b>22a</b>	Outer <b>Bra</b> of the inflorescence leaf-like (NE Brazil)	23
<b>22b</b>	Outer <b>Bra</b> of the inflorescence bract-like; <b>Pet</b> without appendages	<i>Aechmea</i> p.p.
<b>23a</b>	<b>Sep</b> free; <b>Pet</b> with appendages; pollen porate	<i>Sincoraea</i>
<b>23b</b>	<b>Sep</b> high-conate; <b>Pet</b> without appendages; pollen not porate	<i>Cryptanthus</i>
<b>24a</b>	Peduncular <b>Bra</b> leaf-like; <b>Sep</b> free, nearly symmetrical	<i>Orthophytum</i>
<b>24b</b>	Peduncular <b>Bra</b> not leaf-like; <b>Sep</b> free or connate, mostly strongly asymmetrical	<i>Aechmea</i> p.p.

**Key to genera of subfamily Pitcairnioideae with succulents**

<b>1a</b>	Bases of the <b>Fil</b> forming a tube and adnate to the petals; <b>Pet</b> yellow or orange to red (rarely greenish, brownish or blackish); <b>Sep</b> spoon-shaped (E South America)	<i>Dyckia</i>
<b>1b</b>	Bases of the <b>Fil</b> separate from each other, but sometimes individually adnate to the petals and sepals	2
<b>2a</b>	<b>Pet</b> appendaged, each with a single basal scale (S Andes from Peru to Chile, Argentina, Brazil)	<i>Deuterocohnia</i> + marginally succulent <i>Pitcairnia</i> p.p.
<b>2b</b>	<b>Pet</b> without appendages	3
<b>3a</b>	<b>Se</b> with a falciform appendage (NE Brazil)	<i>Encholirium</i>
<b>3b</b>	<b>Se</b> with a bicaudate appendage	<i>Fosterella</i> + marginally succulent <i>Pitcairnia</i> p.p.

& Oliveira 2003), but also in the Oyapock area on the Brazilian-French Guiana border (Buchillet 2007). Another human malaria vector species, *Anopheles cruzii*, was reported for the first time in bromeliads from the coastal area of the State of São Paulo (Marques & Paulo Forattini 2009).

**Horticulture:** Many bromeliads are popular in horticulture, and some are produced by the million as house plants, esp. because of their colourful foliage and bracts. Bromeliad species and genera easily hybridize, and many artificial hybrids have been obtained in the course of time, including numerous intergeneric hybrids. In contrast, natural hybridization is comparatively limited (see Palma-Silva & al. (2016) for an overview of published evidence). Smith (1983) published a

list of nothogeneric names, combinations and cultivars known at that time. In the subsequent account of the family in this handbook, intergeneric hybrid genera are only covered when succulent species are involved as parents.

The following names are of unresolved application but are referred to this family: *Billbergia joinvillei* Hort. Van Houtte (1871) (*nom. inval.*, Art. 32.1c); *Billbergia lansbergiana* Hort. Paramaribo ex Witte (1894) (*nom. inval.*, Art. 32.1c); *Hechtia carnea* hort. ex Wittmack (1890) (*nom. inval.*, Art. 32.1c); *Hechtia gracilis* hort. ex Haage & Schmidt (1912) (*nom. inval.*, Art. 32.1c); *Hechtia joinvillei* hort. ex E. Morren (1876) (*nom. inval.*, Art. 32.1d); *Nidularium caeruleum* Lemaire (1860) (*nom. inval.*, Art. 32.1c);



*Pourretia africana* hort. ex Wittmack (1890) (*nom. inval.*, Art. 32.1c); *Pourretia flexilis* hort. ex E. Morren (1876) (*nom. inval.*, Art. 32.1c); *Pourretia mexicana* hort. ex E. Morren (1876) (*nom. inval.*, Art. 32.1c); *Quesnelia chacoensis* Rojas (1918); *Tillandsia acutifolia* hort. Angl. ex Link (1821) (*nom. inval.*, Art. 32.1c); *Tillandsia armadae* André (1888); *Tillandsia boryana* Gandoger (1919); *Tillandsia calamifolia* Salisbury (1820); *Tillandsia ensifolia* Sessé & Moçônio (1894); *Tillandsia heptantha* Ruiz & Pavón (1802)  $\equiv$  *Platystachys heptantha* (Ruiz & Pavón) Beer (1856); *Tillandsia imbricata* Vellozo (1829)  $\equiv$  *Vriesea imbricata* (Vellozo) Beer (1856); *Tillandsia latispatha* hort. ex Gentil (1907) (*nom. inval.*, Art. 32.1c); *Tillandsia lineata* André (1888); *Tillandsia obscura* Loddiges ex G. Don (1830) (*nom. inval.*, Art. 32.1c); *Tillandsia platystachia* Rojas Acosta (1897) (*nom. inval.*, Art. 32.1c); *Tillandsia ramealis* Klotzsch (1848); *Tillandsia rigida* hort. ex Sweet (1826) (*nom. inval.*, Art. 32.1c); *Tillandsia tortuosa* Loddiges ex Schultes fil. (1830) (*nom. inval.*, Art. 32.1c); *Tillandsia variabilis* Schlechtendal (1844); *Tillandsia violata* Rojas Acosta (1897) (*nom. inval.*, Art. 32.1c); *Vriesea glauca* Alvaro Silveira (1931).

## References

- Aguilar-Rodríguez, P. A. [& al. 2014], Krömer, T. & MacSwiney G. M. C. (2014) The secrets of night-blooming bromeliads and bats. *J. Bromeliad Soc.* 64 (3): 156–165, ills.
- Aguirre-Santoro, J. & Michelangeli, F. (2015) Two new species of *Disteganthus* (*Bromeliaceae*) from Suriname and French Guiana. *Brittonia* 67(3): 233–242, ills., map, key. <https://doi.org/10.1007/s12228-015-9378-0>.
- Baensch, U. (1994) Blühende Bromelien. Flowering Bromeliads. Nassau (BS): Tropic Beauty Publishers.
- Barfuss, M. H. J. [& al. 2005], Samuel, R., Till, W. & Stuessy, T. F. (2005) Phylogenetic relationships in subfamily *Tillandsioideae* (*Bromeliaceae*) based on DNA sequence data from seven plastid regions. *Amer. J. Bot.* 92(2): 337–351. <https://doi.org/10.3732/ajb.92.2.337>.
- Barfuss, M. H. J. [& al. 2016], Till, W., Leme, E. M. C., Pinzón, J. P., Manzanares, J. M., Halbritter, H., Samuel, R. & Brown, G. K. (2016) Taxonomic revision of *Bromeliaceae* subfam. *Tillandsioideae* based on a multi-locus DNA sequence phylogeny and morphology. *Phytotaxa* 279(1): 1–97, ills., key. <https://doi.org/10.11646/phytotaxa.279.1.1>.
- Bennett, B. (2000) Ethnobotany of *Bromeliaceae*. In: Benzing, D. H.: *Bromeliaceae: Profile of an adaptive radiation*; pp. 587–608. Cambridge (GB): Cambridge University Press. <https://doi.org/10.1017/CBO9780511565175>.
- Benzing, D. H. (2000) *Bromeliaceae: Profile of an adaptive radiation*. Cambridge (UK): Cambridge University Press. <https://doi.org/10.1017/CBO9780511565175>.
- Bernardello, L. M. [& al. 1991], Galetto, L. & Juliani, H. R. (1991) Floral nectar, nectary structure and pollinators in some Argentinean *Bromeliaceae*. *Ann. Bot. (Oxford)*, n.s. 67(4): 401–411.
- Böhme, S. (1988) Vergleichende Untersuchungen zu Bau, Lage und systematischer Verwertbarkeit der Septalnektrarien von Bromeliaceen. *Trop. subtrop. Pfl.-welt* 62: 1–154, ills.
- Bouchenack-Khelladi, Y. [& al. 2014], Muthama Muasya, A. & Linder, H. P. (2014) A revised evolutionary history of Poales: Origins and diversification. *Bot. J. Linn. Soc.* 175: 4–16. <https://doi.org/10.1111/boj.12160>.
- Brown, G. K. (2017) Bromeliad systematics — stepping back to move forward. *J. Bromeliad Soc.* 66(3): 149–159.
- Buchillet, D. (2007) Bibliografía crítica da saúde indígena no Brasil (1844–2006). Quito (EC): Abya-Yala. <https://doi.org/10.13140/2.1.3079.6804>.
- Butcher, D. (2000) Key to the genera of *Bromeliaceae*. *J. Bromeliad Soc.* 50(3): 105–112.
- Butcher, D. & Gouda, E. (2014) Most *Ananas* are cultivars. *Newslett. Pineapple Working Group* 21: 9–11, ills.
- Carvalho-Pinto, C. J. & Oliveira, R. L. (2003) Isoenzymatic analysis of four *Anopheles* (*Kerteszia*) *bellator* Dyar & Knab (Diptera: Culicidae) populations. *Mem. Inst. Oswaldo Cruz* 98(8): 1045–1048. <https://doi.org/10.1590/S0074-02762004000500002>.
- Chew, T. [& al. 2010], Luna, E. de & González, D. (2010) Phylogenetic relationships of the pseudobulbous *Tillandsia* species (*Bromeliaceae*) inferred from cladistic analyses of ITS 2, 5.8S ribosomal RNA gene, and ETS sequences. *Syst. Bot.* 35(1): 86–95. <https://doi.org/10.1600/036364410790862632>.
- Crayn, D. M. [& al. 2004], Winter, K. & Smith, J. A. C. (2004) Multiple origins of Crassulacean Acid Metabolism and the epiphytic habit in the neotropical family *Bromeliaceae*. *Proc. Nation. Acad. Sci. USA* 101(10): 3703–3708. <https://doi.org/10.1073/pnas.0400366101>.
- Crayn, D. M. [& al. 2015], Winter, K., Schulte, K. & Smith, J. A. C. (2015) Photosynthetic pathways in *Bromeliaceae*: Phylogenetic and ecological significance for CAM and C3 based on carbon isotope ratios for 1893 species. *Bot. J. Linn. Soc.* 178: 169–221. <https://doi.org/10.1111/boj.12275>.
- Downs, W. G. & Pittendrigh, C. S. (1946) Bromeliad malaria in Trinidad, British West Indies. *Amer. J. Trop. Med.* 26: 47–66. <https://doi.org/10.1186/1475-2875-9-115>.
- Eggli, U. & Nyffeler, R. (2009) Living under temporarily arid conditions — succulence as an adaptive strategy.

- Bradleya 27: 13–36, ills. <https://doi.org/10.5167/uzh-28825>.
- Evans, T. M. [ & al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>.
- Fagundes, N. F. & Mariath, J. E. D. (2010) Morpho-anatomy and ontogeny of fruit in *Bromeliaceae* species. *Acta Bot. Brasil.* 24(3): 765–779, ills. <https://doi.org/10.1590/S0102-33062010000300020>.
- Flores, E. M. (1975) Some aspects of comparative foliar anatomy of two species of *Bromeliaceae*, *Aechmea mexicana* Baker and *Hechtia glomerata* Zucc. *Revista Biol. Trop.* 23(1): 29–52.
- Freschi, L. [ & al. 2010], Takahashi, C. A., Cambui, C. A., Semprebom, T. R., Cruz, A. B., Mioto, P. T., Versieux, L. M., Calvente, A., Latansio-Aidar, S. R., Aidar, M. P. M. & Mercier, H. (2010) Specific leaf areas of the tank bromeliad *Guzmania monostachia* perform distinct functions in response to water shortage. *J. Pl. Physiol.* 167(7): 526–533. <https://doi.org/10.1016/j.jplph.2009.10.011>.
- Gadella, P. (1994) From “forest malaria” to “bromeliad malaria”: A case-study of scientific controversy and malaria control. *Parassitologia* 36(1–2): 175–195.
- Gitaí, J. [ & al. 2014], Paule, J., Zizka, G., Schulte, K. & Benko-Iseppon, A. M. (2014) Chromosome numbers and DNA content in *Bromeliaceae*: Additional data and a critical review. *Bot. J. Linn. Soc.* 176(3): 349–368, ills. <https://doi.org/10.1111/boj.12211>.
- Givnish, T. J. [ & al. 2007], Millan, K. C., Berry, P. E. & Sytsma, K. J. (2007) Phylogeny, adaptive radiation, and historical biogeography of *Bromeliaceae* inferred from *ndhF* sequence data. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution: Poales*. *Aliso* 23: 3–26. <https://doi.org/10.5642/aliso.20072301.04>
- Givnish, T. J. [ & al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ills., maps. <https://doi.org/10.3732/ajb.1000059>.
- Givnish, T. J. [ & al. 2014], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2014) Adaptive radiation, correlated and contingent evolution, and net species diversification in *Bromeliaceae*. *Molec. Phylogen. Evol.* 71: 55–78. <https://doi.org/10.1016/j.ympev.2013.10.010>.
- Gomes-da-Silva, J. [ & al. 2012], Alves da Costa Vargens, F., Carmo de Oliveira Arruda, R. de & Ferreira da Costa, A. (2012) A morphological cladistic analysis of the *Vriesea corcovadensis* group (*Bromeliaceae: Tillandsioideae*), with anatomical descriptions: New evidence of the non-monophyly of the genus. *Syst. Bot.* 37(3): 641–654, ills. <https://doi.org/10.1600/036364412X648599>.
- Gouda, E. J. & Butcher, D. (2016+) A list of accepted *Bromeliaceae* names. Utrecht (NL): University Botanic Gardens, Utrecht; continuously updated. <http://bromeliad.nl/bromnames>.
- Gouda, E. J. [ & al. 2012+], Butcher, D. & Gouda, C. S. (2012+) Encyclopaedia of Bromeliads, Version 3.1 (2012). Utrecht (NL): University Botanic Gardens, Utrecht. <http://bromeliad.nl/encyclopedia/>.
- Gouda, E.J., Butcher, D. & Gouda, C.S. (cont.updated) Encyclopaedia of Bromeliads, Version 4. <http://bromeliad.nl/encyclopedia/> University Botanic Gardens, Utrecht (accessed: Jan. 2019).
- Horres, R. & Zizka, G. (1995) Untersuchungen zur Blattsukkulenz bei *Bromeliaceae*. *Beitr. Biol. Pfl.* 69(1): 43–76, ills.
- Horres, R. [ & al. 2007], Schulte, K., Weising, K. & Zizka, G. (2007) Systematics of *Bromelioideae (Bromeliaceae)* — evidence from molecular and anatomical studies. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution: Poales*. *Aliso* 23(1): 27–43, ills. <https://doi.org/10.5642/aliso.20072301.05>
- Krahl, A. H. [ & al. 2013], Holanda, A. S. S., Krahl, D. R. P., Corrêa, M. M., Oliveira, R. L. C. & Valsko, J. J. (2013) Anatomia foliar de *Ananas lucidus* Mill. (*Bromeliaceae*). *Natureza* on line 11(4): 161–165, ills.
- Loeschen, V. S. [ & al. 1993], Martin, C. E., Smith, M. & Eder, S. L. (1993) Leaf anatomy and CO<sub>2</sub> recycling during Crassulacean Acid Metabolism in twelve epiphytic species of *Tillandsia (Bromeliaceae)*. *Int. J. Pl. Sci.* 154: 100–106. <http://www.jstor.org/stable/2995609>.
- Males, J. (2016) Think tank: Water relations of *Bromeliaceae* in their evolutionary context. *Bot. J. Linn. Soc.* 181(3): 415–440, ills. <https://doi.org/10.1111/boj.12423>.
- Males, J. & Griffiths, H. (2017) Functional types in *Bromeliaceae*: Relationships with drought-resistance traits and bioclimatic distributions. *Funct. Ecol.* 31(10): 1868–1880, ills. <https://doi.org/10.1111/1365-2435.12900>.
- Mantovani, A. [ & al. 2012], Lima da Venda, A. K., Rezende Almeida, V., Ferreira da Costa, A. & Forzza, R. C. (2012) Leaf anatomy of *Quesnelia (Bromeliaceae)*: Implications for the systematics of core bromelioids. *Pl. Syst. Evol.* 298: 787–800. <https://doi.org/10.1007/s00606-012-0590-z>.
- Marques, G. R. A. M. & Paulo Forattini, O. (2009) Encontro de imaturos de *Anopheles cruzii* em bromélias de área urbana, litoral de São Paulo. *Anopheles cruzii* larvae found in bromelias in an urban area on the Brazilian coast. *Revista Saúde Públ.* 43(2): 369–372. <https://doi.org/10.1590/S0034-89102009005000006>.

- Matiz, A. [ & al. 2013], Mioto, P. T., Yepes Mayorga, A., Freschi, L. & Mercier, H. (2013) CAM photosynthesis in Bromeliads and Agaves: What can we learn from these plants? In: Dubinsky, Z. (ed.): *Photosynthesis*; pp. 91–134. Rijeka (HR): InTech. <https://doi.org/10.5772/56219>.
- Meisner, K. & Zotz, G. (2012) Heteroblasty in bromeliads: Its frequency in a local flora and the timing of the transition from atmospheric to tank form in the field. *Int. J. Pl. Sci.* 173(7): 780–788. <https://doi.org/10.1086/666665>.
- Meisner, K. [ & al. 2013], Winkler, U. & Zotz, G. (2013) Heteroblasty in bromeliads — Anatomical, morphological and physiological changes in ontogeny are not related to the change from atmospheric to tank form. *Funct. Pl. Biol.* 40(3): 251–262. <https://doi.org/10.1071/FP12201>.
- Metzler, W. (1924) Beiträge zur vergleichenden Anatomie blattsukkulenter Pflanzen. *Bot. Arch.* 6(1–3): 50–83, ills.
- Mocellin, M. G. [ & al. 2009], Simões, T. S., Fernandes S. T., França T. M. L., Lounibos, L. P. & Lourenço de O., R. (2009) Bromeliad-inhabiting mosquitoes in an urban botanical garden of dengue endemic Rio de Janeiro. Are bromeliads productive habitats for the invasive vectors *Aedes aegypti* and *Aedes albopictus*? *Mem. Inst. Oswaldo Cruz* 104(8): 1171–1176. <https://doi.org/10.1590/S0074-02762009000800015>.
- Monteiro, R. F. [ & al. 2011], Forzza, R. C. & Mantovani, A. (2011) Leaf structure of *Bromelia* and its significance for the evolution of Bromelioideae (*Bromeliaceae*). *Pl. Syst. Evol.* 293(1–4): 53–64, ills. <https://doi.org/10.1007/s00606-011-0426-2>.
- Oliveira-Estevê, F. & Steyermark, J. (1987) *Bromeliaceae* [sic!] of Venezuela. Caracas (VE): Armitano Editores.
- Palací, C. A. [ & al. 2004], Brown, G. K. & Tuthill, D. E. (2004) Vegetative morphology and leaf anatomy of *Catopsis* (*Tillandsioideae: Bromeliaceae*). *Selbyana* 25(1): 138–150, ills.
- Palma-Silva, C. [ & al. 2016], Leal, B. S. S., Chaves, C. J. N. & Fay, M. F. (2016) Advances in and perspectives on evolution in *Bromeliaceae*. *Bot. J. Linn. Soc.* 181(3): 305–322. <https://doi.org/10.1111/boj.12431>.
- Papini, A. [ & al. 2010], Tani, G., Falco, P. di & Brighigna, L. (2010) The ultrastructure of the development of *Tillandsia* (*Bromeliaceae*) trichome. *Flora* (Jena) 205(2): 94–100. <https://doi.org/10.1016/j.flora.2009.02.001>.
- Pereira, T. A. R. [ & al. 2011], Oliveira, T. S. de, Silva, L. C. da & Azevedo, A. A. (2011) Comparative leaf anatomy of four species of *Bromelioideae* (*Bromeliaceae*) occurring in the Atlantic Forest, Brazil. *Botany* 89(4): 243–253, ills. <https://doi.org/10.1139/B11-011>.
- Pierce, S. (2007) The jeweled armor of *Tillandsia* — multifaceted or elongated trichomes provide photoprotection. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution*; Poales. *Aliso* 23: 44–52, ills. <https://doi.org/10.5642/aliso.20072301.06>.
- Pierce, S. [ & al. 2001], Maxwell, K., Griffiths, H. & Winter, K. (2001) Hydrophobic trichome layers and epicuticular wax powders in *Bromeliaceae*. *Amer. J. Bot.* 88(8): 1371–1389. <http://www.amjbot.org/content/88/8/1371.abstract>.
- Pittendrigh, C. S. (1948) The bromeliad — *Anopheles-malaria* complex in Trinidad. I. The bromeliad flora. *Evolution* 2: 58–89. <http://www.jstor.org/stable/2405616>.
- Quezada, I. M. & Gianoli, E. (2011) Crassulacean Acid Metabolism photosynthesis in *Bromeliaceae*: An evolutionary key innovation. *Biol. J. Linn. Soc.* 104(2): 480–486. <https://doi.org/10.1111/j.1095-8312.2011.01713.x>.
- Rauh, W. (1990) *Bromelien*. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Reinert, F. & Meirelles, S. T. (1993) Water acquisition strategy shifts in the heterophyllous saxicolous bromeliad, *Vriesea geniculata* (Wawra) Wawra. *Selbyana* 14: 80–88, ills. <http://www.jstor.org/stable/41760421>.
- Reitz, R. (1983) Bromeliáceas e a malária-bromélia endêmica. In: Reitz, R. (ed.): *Flora ilustrada catarinense, I parte as plantas, fascículo BROM. Itajaí (BR): Herbario “Barbosa Rodrigues”*.
- Reyes-García, C. & Griffiths, H. (2009) Ecophysiological studies of perennials of the *Bromeliaceae* family in a dry forest: Strategies for survival. In: Barrera, E. de la & Smith, W. K. (eds.): *Perspectives in biophysical plant ecophysiology. A tribute to Park S. Nobel*; pp. 121–151. México (MX): Universidad Nacional Autónoma de México.
- Robinson, H. (1969) A monograph of foliar anatomy of the genera *Connellia*, *Cottendorfia*, and *Navia* (*Bromeliaceae*). *Smithsonian Contr. Bot.* 2: 1–41, ills. <http://hdl.handle.net/10088/7011>.
- Rodrigues Pereira, T. A. [ & al. 2013], Campos da Silva, L., Alves Azevedo, A., Francino, D. M. T., Santos Coser, T. dos & Dias Pereira, J. (2013) Leaf morpho-anatomical variations in *Billbergia elegans* and *Neoregelia mucugensis* (*Bromeliaceae*) exposed to low and high solar radiation. *Botany* 91(6): 327–334, ills. <https://doi.org/10.1139/cjb-2012-0276>.
- Roguenant, A. [ & al. 2016], Lecoufle, M. & Raynal-Roques, A. (2016) Les Broméliacées. Approche panoramique d’une grande famille “américaine”. Paris (FR): Belin.
- Santos-Silva, F. [ & al. 2013], Saraiva, D. P., Monteiro, R. F., Pita, P., Mantovani, A. & Forzza, R. C. (2013) Invasion of the South American dry diagonal: What can the leaf anatomy of *Pitcairnioideae* (*Bromeliaceae*) tell us about it? *Flora* (Jena) 208(8–9): 508–521, ills., maps. <https://doi.org/10.1016/j.flora.2013.08.003>.
- Santos-Silva, F. [ & al. 2015], Antunes Mastroberti, A. & Araujo Mariath, E. de (2015) Capsule structure in three species of *Dyckia* (*Bromeliaceae*): Ontogenetic and taxonomic issues. *J. Torrey Bot. Soc.* 142(3): 249–257, ills. <https://doi.org/10.3159/TORREY-D-14-00002.1>.
- Saraiva, D. P. [ & al. 2015], Mantovani, A. & Forzza, R. C. (2015) Insights into the evolution of *Pitcairnia* (*Pitcairnioideae* — *Bromeliaceae*), based on morphological evidence. *Syst. Bot.* 40(3): 726–736, ills. <https://doi.org/10.1600/036364415X689186>.

- Scharf, U. & Gouda, E. J. (2008) Bringing *Bromeliaceae* back to homeland botany. *J. Bromeliad Soc.* 58(3): 123–129, ills.
- Schulte, K. & Zizka, G. (2008) Multi locus plastid phylogeny of *Bromelioideae* (*Bromeliaceae*) and the taxonomic utility of petal appendages and pollen characters. *Candollea* 63(2): 209–225. [http://www.ville-ge.ch/cjb/publications\\_candollea\\_632.php](http://www.ville-ge.ch/cjb/publications_candollea_632.php).
- Schütz, N. [ & al. 2016 ], Krapp, F., Wagner, N. & Weising, K. (2016) Phylogenetics of *Pitcairnioideae* s.s. (*Bromeliaceae*): Evidence from nuclear and plastid DNA sequence data. *Bot. J. Linn. Soc.* 181(3): 323–342, maps, ills. <https://doi.org/10.1111/boj.12403>.
- Silvera, K. [ & al. 2010 ], Neubig, K. M., Whitten, W. M., Williams, N. H., Winter, K. & Cushman, J. C. (2010) Evolution along the Crassulacean Acid Metabolism continuum. *Funct. Pl. Biol.* 37(11): 995–1010. <https://doi.org/10.1071/FP10084>.
- Silvestro, D. [ & al. 2014 ], Zizka, G. & Schulte, K. (2014) Disentangling the effects of key innovations on the diversification of *Bromelioideae* (*Bromeliaceae*). *Evolution* 68(1): 163–175. <https://doi.org/10.1111/evo.12236>.
- Smith, E. L. (1983) Bigeneric hybrids — A listing. *J. Bromeliad Soc.* 33(2): 69–75. <http://journal.bsi.org/V33/2/>.
- Smith, L. B. & Downs, R. J. (1974) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 1: *Pitcairnioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4393694>.
- Smith, L. B. & Downs, R. J. (1977) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 2: *Tillandsioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399938>.
- Smith, L. B. & Downs, R. J. (1979) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>.
- Smith, L. B. & Till, W. (1998) *Bromeliaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 4: 75–99, ills., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03531-3\\_8](https://doi.org/10.1007/978-3-662-03531-3_8).
- Stevens, P. F. (2001+) *Angiosperm Phylogeny Website*, Version 12, July 2012 [and more or less continuously updated since]. St. Louis (US): Missouri Botanical Garden. <http://www.mobot.org/MOBOT/research/APweb/>
- Versieux, L. M. & Medeiros, A. S. M. (2018) Leaf anatomical characterization of *Guzmania* Ruiz & Pav., and *Mezobromelia* L. B. Sm. (*Tillandsioideae*, *Bromeliaceae*). *J. Bromeliad Soc.* 67(1): 8–26, ills.
- Versieux, L. M. [ & al. 2010 ], Elbl, P. M., Wanderley, M. G. L. & Menezes, N. L. de (2010) *Alcantarea* (*Bromeliaceae*) leaf anatomy characterization and its systematic implications. *Nordic J. Bot.* 28(4): 385–397. <https://doi.org/10.1111/j.1756-1051.2010.00727.x>.
- Versieux, L. M. [ & al. 2012 ], Barbará, T., Wanderley, M. G. L., Calvente, A., Fay, M. F. & Lexer, C. (2012) Molecular phylogenetics of the Brazilian giant bromeliads (*Alcantarea*, *Bromeliaceae*): Implications for morphological evolution and biogeography. *Molec. Phylogen. Evol.* 64: 177–189, ills. <https://doi.org/10.1016/j.ympev.2012.03.015>.
- Vieira da Silva, I. [ & al. 2011 ], Oliveria, D. M. de & Scatena, V. L. (2011) Anatomia foliar de *Ananas ananassoides* (Baker) L. B. Sm., *Vriesea bituminosa* Wawra e *Guzmania lingulata* (L.) Mez (*Bromeliaceae*) do Parque Estadual Cristalino, Alta Floresta - MT, Brasil. *Revista Ci. Agro-Ambient., Alta Floresta* 9(1): 83–95, ills.







## Acanthostachys BROMELIACEAE

U. Eggli

**Acanthostachys** Klotzsch (Icon. Pl. Rar. Hort. Reg. Bot. Berol. [II] 1: 21, t. 9, 1840). **Type:** *Hohenbergia strobilacea* Schultes fil. — **Bromelioideae** — **Lit:** Rauh & Barthlott (1982: systematics). **Distr:** E Brazil, Paraguay, NE Argentina. **Etym:** Gr. ‘akanthos, akantha’, thorn, prickle; and Gr. ‘stachys’, spike; for the spiny leaves and the inflorescence architecture.

Perennial epiphytic or saxicolous rosette plants with short-stemmed offsets, forming untidy clumps; **Ros** few-leaved; **L** irregularly erect to spreading and sometimes irregularly secund, stiff, thickened and succulent, sheath indistinct, narrowly elliptic, entire, dark brown, lamina to 1 m × 1.2 cm, strongly canaliculate with involute margins, tomentose-lepidote or glabrous, margin laxly serrate, **Sp** to 1.5 mm, green; **Inf** terminal, either sessile in the rosette, or erect to leaning or curved with a long peduncle and a congested fertile part subtended by 2 narrow long peduncular **Bra**, fertile part simple, strongly condensed, ovoid, 3–7 × 2–3.5 cm, with ascending-spreading, serrulate to entire, orange to reddish fertile **Bra** and an indistinct coma of sterile bracts; **Fl** sessile, to 25 mm; **Sep** free, yellow, triangular, pointed, 8–11 mm; **Pet** erect, free, yellow or white with blue tips, 16 mm, above the base with 2 scales; **St** included; **Ov** almost globose to

compressed, semi-inferior, with only 2 ovules per carpel; **Fr** fleshy berries aggregated into an infructescence, white or yellowish; **Se** embedded in mucilage, with a long-extended filiform appendage at maturity.

For long monotypic, a second species was added by Rauh & Barthlott (1982). The condensed inflorescences, either sessile or long-stalked, and the fruits aggregated into an edible cone-like infructescence, are diagnostic. The genus is part of the Eu-Bromelioids, where it is placed close to *Cryptanthus* as sister to the tank-forming Eu-Bromelioids (Schulte & al. 2009, Givnish & al. 2011). Evans & al. (2015) could not confirm monophyly of the genus, and its species are shown in an extensive polytomy in their Eu-Bromelioid clade. Within *Bromelioideae*, the genus is unique by having semi-inferior ovaries (inferior in all other genera of the subfamily) (Duque-Thüs 2009: 309).

Sazima & Sazima (1999) report that flowers of *A. strobilacea* are visited by 4 different species of hummingbirds, as well as by the perching passerine bird *Coereba flaveola*.

The leaves are quite succulent. With increasing water stress, the water storage tissue is losing volume and the leaves become increasingly canaliculate with inrolled margins until the leaves are almost terete and rush-like (Rauh & Barthlott 1982: 32).

**A. pitcairnioides** (Mez) Rauh & Barthlott (Trop. subtrop. Pfl.-welt 39: 5–6, 1982). **Type:**

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**Fig. 1** *Acanthostachys strobilacea* (Rauh s.n.: Brazil; São Paulo, Guaira). (Copyright: U. Eggli)

Brazil, Bahia (*Blanchet* s.n. [G, F [photo]]). — **Distr:** Brazil (Bahia, Espírito Santo); Atlantic rain forest, epiphytic. **I:** Rauh & Barthlott (1982).

≡ *Aechmea pitcairnioides* Mez (1896).

**L** margins coarsely brown-spined; **Inf** sessile within the rosette; **Pet** white with blue tips.

**A. strobilacea** (Schultes & Schultes *fil.*) Klotzsch (in Link & Otto, *Icon. Pl. Rar. Hort. Reg. Bot. Berol.* [II] 1: 21, t. 9, 1840). **Type:** Brazil, Minas Gerais (*Martius* s.n. [M]). — **Distr:** E Brazil (widespread, in the N to Maranhão), Paraguay (Amambay, Canindeyú, San Pedro), NE Argentina (Misiones); tropical and subtropical forests, epiphytic or epilithic; flowering in the dry season. **I:** Rauh & Barthlott (1982). — Fig. 1

≡ *Hohenbergia strobilacea* Schultes & Schultes *fil.* (1830); **incl.** *Acanthostachys exilis* Bertoni (1919).

**L** margins delicately spined; **Inf** long pedunculate; **Pet** yellow.

## References

- Duque-Thüs, R. (2009) Beiträge morphologischer und anatomischer Merkmale, insbesondere der Fruchtknoten und Samenanlagen zur Taxonomie und Systematik der *Bromelioideae* (*Bromeliaceae*). Frankfurt am Main (DE): J. W. Goethe-Universität, Fachbereich Biologie; unpublished Ph.D. thesis.
- Evans, T. M. [& al. 2015], Jabaily, R. S., Faria, A. P. G. de, Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>
- Givnish, T. J. [& al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ill., maps. <https://doi.org/10.3732/ajb.1000059>
- Rauh, W. & Barthlott, W. (1982) Zur Kenntnis der Gattung *Acanthostachys* Klotzsch mit Beschreibung einer zweiten ökologisch bemerkenswerten Art. *Trop. subtrop. Pfl.-welt* 39: 5–35, ill., key.
- Sazima, M. & Sazima, I. (1999) The perching bird *Coereba flaveola* as a co-pollinator of bromeliad flowers in southeastern Brazil. *Canad. J. Zool.* 77: 47–51, ill. <https://doi.org/10.1139/z98-184>
- Schulte, K. [& al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromeliaceae*) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylog. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>

## Aechmea BROMELIACEAE

U. Eggli

**Aechmea** Ruiz & Pavón (Fl. Peruv. Prodr., 47, 1794). **Type:** *Aechmea paniculata* Ruiz & Pavón. — **Bromelioideae** — **Lit:** Smith & Downs (1979: 1766–1956, Fl. Neotropica); Sass & Specht (2010: classification); Heller & al. (2015: classification); Aguirre-Santoro & al. (2016: phylogeny); Goetze & al. (2016: classification). **Distr:** Mexico to Uruguay and N Argentina, incl. C America and Caribbean. **Etym:** Gr. ‘aichme’, spear, tip of a spear; for the pungent tips of the leaves, floral bracts and/or sepals of some species.

**Incl.** *Hoiriri* Adanson (1763) (*nomen rejiciendum*, Art. 56.1). **Type:** *Bromelia nudicaulis* Linné.

**Incl.** *Oechmea* J. St.-Hilaire (1805) (*nom. inval.*, Art. 61.1).

**Incl.** *Eriostax* Rafinesque (1838). **Type:** *Eriostax glauca* Rafinesque [*nom. illeg.*, = *Bromelia melanantha* Kew-Gawler, fide IPNI].

**Incl.** *Aechmaea* Brongniart (1841) (*nom. inval.*, Art. 61.1).

**Incl.** *Chevalieria* Gaudichaud (1843) (*nom. inval.*, Art. 32.1d?).

**Incl.** *Disquamia* Lemaire (1853) (*nom. inval.*, Art. 32.1c). **Type:** *Aechmea distichantha* Lemaire.

**Incl.** *Macrochordion* de Vriese (1853). **Type:** *Bromelia tinctoria* Martius.

**Incl.** *Hoplophytum* Beer (1854). **Type:** *Billbergia rhodocyanea* Lemaire.

**Incl.** *Chevaliera* Gaudichaud ex Beer (1856). **Type:** *Chevaliera sphaerocephala* Gaudichaud.

**Incl.** *Lamprococcus* Beer (1856). **Type:** *Aechmea fulgens* Brongniart.

**Incl.** *Macrochordium* Beer (1856) (*nom. inval.*, Art. 61.1).

**Incl.** *Pothuava* Gaudichaud ex K. Koch (1860). **Type:** *Bromelia nudicaulis* Linné.

**Incl.** *Ortgiesia* Regel (1867). **Type:** *Ortgiesia tillandsioides* Regel.

**Incl.** *Gravisia* Mez (1891). **Type:** *Bromelia exsudans* Loddiges.

**Incl.** *Wittmackia* Mez (1891). **Type:** *Bromelia lingulata* Linné.

**Incl.** *Platyaechmea* (Baker) L. B. Smith & Kress (1990). **Type:** *Aechmea distichantha* Lemaire.

**Incl.** *Podaechmea* (Mez) L. B. Smith & Kress (1990). **Type:** *Pironneava lueddemanniana* K. Koch [lectotype, according to L. B. Smith & Kress, *Phytologia* 66(4): 271, 1990].

Perennial epiphytic or terrestrial or saxicolous rosette plants, mesophytic to xerophytic, usually of medium size, almost always acaulescent, often offsetting with basally produced stolons; **L** in

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dense rosettes or at least in fascicles, sheaths often forming a tank, lamina often leathery and coarse, rarely slightly succulent, often cross-zoned or blotched, tip broadly rounded and usually with a spiny mucro, margins usually spinose-serrate; **Inf** usually with a well-defined peduncle, fertile part simple or compound; peduncular and floral **Bra** usually brightly coloured; **Fl** often densely arranged, spiral or sometimes distichous, sessile or pedicellate, hermaphrodite, usually not showy, often with abundant nectar; **Sep** free or connate, mostly strongly asymmetrical; **Pet** (almost) free, regular, usually with 2 basal appendages (these rarely almost aborted); **St** included, free or the epipetalous ones adnate to the petals; **Anth** dorsifixed; **Ov** inferior, with numerous ovules; **Fr** often hardly larger than the ovary, fleshy (rarely dry) berries, often brightly coloured and long-lasting; **Se** small.

A genus of  $\pm 180$  species, divided into 8 subgenera, and already thought to likely be polyphyletic by Smith & Downs (1979). Smith & Kress (1990) elevated the 7 heterotypic subgenera of the 1979-treatment to the rank of genus, but this did not eliminate the confusion and was mostly not followed by later authors. All recent molecular studies agree that *Aechmea* in the traditional circumscription is highly polyphyletic (Schulte & al. 2005, Horres & al. 2007, Schulte & Zizka 2008, Schulte & al. 2009, Evans & al. 2015, Heller & al. 2015, Aguirre-Santoro & al. 2016). Sass & Specht (2010) not only confirm the genus to be polyphyletic, but moreover found its species to be dispersed throughout the higher core bromelioids, making several other genera paraphyletic. According to their study, most of the traditionally accepted subgenera are also not monophyletic, but can be divided into separate clades that correlate with geographical distribution, rather than having shared morphologies. There is no doubt that *Aechmea* has been used as a “trash can genus” in the past, and some species are probably better reclassified in *Araeococcus* or *Ananas* (Givnish & al. 2011: 885). Aguirre-Santoro & al. (2016) studied the so-called “*Ronnbergia* Alliance”, which includes species of *Aechmea*, *Hohenbergia* and *Ronnbergia*, and which is sister to a clade with the majority of the

remaining *Aechmea* species plus *Billbergia* and *Hohenbergia*. The centre of diversity of the group as a whole appears to be in Brazil. A modern monograph is lamentably absent.

**Succulence:** Species from seasonally dry regions often have considerably xeromorphic leaves, and a minor degree of succulence is found in many taxa. Horres & Zizka (1995) show a well-developed hydrenchyma making up 43% of the cross-sectional area of the leaves of *A. recurvata*. Horres & al. (2007: 40, Fig. 5G-H) define 5 different types of leaf anatomy for *Bromelioideae* genera, and illustrate strongly developed water-storage tissue for *A. weberbaueri*, and fairly well-developed water storage tissue for *A. aquilega*, *A. eurycorymbosa*, *A. mulfordii*, *A. paniculata* and *A. rubens*. Proença & Sajo (2004) present more detailed data for different leaf parts; in general, the apical parts of the lamina show least well-developed succulence (25–40% cross-sectional area occupied by the hydrenchyma), while the middle lamina parts are moderately succulent, and the basal part shows the most pronounced development of hydrenchyma (to 60–70% cross-sectional area in *A. gracilis* and *A. distichantha*). Minor to moderate development of hydrenchyma is obviously widespread, and Faria & al. (2012) observed that all the species of subgen. *Macrochordion* have an “aquiferous parenchyma” consisting of 1–5 cell layers. The selection of species treated below is somewhat casual, and merely presents a few species by way of example.

**Horticulture:** Several species of *Aechmea* are of horticultural importance and are valued as foliage plants and for their long-lasting inflorescence with colourful bracts. Plants of numerous cultivars and selections are produced annually in enormous numbers. The most popular species is probably *A. fasciata* with the typically cross-banded leaves. Formally named intergeneric hybrids are known with *Nidularium* (=  $\times$ *Nidumea*), *Orthophytum* (=  $\times$ *Orthomea*, see separate entry in this handbook), *Portea* (=  $\times$ *Portemea*), *Pseudoananas* (=  $\times$ *Pseudoanamea*), *Quesnelia* (=  $\times$ *Quesmea*), *Streptocalyx* (=  $\times$ *Streptomea*), and *Ursulaea* (=  $\times$ *Ursumea*).

The following names are of unresolved application but are referred to this genus: *Tillandsia bracteata* Vellozo (1829); *Tillandsia comata* Vellozo (1829)  $\equiv$  *Bromelia comata* (Vellozo) Beer (1856); *Tillandsia tetrasticha* Vellozo (1829).

**A. cylindrata** Lindman (Kongl. Svenska Vetensk. Acad. Handl., n.s. [ser. 2], 24(8): 32, t. 8, Figs. 28–35, 1891). **Type:** Brazil, São Paulo (*Mosén* 2975 [S, GH [photo]]). — **Distr:** Brazil (São Paulo, Paraná, Santa Catarina); epiphytic or very rarely terrestrial, 50–1200 m. **I:** Reitz (1983: t. 7); Rauh (1990: 121: Fig. 96).

$\equiv$  *Ortgiesia cylindrata* (Lindman) L. B. Smith & W. J. Kress (1989); **incl.** *Aechmea cylindrata* var. *micrantha* Lindman (1891); **incl.** *Aechmea hyacinthus* F. Mueller (1893).

Acaulescent, to 60 (–80) cm when flowering; **Ros** with numerous flatly arching-spreading leaves; **L** sheaths oblong-ovate, 10–12  $\times$  5–10 cm, green, with pale pink lines or blotches, grey-lepidote, **L** lamina 30–40 (–120)  $\times$  to 6 cm, linear, moderately canaliculate, dark green, upper face weakly and lower face densely lepidote, margins serrate; **Inf** to 60 cm, fertile part 15–20  $\times$  2–3 cm; floral **Bra** long-acuminate, red, weakly white-lanate, margins entire, basal **Bra** longer than the flowers, upper **Bra** shorter; **Fl** to 12 mm; **Sep** rose-coloured; **Pet** pale blue with darker, broadly rounded tip; **Fr** red, ellipsoid, 15  $\times$  6 mm.

**A. distichantha** Lemaire (Jard. Fleur. 3: t. 269 + text + ill., 1853). **Type:** Brazil, São Paulo (*Libon* s.n. [[icono]: l.c. t. 269]). — **Lit:** Sazima & Sazima (1999: pollination ecology); Bianchi & al. (2000: breeding system); Figueiredo (2006: pollination ecology). **Distr:** Brazil, Uruguay, N Argentina, Paraguay, Bolivia.

$\equiv$  *Hoplophytum distichanthum* (Lemaire) Beer (1856)  $\equiv$  *Hohenbergia distichantha* (Lemaire) Baker (1872)  $\equiv$  *Quesnelia distichantha* (Lemaire) Lindman (1891)  $\equiv$  *Platyaechea distichantha* (Lemaire) L. B. Smith & W. J. Kress (1990).

Acaulescent, to 70 cm when flowering; **Ros** with numerous straightly ascending leaves; **L** sheaths oblong-elliptic, to 30 cm, **L** lamina

100–150  $\times$  2.5–8 cm, tongue-shaped, rigid, dull green, grey-lepidote, margins densely brown-spinose; **Inf** compound, pyramidal in outline, primary **Bra** broadly ovate, rose-coloured, white-lanate, shorter than the ascending to spreading branches; peduncular **Bra** appressed to the axis, longer than the internodes, imbricate, rose to green; floral **Bra** 5–7 mm, rose; **Fl** distichous; **Sep** 5–13 mm, free or shortly fused, veined, rose, white-lanate; **Pet** 18 mm, obtuse, blue, white or purple; **Fr** whitish, ellipsoid, to 10  $\times$  7 mm.

Variable, and divided into the following varieties:

**A. distichantha** var. **distichantha** — **Distr:** Brazil (Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Uruguay, N Argentina (Misiones), Paraguay (widespread); epiphytic, 200–1200 m. **I:** Reitz (1983: t. 8); Oliva-Esteve & Steyermark (1987: 52–53); Rauh (1990: 11: Fig. 71).

**Incl.** *Tillandsia polystachia* Vellozo (1829) (*nom. illeg.*, Art. 53.1)  $\equiv$  *Aechmea polystachia* (Vellozo) Mez (1892)  $\equiv$  *Hoiriri polystachia* (Vellozo) Kuntze (1898); **incl.** *Billbergia distichostachya* Lemaire (1851) (*nomen rejiciendum*, Art. 56.1); **incl.** *Billbergia polystachya* Lindley & Paxton (1852) (*nomen rejiciendum*, Art. 56.1); **incl.** *Aechmea hookeri* Lemaire (1864); **incl.** *Aechmea excavata* Baker (1879)  $\equiv$  *Aechmea polystachia* var. *excavata* (Baker) Mez (1896); **incl.** *Aechmea myriophylla* E. Morren ex Baker (1887); **incl.** *Aechmea microphylla* Mez (1892) (*nom. inval.*, Art. 61.1); **incl.** *Nidularium hydrophorum* Rojas (1918); **incl.** *Aechmea platyphylla* Hassler (1919); **incl.** *Aechmea polystachia* var. *myriophylla* Hassler (1919); **incl.** *Aechmea polystachya* var. *longifolia* Castellanos (1925); **incl.** *Aechmea distichantha* fa. *albiflora* L. B. Smith (1943).

**L** tip mostly shortly attenuate; **Inf** broadly pyramidal, lax, branches  $\pm$ spreading, many-flowered; **Pet** purple or blue.

A white-flowering form from Paraná has been described as fa. *albiflora*.

**A. distichantha** var. **glaziovii** (Baker) L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1:



102, 1943). **Type:** Brazil, Rio de Janeiro (*Glaziou & Joly* 8986 [K, GH [photo]]). — **Distr:** Brazil (Minas Gerais, Rio de Janeiro, São Paulo, Paraná); epiphytic, 840–1900 m.

≡ *Aechmea glaziovii* Baker (1879) ≡ *Platyaechmea distichantha* var. *glaziovii* (Baker) L. B. Smith & W. J. Kress (1990); **incl.** *Aechmea minor* E. Morren (1881) (*nom. inval.*, Art. 32.1c); **incl.** *Aechmea pulchella* E. Morren ex Mez (1892); **incl.** *Aechmea regelii* Mez (1892).

**L** tip rounded with a mucro; fertile **Inf** part dense, ovate-cylindrical, branches ascending, few-flowered.

**A. distichantha** var. **schlumbergeri** E. Morren ex Mez (in Martius, Fl. Bras. 3(3): 343, 1892). **Type:** LG, B, GH [photo]. — **Distr:** Brazil (Minas Gerais), Bolivia (La Paz, Cochabamba, Santa Cruz), Paraguay, N Argentina (Jujuy, Salta, Tucumán, Formosa, Corrientes, Misiones, Santa Fé); epiphytic or sometimes terrestrial, 200–1800 m.

≡ *Platyaechmea distichantha* var. *schlumbergeri* (E. Morren ex Mez) L. B. Smith & W. J. Kress (1990); **incl.** *Chevaliera grandiceps* Grisebach (1879) ≡ *Aechmea grandiceps* (Grisebach) Mez (1892); **incl.** *Aechmea polystachya* Mez (1892); **incl.** *Aechmea involucrata* Rusby (1907) (*nom. illeg.*, Art. 53.1); **incl.** *Aechmea rubra* A. Silveira (1931); **incl.** *Aechmea involucrifera* Mez (1934).

Plants large; **L** usually acuminate; fertile **Inf** part dense, elongate cylindrical to fusiform, few-flowered.

**A. distichantha** var. **vernica** E. Pereira (Bradea 2(47): 308, 1979). **Type:** Brazil, Rio de Janeiro (*Dungs* 30 [HB]). — **Distr:** Brazil (Rio de Janeiro); epiphytic, 750 m.

≡ *Platyaechmea distichantha* var. *vernica* (E. Pereira) L. B. Smith & W. J. Kress (1990).

**L**, floral **Bra** and **Sep** varnished-glossy.

**A. gracilis** Lindman (Kongl. Svenska Vetensk. Acad. Handl., n.s. [ser. 2], 24(8): 30, t. 6, Figs. 10–16, 1891). **Type:** Brazil, São Paulo (*Mosén* 3707 [S, GH [photo]]). — **Distr:** Brazil (Rio de Janeiro, São Paulo, Paraná); epiphytic, to 1000 m. **I:** Rauh (1990: 255: fig. 275).

≡ *Ortgiesia gracilis* (Lindman) L. B. Smith & W. J. Kress (1989).

Acaulescent, to 50 cm when flowering; **Ros** with few ascending-spreading leaves; **L** sheath narrowly ovate, 8–10 × 4–5 cm, upper parts sometimes dark pink, lamina to 30 × 3–4 cm, narrowly linear with rounded mucronate tip, dark green, grey-lepidote, margins laxly spinose; **Inf** to 40 cm, peduncle ±20 cm, erect, green, first white-lanate but becoming naked, fertile part simple, lax and few-flowered, or rarely compound with few 2- to 3-flowered branches; floral **Bra** small, red, rapidly caducous; **Fl** spiral, sessile, to 25 mm; **Sep** ± 6 mm, fused for 3 mm, pale red, glabrous, with spinose tip; **Pet** 14 mm, rounded, pale blue with darker margins and base; **Fr** not described.

**A. nudicaulis** (Linné) Grisebach (Fl. Brit. West Ind. Islands, 593, 1864). **Type:** West Indies (*Plumier* s.n. [not located, original material: [icon]: Plumier in Burman, Pl. Amer., 51, t. 62, 1756]). — **Distr:** Mexico, C America, Caribbean, Venezuela, Colombia, Guayana, Brazil, Peru, Ecuador; epiphytic, terrestrial or lithophytic, to 1140 m. **I:** Reitz (1983: t. 15 (var. *cuspidata*), t. 16 (var. *tabuleirensis*)); Oliva-Esteve & Steyermark (1987: 74–75); Rauh (1990: 115: fig. 74 (var. *nudicaulis*)); Klein V. & Klein (2013: 17).

≡ *Bromelia nudicaulis* Linné (1753) ≡ *Billbergia nudicaulis* (Linné) Lindley (1827) ≡ *Hoplophytum nudicaule* (Linné) K. Koch (1857) ≡ *Hohenbergia nudicaulis* (Linné) Baker (1871) ≡ *Pothuava nudicaulis* (Linné) Regel (1882); **incl.** *Tillandsia saxatilis* Vellozo (1829).

Acaulescent, 30–70 cm when flowering; **Ros** tubular with few leaves; **L** sheath large, elliptic, to 15 cm, above brown to lilac, densely brown-lepidote, lamina broadly tongue-shaped, 20–90 × 6–10 cm, green, lower face sometimes with grey cross-bands, margins with black spines 4 mm long; **Inf** to 70 cm, simple, lax, peduncle hardly longer than the leaves, white-lanate-lepidote; peduncular **Bra** erect, longer than the internodes, bright red, elliptic, with weakly spinose margins; floral **Bra** small, pointed, shorter than the sepals, red, sometimes reduced or absent; **Fl** sessile, spiral; **Sep** 5–10 mm, free, yellowish-green, minutely

lepidote, tip pungent; **Pet** tongue-shaped, acute, 12 mm, yellow; **Fr** ± orange, ovoid.

A very variable species, for which almost a dozen heterotypic varieties have been described (not treated separately here).

**A. recurvata** (Klotzsch) L. B. Smith (Contr. Gray Herb. 98: 5, 1932). **Type:** (*Anonymus* s.n. in *Hort. Blass* s.n. [B?]). — **Distr:** Brazil, Paraguay, Uruguay, NE Argentina; epiphytic or lithophytic, 0–2000 m.

≡ *Macrochordium recurvatum* Klotzsch (1856) ≡ *Orgiesia recurvata* (Klotzsch) L. B. Smith & W. J. Kress (1989); **incl.** *Vriesea legrelliana* hort. ex Padilla (1965) (*nom. inval.*, Art. 32.1c).

Acaulescent, epiphytic or less commonly terrestrial (saxicolous), forming small groups, stoloniferous, 15–20 cm when flowering; **Ros** few-leaved, elongate-urceolate by virtue of the overlapping leaf sheaths; **L** sheath spoon-shaped, to 7 cm, lamina narrowly triangular, long acuminate, longer than the sheath, basally 1 cm wide, recurving, with long pungent tip, margins laxly to densely spinose-serrate, inner leaves turning rose-red in flowering plants; **Inf** shorter than the leaves, with a short distinct peduncle, fertile part simple, 5–6 × 3 cm, dense; floral **Bra** triangular-acuminate, serrate, to 17 mm, red, thin-textured; **Fl** sessile, to 35 mm; **Sep** to 17 × 5 mm, ovate, tip rounded, basal ¼ fused, rose-coloured, glabrous or scantily lepidote; **Pet** 25 × 4 mm, rose to pink-red with white base; **Fr** blackish, globose to oblong, to 17 × 9 mm, glossy.

A variable species with 3 heterotypic varieties:

**A. recurvata** var. **benrathii** (Mez) Reitz (Anais Bot. Herb. “Barbosa Rodrigues” 4: 30, 1952). **Type:** Brazil (*Anonymus* s.n. in *BG Königsberg* s.n. [B, F [photo]]). — **Distr:** S Brazil (Santa Catarina); saxicolous, to 50 m. **I:** Reitz (1983: t. 21).

≡ *Aechmea benrathii* Mez (1919) ≡ *Orgiesia recurvata* var. *benrathii* (Mez) L. B. Smith & W. J. Kress (1989); **incl.** *Aechmea rupestris* F. Müller ex Ule (1899) (*nom. inval.*, Art. 32.1c).

**Inf** mostly or completely included in the rosettes; **L** and **Bra** entire or almost entire.

A hybrid with *Orthophytum vagans* is reported in the horticultural literature (as ×*Orthomea*).

**A. recurvata** var. **ortgiesii** (Baker) Reitz (Anais Bot. Herb. “Barbosa Rodrigues” 4: 29, 1952). **Type:** (*Anonymus* s.n. in *BG St. Petersburg* s.n. [LE?]). — **Distr:** S Brazil (Santa Catarina, Paraná); epiphytic or sometimes terrestrial, to 2000 m. **I:** Reitz (1983: t. 22).

≡ *Aechmea ortgiesii* Baker (1879) ≡ *Orgiesia recurvata* var. *ortgiesii* (Baker) L. B. Smith & W. J. Kress (1989); **incl.** *Tillandsia rosea* hort. ex Regel (1866) (*nom. inval.*, Art. 32.1c); **incl.** *Orgiesia tillandsioides* Regel (1867) ≡ *Portea tillandsioides* (Regel) Nicholson (1886); **incl.** *Tillandsia rosea* Hort. Linden ex Regel (1867) (*nom. inval.*, Art. 32.1c).

**Inf** mostly or completely included in the rosettes; **L** and **Bra** strongly serrate.

**A. recurvata** var. **recurvata** — **Distr:** Brazil (Rio Grande do Sul, Santa Catarina, Paraná), Uruguay, Paraguay, NE Argentina (Corrientes, Misiones); mostly epiphytic, to 70 m. **I:** Reitz (1983: t. 23); Klein V. & Klein (2013: 14–16). – Fig. 1.

**Incl.** *Orgiesia tillandsioides* var. *subexserta* Regel (1867); **incl.** *Hohenbergia legrelliana* Baker (1871) ≡ *Aechmea legrelliana* (Baker) Baker (1879) ≡ *Portea legrelliana* (Baker) Nicholson (1886) ≡ *Orgiesia legrelliana* (Baker)



**Fig. 1** *Aechmea recurvata* var. *recurvata* (Supthut 90105: Brazil; Santa Catarina, E of Lajes, 1000 m.) (Copyright: U. Eggli)

Baker (1889); **incl.** *Billbergia legrelliana* hort. ex Baker (1871) (*nom. inval.*, Art. 34.1c); **incl.** *Billbergia legrelloae* hort. ex Morren (1873); **incl.** *Ortgiesia palleolata* Morren (1873); **incl.** *Aechmea ampullacea* Mez (1896); **incl.** *Aechmea ampullacea* var. *longifolia* Hassler (1919).

**Inf** completely exserted from the rosettes; floral **Bra** serrate.

**A. weberbaueri** Harms (Notizbl. Bot. Gart. Berlin-Dahlem 14: 330, 1939). **Type:** Peru, Lambayeque (*Weberbauer* 8041 [B, B [photo]]). — **Distr:** C Peru (Lambayeque); epiphytic, ±1200 m. **I:** Rauh (1990: 258; Fig. 285).

≡ *Pothuava weberbaueri* (Harms) L. B. Smith & W. J. Kress (1989).

Acaulescent, to 70 cm when flowering; **Ros** few-leaved, 60–80 cm broad; **L** sheath oblong-ovate, 15–20 × 8–9 cm, dull green, appressedly grey-lepidote, lamina 50–60 × 6–7 cm, linear, dull green, appressedly grey-lepidote, margins with brown spines to 2 mm long; **Inf** with peduncle to 40 cm, white-lanate, fertile part simple, 10–15 × 8 cm, lax; peduncular **Bra** longer than the internodes, erect, green, grey-lepidote, margins serrate; floral **Bra** horizontally porrect, basal ones to 35 × 6 mm, long-attenuate, entire, drying before anthesis, glabrescent; **Fl** sessile; **Sep** 20 mm, rose-pink, with 10 mm long spinose brown tip, white-lanate; **Pet** free but forming a tube and only the tips spreading, 40 × 6 mm, sky-blue; **Fr** not described.

Belonging to the so-called “Pacific Clade” within the “*Ronnbergia* Alliance” in the phylogeny presented by Aguirre-Santoro & al. (2016).

## References

- Aguirre-Santoro, J. [& al. 2016], Michelangeli, F. A. & Stevenson, D. W. (2016) Molecular phylogenetics of the *Ronnbergia* alliance (*Bromeliaceae*, *Bromelioideae*) and insights into their morphological evolution. *Molec. Phylogen. Evol.* 100: 1–20, ills. <https://doi.org/10.1016/j.ympcv.2016.04.007>
- Bianchi, M. B. [& al. 2000], Gibbs, P. E., Prado, D. E. & Vesprini, J. L. (2000) Studies on the breeding systems of understory species of a Chaco woodland in NE Argentina. *Flora* 195(4): 339–348, ills.
- Evans, T. M. [& al. 2015], Jabaily, R. S., Faria, A. P. G. de, Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>
- Faria, A. P. G. de [& al. 2012], Vieira, A. C. M. & Wendt, T. (2012) Leaf anatomy and its contribution to the systematics of *Aechmea* subgenus *Macrochordion* (de Vriese) Baker (*Bromeliaceae*). *Anais Acad. Brasil. Ci.* 84(4): 961–971, ills. <https://doi.org/10.1590/S0001-37652012005000053>
- Figueiredo, R. A. de (2006) Reproductive aspects of sympatric Bromeliads in southeastern Brazil. *J. Bromeliad Soc.* 55(5): 219–228, ills.
- Givnish, T. J. [& al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ills., maps. <https://doi.org/10.3732/ajb.1000059>
- Goetze, M. [& al. 2016], Schulte, K., Palma-Silva, C., Zanella, C. M., Büttow, M. V., Capra, F. & Bered, F. (2016) Diversification of *Bromelioideae* (*Bromeliaceae*) in the Brazilian Atlantic forest: A case study in *Aechmea* subgenus *Ortgiesia*. *Molec. Phylogen. Evol.* 98: 346–357, map. <https://doi.org/10.1016/j.ympcv.2016.03.001>
- Heller, S. [& al. 2015], Leme, E. M. C., Schulte, K., Benko-Iseppon, A. M. & Zizka, G. (2015) Elucidating phylogenetic relationships in the *Aechmea* alliance: AFLP analysis of *Portea* and the *Gravisia* complex (*Bromeliaceae*, *Bromelioideae*). *Syst. Bot.* 40(3): 716–725, map, ills. <https://doi.org/10.1600/036364415X689177>
- Horres, R. & Zizka, G. (1995) Untersuchungen zur Blattsukkulenz bei *Bromeliaceae*. *Beitr. Biol. Pfl.* 69(1):43–76, ills
- Horres, R. [& al. 2007], Schulte, K., Weising, K. & Zizka, G. (2007) Systematics of *Bromelioideae* (*Bromeliaceae*) — evidence from molecular and anatomical studies. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution: Poales*. *Aliso* 23(1): 27–43, ills. <https://doi.org/10.5642/aliso.20072301.05>
- Klein V., L. F. & Klein, J. (2013) Die Bromelien in den atlantischen Wäldern der Nord-Ost-Küste von Rio Grande do Sul / Brasilien — Teil 1/Teil 2/Teil 3. The Bromeliads in the Atlantic forest of the northeast coast of Rio Grande do Sul/Brazil — part 1/part 2/part 3. *Bromelie* 2013(1): 8–17, (2): 74–81, (3): 144–154, ills.
- Oliva-Esteve, F. & Steyermark, J. (1987) *Bromeliaceae* [sic!] of Venezuela. Caracas (VE): Armitano Editores.
- Pronça, S. L. & Sajo, M. G. (2004) Estrutura foliar de espécies de *Aechmea* Ruiz & Pav. (*Bromeliaceae*) do Estado de São Paulo, Brasil. *Acta Bot. Brasil.* 18(2):

- 319–331, ills. <https://doi.org/10.1590/S0102-33062011000100002>
- Rauh, W. (1990) Bromelien. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Reitz, R. (1983) Bromeliáceas e a malária-broméia endêmica. In: Reitz, R. (ed.): Flora ilustrada catarinense, I parte as plantas, fascículo BROM. Itajaí (BR): Herbario “Barbosa Rodrigues”.
- Sass, C. & Specht, C. D. (2010) Phylogenetic estimation of the core Bromelioids with an emphasis on the genus *Aechmea* (Bromeliaceae). *Molec. Phylogen. Evol.* 55: 559–571. <https://doi.org/10.1016/j.ympev.2010.01.005>
- Sazima, M. & Sazima, I. (1999) The perching bird *Coereba flaveola* as a co-pollinator of bromeliad flowers in southeastern Brazil. *Canad. J. Zool.* 77: 47–51, ills. <https://doi.org/10.1139/z98-184>
- Schulte, K. & Zizka, G. (2008) Multi locus plastid phylogeny of *Bromelioideae* (Bromeliaceae) and the taxonomic utility of petal appendages and pollen characters. *Candollea* 63(2): 209–225. [http://www.ville-ge.ch/cjb/publications\\_candollea\\_632.php](http://www.ville-ge.ch/cjb/publications_candollea_632.php)
- Schulte, K. [ & al. 2005], Horres, R. & Zizka, G. (2005) Molecular phylogeny of *Bromelioideae* and its implications on biogeography and the evolution of CAM in the family. *Senckenberg. Biol.* 85(1): 113–125, maps.
- Schulte, K. [ & al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (Bromeliaceae) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylogen. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>
- Smith, L. B. & Downs, R. J. (1979) Flora Neotropica. Monograph No. 14 [Bromeliaceae]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>
- Smith, L. B. & Kress, W. J. (1990) New genera of *Bromeliaceae*. *Phytologia* 69(4): 271–274.







## Billbergia BROMELIACEAE

U. Eggli

**Billbergia** Thunberg (Pl. Bras. 3: 30, 1821). **Type:** *Billbergia speciosa* Thunberg. — **Bromelioideae** — **Lit:** Smith & Downs (1979: 1975–2036, Fl. Neotropica); Barros & Costa (2008: monograph Rio de Janeiro State); Gaiotto F. & al. (2010: monograph Paraná State). **Distr:** S Mexico to Bolivia and N Argentina, with a centre of diversity in Brazil. **Etym:** For Gustaf Johan Billberg (1772–1844), Swedish botanist and zoologist.

**Incl.** *Anacyclia* Hoffmannsegg (1833). **Type:** *Anacyclia farinosa* Hoffmannsegg [*nom. illeg.*, ≡ *Bromelia zebrina* Herbert].

**Incl.** *Eucallias* Rafinesque (1838) (*nom. illeg.*, Art. 52.1). **Type:** *Eucallias versicolor* Rafinesque [*nom. illeg.*, ≡ *Bromelia zebrina* Herbert].

**Incl.** *Jonghea* Lemaire (1852). **Type:** *Jonghea splendida* Lemaire.

**Incl.** *Cremobotrys* Beer (1854) (*nom. illeg.*, Art. 52.1). **Type:** *Bromelia zebrina* Herbert.

**Incl.** *Helicodea* Lemaire (1864). **Type:** *Helicodea baraquinia* Lemaire [typification according to L. B. Smith & Downs, Fl. Neotrop. 14(3): 1977, 1979].

Perennial terrestrial or epiphytic rosette plants, usually acaulescent, offsetting and with usually short stolons; **Ros** broadly funnel-shaped to tubular; **L** sheaths inconspicuous to distinct, **L** lamina narrowly to broadly linear-oblong, often with conspicuous pale cross-bands, tip often rounded tongue-shaped with a small mucro, margins coarsely to finely serrate or rarely entire; **Inf** simple or compound, peduncle erect or curved, fliferous part often arching to nutant; peduncular **Bra** usually large, thin, often bright red to magenta, overlapping; **Fl** large and showy, actinomorphic or slightly zygomorphic, sepals and petals forming a short to long epigynous tube; **Sep** lobes free, erect, glabrous to densely farinose or floccose-lanate; **Pet** free, at the basis with 2 scales, with a long claw and a somewhat broader, long but still narrow tip, ascending to recurved or tightly recoiled at anthesis; **St** usually exerted; **Fil** all free or those of the inner whorl adnate to the petal base to the height of the scales; **Ov** completely inferior; **Sty** longer than the stamens; **Fr** green to violet fleshy berries, globose, with persistent calyx.

A genus of some 60 species. *Billbergia* forms part of the higher core *Bromelioideae* in all recent molecular phylogenies. It is with the exception of 2 species strongly supported as monophyletic, and is closely related to *Quesnelia* and a small group of *Aechmea* species (Sass & Specht 2010). Evans & al. (2015) also found 3 species outside a well-supported core *Billbergia* clade. The genus is traditionally divided into 2 subgenera, Subgen.

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*Billbergia* (inflorescences simple or branched, peduncle often glabrous; petals recurved or slightly coiled) and Subgen. *Helicodea* (Lemaire) Baker 1889 (inflorescences simple, peduncle densely white-lanate; petals coiled), but the molecular phylogeny of Sass & Specht (2010) found no support for this division.

**Succulence:** Succulence is absent or ill-defined in most species of the genus, although many have distinctly coriaceous leaves and are native to semi-arid places. In cultivation, the degree of succulence of several species is strongly influenced by the watering and light regime, with more pronounced succulence under dry and bright conditions. Below, a very small selection of succulent-leaved species (all from subgen. *Billbergia*) is presented by way of example.

**Horticulture:** Most species have relatively short-lived flowers, making them unattractive for horticultural purposes. The only species more commonly seen in the trade is *B. nutans*, and several cultivars and selections are encountered. Formally named intergeneric hybrids are known with *Aechmea* (= ×*Billmea*), *Cryptanthus* (= ×*Biltanthus*, see separate entry in this handbook), *Neoregelia* (= ×*Neobergia*, see separate entry in this handbook), and *Quesnelia* (= ×*Billnelia*).

The following name is of unresolved application but is referred to this genus: *Tillandsia osyana* hort. ex K. Koch (1862) (*nom. inval.*, Art. 32.1c).

**B. brasiliensis** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 105, 1943). **Type:** Brazil, Santa Catarina? (*De Vos* s.n. in *Hort. Verschaffelt* s.n. [[*icono*]: *Rev. Hort.* 41: 87, Fig. 21, 1869]). — **Lit:** Barros & Costa (2008: 1175–1176). **Distr:** Brazil (Rio de Janeiro, Santa Catarina?); ecology not described. – Fig. 1.

**Incl.** *Helicodea leopoldii* Hort. Verschaffelt ex Lemaire (1864) ≡ *Billbergia leopoldii* (Hort. Verschaffelt ex Lemaire) Linden (1869) (*nom. illeg.*, Art. 53.1); **incl.** *Billbergia ianthina* hort. ex E. Morren (1871) (*nom. inval.*, Art. 32.1c); **incl.** *Billbergia nuptialis* Hort. Makoy ex E. Morren (1871) (*nom. inval.*, Art. 32.1c); **incl.** *Billbergia kuhlmannii* L. B. Smith (1950).

Acaulescent, to 80 cm tall, with short ascending rhizomes; **Ros** rather narrowly tubular, with 8–10 leaves; **L** sheath broadly elliptic, rigid, margins spiny, **L** lamina to 80 × 6–7 cm, basal parts with broad pale cross-bands, thick and fleshy (E. Gouda, pers. comm.), somewhat lepidote, esp. on the lower face, tip broadly acute to roundish, apiculate, margins with laxly arranged **Sp**, these brown, antrorse, 1.5–3 mm; **Inf** decurved, simple, floriferous part usually nodding, somewhat densely 28- to 30-flowered, densely white-farinose, peduncle 35–41 cm, white-farinose; peduncular **Bra** congested below the floriferous part, lanceolate, acute, rose-red; floral **Bra** minute, almost covered by the indumentum; **Fl** sessile, suberect, 65 mm; **Sep** very slightly asymmetrical, oblong, 10–17 × 6 mm, rose-red, white-farinose;

**Fig. 1** *Billbergia brasiliensis*. (Copyright: E. J. Gouda)



**Pet** linear, acute,  $\pm 50$  mm, greenish-rose with dark blue-purple apical part, with 2 fimbriate scales, contorted or somewhat spirally recurved for a short distance only; **St** included; **Fr** not described.

Originally described from Santa Catarina, but without locality data. Barros & Costa (2008) report the taxon from Rio de Janeiro, and its occurrence in Santa Catarina is unlikely. Suspected as probable intersubgeneric hybrid by Smith & Downs (1979: 2007) and Reitz (1983: 485–486), but compared with the similar *B. pyramidalis* by Barros & Costa (2008).

**B. euphemiae** E. Morren (Belgique Hort. 22: 11, tt. 1–2, 1872). **Type:** Cult. BG Liège (*Anonymus* s.n. [LG, GH [photo]]). — **Distr:** Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro); epiphytic or lithophytic in forest. **I:** Smith & Downs (1979: 2013); Barros & Costa (2008: 1178); Machado & al. (2016: 138).

**Incl.** *Billbergia euphemiae* var. *nudiflora* L. B. Smith (1955); **incl.** *Billbergia euphemiae* var. *saundersioides* L. B. Smith (1955); **incl.** *Billbergia euphemiae* var. *purpurea* M. B. Foster (1957).

Acaulescent, to 60–70 cm tall, with short, stout, ascending rhizomes; **Ros** broadly tubular, with few leaves; **L** sheath large, narrowly elliptic, entire, **L** lamina 30 – 64  $\times$  (2.4–) 3–6 cm, thickly coriaceous, long-oblong, with white-lepidote transverse bands, tip rounded to broadly acute, apiculate, margins with laxly arranged small teeth; **Inf** decurved, 22–35 cm, floriferous part nodding to pendent, laxly to densely 6- to 20-flowered, simple, peduncle red, densely white-farinose; peduncular **Bra** suberect, large, lanceolate-elliptic, acute, whitish-red, upper **Bra** congested below the floriferous part, lax to somewhat dense; **Fl** spreading, 50–60 mm, very shortly pedicellate; **Sep** asymmetrical, 12–18 mm, narrowly elliptic, rounded, minutely apiculate; **Pet** linear,  $\pm 30$  mm, linear, obtuse, green, purple or dark blue towards the tip, with 2 fimbriate scales, never coiled; **St** included; **Fr** not described.

Divided into 4 ill-defined varieties by Smith & Downs (1979: 2012), but the differences appear to be minor, and var. *nudiflora* was synonymized already by Barros & Costa (2008: 1176). The

leaves are quite succulent at least in some clones, and Pereira & al. (2011) record up to  $\pm 50\%$  water storage volume.

**B. nutans** H. Wendland *ex* Regel (Gartenflora 18: 162, t. 617, 1869). **Type:** BG Herrenhausen (*Anonymus* s.n. [LE?; [icono]: l.c. t. 617]). — **Lit:** Fagundes & Mariath (2010: fruit anatomy). **Distr:** Brazil (Paraná, Santa Catarina, Rio Grande do Sul), Uruguay, Paraguay, Argentina (Jujuy, Salta, Misiones, Córdoba); epiphytic or rarely lithophytic. **I:** Rauh (1990: 119: Fig. 88); Gaiotto F. & al. (2010: 89); Klein V. & Klein (2013: 76–77); Roguenant & al. (2016: 527). – Fig. 2.

**Incl.** *Billbergia schimperiana* Wittmack *ex* Baker (1889)  $\equiv$  *Billbergia nutans* var. *schimperiana* (Wittmack *ex* Baker) Mez (1896); **incl.** *Billbergia nutans* fa. *rupestris* Hassler (1919); **incl.** *Billbergia nutans* var. *striata* Reitz (1965).

Acaulescent, 40 (–50) cm tall, with numerous short stolons and forming dense somewhat untidy-



**Fig. 2** *Billbergia nutans*. (Copyright: E. J. Gouda)

looking clumps; **Ros** narrowly tubular, with 12–15 erect to somewhat arching leaves; **L** sheath oblong, 4 – 5 × 2 – 2.5 cm, subglabrous, **L** lamina linear to very narrowly triangular, to 60 (–70 or 100 cm under shady conditions) × (0.6–) 1–1.7 (–2) cm, somewhat canaliculate, leathery-coriaceous to distinctly fleshy, sparsely appressed-lepidote, margins near the base spinose-serrate, **Sp** 1 mm; **Inf** decurved, to 40 cm, appearing simple but composed of usually 1-flowered branches, peduncle very slender, glabrous, flowering part arching to drooping, few-flowered; peduncular **Bra** similar to the leaves, densely imbricate, basal **Bra** long-attenuate, green, upper **Bra** shorter, red, all grey-lepidote, longer than the internodes; floral **Bra** small, inconspicuous; **Fl** somewhat distichously arranged, sessile to shortly pedicellate; **Sep** erect, narrowly elliptic to ovate-lanceolate, acute, 15–20 (–27?) mm, rose with dark blue margins, towards the tip green with bluish blotch; **Pet** 35–46 mm, linear, obtuse, pale green with blue margins, with 2 coarsely serrate scales, tips pure green, spreading to recurved; **St** included; **Fil** of the inner series shortly connate with the petals; **Fr** ellipsoid, 35–45 × 12–14 mm, green, glabrous.

A naturally occurring form from Rio Grande do Sul with yellow longitudinal lines on the leaves was separated as var. *striata*. According to Gaiotto F. & al. (2010), *B. schimperiana* falls within the variability of the species, and recognition as separate taxon at any rank seems unwarranted. Guillot Ortiz & al. (2016) report the taxon as local neophyte in Spain.

## References

- Barros, J. V. de. & Costa, A. F. da (2008) O gênero *Billbergia* Thunb. (*Bromeliaceae*) no Estado do Rio de Janeiro, Brasil. Acta Bot. Brasil. 22(4): 1172–1192, key, ills. <https://doi.org/10.1590/S0102-33062008000400028>
- Evans, T. M. [& al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. Syst. Bot. 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>
- Fagundes, N. F. & Mariath, J. E. D. (2010) Morphoanatomy and ontogeny of fruit in *Bromeliaceae* species. Acta Bot. Brasil. 24(3): 765–779, ills. <https://doi.org/10.1590/S0102-33062010000300020>
- Gaiotto F. D. [& al. 2010], Capuano T., R. & Cervi, A. C. (2010) O gênero *Billbergia* Thunberg (*Bromeliaceae*) no Estado do Paraná, Brasil. Fontqueria 56(11): 81–100, key, ills. [http://www.bibdigital.rjb.csic.es/PDF/Fontqueria\\_56\\_11.pdf](http://www.bibdigital.rjb.csic.es/PDF/Fontqueria_56_11.pdf)
- Guillot Ortiz, D. [& al. 2016], Ferrer-Gallego, P. P. & Laguna Lumbreras, E. (2016) Nuevas citas sobre flora alóctona de origen ornamental en la Comunidad Valenciana. Bouteloua 24: 70–77, ills.
- Klein V., L. F. & Klein, J. (2013) Die Bromelien in den atlantischen Wäldern der Nord-Ost-Küste von Rio Grande do Sul/Brasilien — Teil 1/Teil 2/Teil 3. The Bromeliads in the Atlantic forest of the northeast coast of Rio Grande do Sul/Brazil — part 1/part 2/part 3. Bromelié 2013(1): 8–17, (2): 74–81, (3): 144–154, ills.
- Machado, T. M. [& al. 2016], Forzza, R. C. & Stehmann, J. R. (2016) *Bromeliaceae* from Caparaó National Park, Minas Gerais/Espírito Santo states, Brazil, with notes on distribution and conservation. Oecol. Australis 20(2): 133–146, ills. <https://doi.org/10.4257/oeco.2016.2002.10>
- Pereira, T. A. R. [& al. 2011], Oliveira, T. S. de, Silva, L. C. da & Azevedo, A. A. (2011) Comparative leaf anatomy of four species of *Bromelioideae* (*Bromeliaceae*) occurring in the Atlantic Forest, Brazil. Botany 89(4): 243–253, ills. <https://doi.org/10.1139/B11-011>
- Rauh, W. (1990) Bromelien. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Reitz, R. (1983) Bromeliáceas e a malária-bromélia endêmica. In: Reitz, R. (ed.): Flora ilustrada catarinense, I parte as plantas, fascículo BROM. Itajaí (BR): Herbario “Barbosa Rodrigues”.
- Roguenant, A. [& al. 2016], Lecouffle, M. & Raynal-Roques, A. (2016) Les Broméliacées. Approche panoramique d’une grande famille “américaine”. Paris (FR): Belin.
- Sass, C. & Specht, C. D. (2010) Phylogenetic estimation of the core Bromelioids with an emphasis on the genus *Aechmea* (*Bromeliaceae*). Molec. Phylogen. Evol. 55: 559–571. <https://doi.org/10.1016/j.ympev.2010.01.005>
- Smith, L. B. & Downs, R. J. (1979) Flora Neotropica. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>



## × *Biltanthus* BROMELIACEAE

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× *Biltanthus* Hort. Roehr (Exotics, Cat. Julius Roehrs Comp., [], 1947). — **Lit:** Butcher (2013). **Distr:** Cultivated only.

**Incl.** × *Cryptbergia* Anonymus (1952).

= *Billbergia* × *Cryptanthus*. For long known as × *Cryptbergia*, the change of name is necessary because of nomenclatural priority (Butcher 2013). Smith & Downs (1979: 1604, as × *Cryptbergia*) mention the hybrids *C. bahianus* × *B. nutans* (= × *Cryptbergia* ‘Red Burst’ = × *Cryptbergia rubra* hort.) and *C. beuckeri* × *B. nutans* (= × *Cryptbergia meadii* B. & C. Wilson 1963 = × *Cryptbergia* ‘Mead’). Smith (1983) mentions a couple of additional cultivars, and several more have become known since

(Butcher 2013). Plants are usually intermediate between the parents, i.e. the leaves are more ascending-spreading in the hybrids in comparison with the *Cryptanthus* parent, but far shorter than in *Billbergia nutans*.

### References

- Butcher, D. (2013) × *Biltanthus*. J. Bromeliad Soc. 62(4): 173–176, ills.
- Smith, E. L. (1983) Bigeneric hybrids — A listing. J. Bromeliad Soc. 33(2): 69–75. <http://journal.bsi.org/V33/2/>
- Smith, L. B. & Downs, R. J. (1979) Flora Neotropica. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>

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## Cryptanthus BROMELIACEAE

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**Cryptanthus** Otto & A. Dietrich (Allg. Gartenzeitung 4: 297, 1836). **Type:** *Cryptanthus bromelioides* Otto & A. Dietrich. — **Bromelioideae** — **Lit:** Smith & Downs (1979: 1586–1604, Fl. Neotropica); Dias Cândido (1995: key); Ramírez Morillo (1996: systematics); Ramírez Morillo (2000: overview); Ramírez Morillo & Brown (2001: cytology); Cruz (2013: phylogeny, biogeography); Cruz & al. (2017: phylogeny, biogeography); Leme & al. (2017: classification). **Distr:** NE Brazil (Rio Grande do Norte to Rio de Janeiro); wet to subarid vegetations, 0–2000 m. **Etyim:** Gr. ‘kryptos’, hidden, covered; and Gr. ‘anthos’, flower; for the sessile inflorescences with smallish flowers.

**Incl.** *Pholidophyllum* Visiani (1847). **Type:** *Pholidophyllum zonatum* Visiani.

**Incl.** *Madvigia* Liebmann (1854). **Type:** *Madvigia densiflora* Liebmann.

**Incl.** *Forzzaea* Leme & al. (2017). **Type:** *Cryptanthus leopoldo-horstii* Rauh.

**Incl.** *Hoplocryptanthus* (Mez) Leme & al. (2017). **Type:** *Cryptanthus glaziovii* Mez [lectotype, designated (probably ineffectively under ICN Art. 29.1?) by Ramírez, Syst. Phylog.

Chromos. Number Evol. *Cryptanthus* [Ph.D. thesis], 1996].

**Incl.** *Rokautskyia* Leme & al. (2017). **Type:** *Cryptanthus sanctaluciae* Leme & L. Kollmann.

Perennial terrestrial or saxicolous rosette plants, mesophytic to xerophytic, acaulescent or shortly caulescent, **Ros** monocarpic but offsetting, often with long stolons and forming large colonies; **L** rosulate or spirally arranged along the upper stem parts, sheath usually inconspicuous, lamina narrowly triangular or basally somewhat contracted and (sub-) petiolate, spinose to serrate, often conspicuously cross-banded or otherwise marked or spotted, or variegated; **Inf** condensed, sessile in the rosette centre, compound, corymbose, subglobose; **Fl** hermaphrodite or male (plants andromonoecious); **Sep** connate only at the base or to ½ of their length or rarely free, the posterior carinate; **Pet** white or greenish-yellow, clawed and basally connate or rarely free, without appendage, limb spreading or reflexed; **St** shortly exerted at anthesis; **Fil** usually adnate to the petals for much of their length; **Ov** inferior; **Fr** small, ± dry capsules with (partially) persistent sepals; **Se** small, flat. — **Cytology:**  $2n = 32, 34, 36$  (Ramírez Morillo & Brown 2001, Gitai & al. 2014).

A genus of ± 41 (Ramírez Morillo 2000) to 66 (Krapp & al. 2013), or 72 (Cruz & al. 2017) to 80 (Leme & al. 2017, including the recently segregated genera) species, many of them narrowly

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endemic, esp. in the Atlantic Rainforest (Ramírez Morillo 1998). The genus is related to *Orthophytum* (see separate entry in this handbook) and the recently segregated genera *Lapanthus* (not considered to include succulents) and *Sincoraea* (see separate entry in this handbook). The combined clade is sister to the eu-bromelioids, though with low support, in the molecular phylogeny of Schulte & al. (2009). The data of Givnish & al. (2011) remains inconclusive but shows the genus in an overall similar place in the topology. These authors further argue that *Cryptanthus* is closely related to *Acanthostachys*. The recent more detailed molecular phylogeny of Louzada & al. (2014) finds *Cryptanthus* as well as *Lapanthus* embedded amongst the species of *Orthophytum* with sessile inflorescences. This is at variance with the results obtained by Evans & al. (2015), where *Cryptanthus* forms a highly supported clade with *Aechmea lamarchei* as sister, and separate from the 2 clades that include *Orthophytum* species.

The unusually low chromosome number of species of *Cryptanthus* ( $2n = 32, 34, 36$  compared with  $2n = 50$  prevalent in the family) is most probably due to descending aneuploidy or dysploidy — this appears to indicate a derived condition (Ramírez Morillo & Brown 2001, Gitai & al. 2014), which is somewhat at variance with the molecular data. *Cryptanthus* is further notable as 2 of the 3 analysed species have B chromosomes (otherwise only found rarely in the family), which might indicate ongoing speciation (Gitai & al. 2014: 365).

*Cryptanthus* was traditionally subdivided into 2 subgenera, and this was supported by the early study of Ramírez Morillo (2000). Cruz (2013) and Cruz & al. (2017) found that only Subgen. *Cryptanthus* is monophyletic in their AFLP study, while the species of Subgen. *Hoplocryptanthus* form a basal grade consisting of 3 consecutive clades, though support values for part of the topology are low. These results are corroborated by the more deeply sampled study of Leme & al. (2017), who recircumscribe *Cryptanthus* s.s., and accept the clades that made up Subgen. *Hoplocryptanthus* as separate genera *Hoplocryptanthus*, *Forzzaea* and *Rokautskyia*. While all of the genera are strongly supported as monophyletic clades (both in the molecular phylogeny, and morphologically and

biogeographically), the topology of the backbone and thus the relative relationships between the segregates are insufficiently supported in the molecular phylogeny: *Hoplocryptanthus* is shown in a trichotomy with a clade that includes *Cryptanthus* s.s., *Lapanthus* and *Forzzaea*, and a clade that shows *Sincoraea* as sister to *Rokautskyia* + *Orthophytum*. Pending a fuller resolution of the backbone relationships, *Cryptanthus* is kept in its traditional wide circumscription here:

[1] Subgen. *Cryptanthus* (= *Cryptanthus* s.s. *sensu* Leme & al. (2017): Andromonoecious with perfect flowers making up the basal fascicles, and male flowers concentrated in the central or apical parts of the inflorescence; **L** coriaceous to thickly coriaceous, often with a median thickened region consisting of a multi-layered hypodermis; **Fl** usually unscented; **Sep** connate for  $\frac{1}{3}$ – $\frac{1}{2}$  of their length; **Pet** connate for  $\frac{1}{7}$ – $\frac{1}{3}$  of their length, white or rarely greenish, 4–8 × longer than broad; **Sti** conduplicate-patent, lobes spreading-recurved; **Fr** 12–20 mm, with persistent sepals that soon degrade from the tips, with 2–10 (–30) seeds. — ± 55 species, geographically widespread in Restinga and Caatinga vegetations, 0–700 m.

This subgenus is divided into 5 sections by Ramírez Morillo (2000), while Cruz (2013) found only 2 clades. — Andromonoecy is an almost unique character for whole family, otherwise only reported from some species of *Aechmea*, *Androlepis* and *Catopsis*.

[2] Subgen. *Hoplocryptanthus* Mez 1891: Hermaphroditic; **Fl** often scented; **Fr** with persistent sepals whose tips do not degrade. — Only in Espírito Santo and Minas Gerais in high-altitude grassland and montane forests (Campo Rupestre vegetation and Atlantic Rainforests, 800–2000 m). As explained above, this subgenus is not monophyletic, and the 3 clades are recognized as separate genera by Leme & al. (2017):

[2a] Clade of *Forzzaea* Leme & al. 2017: **L** (thickly) coriaceous, succulent; **Inf** simple or basal fascicles with 2–5 (–6) flowers; **Sep** connate to  $\frac{1}{2}$  of their length or rarely free; **Pet** white or rarely greenish-

yellow, connate basally to  $\frac{1}{7}$  of their length or sometimes free, 2.5–5× longer than broad; **Sti** branches short, erect to slightly patent; **Fr** 4–10 mm, with 2–8 seeds. — 3 species from Minas Gerais, in Campo Rupestre vegetation, 750–1300 m.

[2b] Clade of *Hoplocryptanthus* (Mez) Leme & al. 2017: **L** coriaceous but hardly succulent; **Inf** simple or basal fascicles with 2–5 (–6) flowers; **Sep** connate for  $\frac{1}{5}$ – $\frac{1}{2}$  of their length; **Pet** white or rarely greenish-yellow, connate for  $\frac{1}{10}$ – $\frac{1}{3}$  of their length, 2.5–4× longer than broad; **Sti** branches conspicuous, ascending-spreading; **Fr** 6–10 mm, with 35–75 seeds. — 8 species from Minas Gerais, in Campo Rupestre vegetation, 500–1830 m.

[2c] Clade of *Rokautskyia* Leme & al. 2017: **L** (thinly) coriaceous; **Inf** basal fascicles with (5–) 6–15 flowers; **Sep** connate for  $\frac{1}{5}$ – $\frac{1}{2}$  of their length; **Pet** white, connate for  $\frac{1}{3}$ – $\frac{1}{2}$  of their length, 2.4–3.3× longer than broad; **Sti** sessile or with short erect lobes (“simple-imbricate”); **Fr** 4–7 mm, with 18–60 seeds. — 14 species from the Atlantic Rainforest of Espírito Santo, 400–1000 m.

**Succulence:** While some species are decidedly mesophytic, many have coriaceous to somewhat succulent leaves. Succulence can be confined to the basal-median part of the lamina, but can also embrace the major part of it. According to Hornberger (1993) the water-storage tissue is derived from the hypodermis and can make up 50% and more of the leaf volume. Only the more pronouncedly succulent taxa are covered in this account, which is condensed from the scant available published literature, where many descriptions are lamentably incomplete.

**Horticulture:** Several species are popular in horticulture (where the vernacular name “Earth Star” is used) and are traded in the form of numerous cultivars, mostly bred for colourful leaves. There is also an USA-based international *Cryptanthus* Society. *Cryptanthus* has been successfully hybridized in

cultivation with *Billbergia* (see × *Biltanthus*, involving species of *Cryptanthus* s.s.) and with *Ortho-phytum* (see × *Ortho-phanthus*, involving at least one species of the clade of *Rokautskyia*), as well as with *Neoregelia* (= × *Neotanthus*) (not covered in this handbook).

**C. bahianus** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 106, t. 104, 1943). **Type:** Brazil, Bahia (*Foster* 98 [GH]). — **Distr:** E Brazil (Bahia, Paraíba); Caatinga vegetation, 500 m. **I:** Smith (1937); Smith & Downs (1979: 1589).

**Incl.** *Cryptanthus glaziovii* L. B. Smith (1937) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Cryptanthus bahiensis* hort. (s.a.) (*nom. inval.*, ICN Art. 61.1).

[1] **Ros** shortly caulescent, to 40 cm tall at flowering time; **L** numerous, to 40 cm, sheath not described, lamina smooth and glabrous, somewhat succulent, margins laxly serrate with slender curved spines to 1.5 mm; **Inf** sessile, few-flowered; floral **Bra** broadly elliptic, acute, longer than the ovary, membranous, sparsely lepidote; **Fl** sessile, the outer hermaphrodite, the inner male; **Sep** 10 mm, slightly connate, elliptic, broadly acute, membranous, densely white-lepidote; **Pet** linear, 30 mm, obtuse, white, conglutinate (Smith & Downs l.c.); **Ov** ellipsoid, 5 mm.

**C. boanovens** Leme (J. Bromeliad Soc. 65(2): 93–97, ills., 2015). **Type:** Brazil, Bahia (*Lima* s.n. in *Leme* 8769 [RB]). — **Distr:** E Brazil (Bahia: Boa Nova); terrestrial in forests, 700–800 m.

[1] Acaulescent, mostly solitary; **Ros** flattish; **L** 9–16, spreading-recurved, thickly coariceous, sheath subreniform, spinulose towards the tip, lamina 14–28 × 1.2 cm, not narrowed towards the base, narrowly triangular, acuminate-caudate, to 3 mm thick near the base, slightly to distinctly canaliculate towards the base, esp. in the dry season, reddish-bronze-coloured, densely (near the base) to sparsely spinose along the margins, upper face smooth with sparse scales towards the base, lower face strongly veined and densely white-tomentose between the veins; **Inf** sessile, few-flowered with 3–4 fascicles with ± 3 flowers; primary **Bra** leaf-like; floral **Bra** narrowly triangular, to 16 × 6 mm, hyaline-membranous; **Fl** ± 40 mm (inner male flowers) to 47 mm (hermaphrodite flowers); **Sep** 13–14 mm,

connate for 6–7 mm, brownish; **Pet**  $\pm 35 \times 6.5$  mm, narrowly subspatulate, white, acute to roundish, spreading.

**C. bromelioides** Otto & Dietrich (Allg. Gartenzeitung 4: 298, 1836). **Type** [neo]: Brazil, Rio de Janeiro (*Pereira* 5637 [HB, B, MBM]). — **Distr**: E Brazil (Rio de Janeiro). **I**: Rauh (1990: 121, fig. 98, as var. *tricolor*).

≡ *Cryptanthus acaulis* var. *bromelioides* (Otto & Dietrich) Mez (1896); **incl.** *Cryptanthus diversifolius* Beer (1856) ≡ *Cryptanthus acaulis* var. *diversifolius* (Beer) Mez (1896); **incl.** *Cryptanthus suaveolens* E. Morren ex Baker (1889); **incl.** *Cryptanthus carnosus* Mez (1919); **incl.** *Cryptanthus bromelioides* var. *tricolor* M. B. Foster (1953).

[1] **Ros** caulescent, stems to 70 cm; **L** numerous, lamina basally constricted above the sheath, 10–20  $\times$  3–4 cm, rigid and thick, undulate, minutely serrulate, uniformly variously green in nature, upper face (sub-) glabrous, lower face with pale scales and obscure stripes; **Inf** many-flowered with 4–6 flowers per fascicle; floral **Bra** lanceolate, acute, much shorter than the flowers, carinate; **Fl** to 41 mm; **Sep** acuminate, connate for  $> \frac{1}{2}$  of their length; **Pet** linear, obtuse, erect at anthesis.

A horticultural selection with several longitudinal red, green and white stripes on the leaf lamina has been named var. *tricolor*, but should preferably be treated as cultivar group. Several named cultivars are frequent in the horticultural trade.

**C. caracensis** Leme & E. Gross (*Cryptanthus* Soc. J. 7(4): 12–14, ill., 1992). **Type**: Brazil, Minas Gerais (*Leme & Nahoum* 1853 [HB]). — **Distr**: Brazil (Minas Gerais: near Caraça); rock outcrops in Campo Rupestre vegetation, above 1000 m. **I**: Leme & Marigo (1993: 102).

≡ *Hoplocryptanthus caracensis* (Leme & E. Gross) Leme & al. (2017).

[2b] Acaulescent, with short stolons; **Ros** with suberect leaves becoming flatly spreading at anthesis; **L** sheath suborbicular, 1.2–1.7  $\times$  1.5–2.5 cm, densely white-lepidote above the glabrous base, apically spinulose, outside wine-red, **L** lamina 15–35  $\times$  1.3–1.5 cm, narrowly triangular, flat, comparatively thin-textured, green or reddish towards

the base, densely lepidote, margins with acicular reddish spines to 2 mm; **Inf** few-flowered, basal fascicles 2- to 3-flowered; primary **Bra** leaf-like; floral **Bra** ovate-triangular, entire,  $\pm 10 \times 8$ –14 mm, carinate, white-floccose; **Fl**  $\pm 30$  mm, fragrant; **Sep**  $\pm 10 \times 2$ –2.5 mm, connate for 3–4 mm; **Pet** 20–25  $\times$  8–10 mm, with very narrow base, spatulate with subacute to obtuse tip, white, suberect to spreading.

Compared with *C. leopoldo-horstii* (*Forzzaea* clade) in the protologue, but with less coriaceous leaves with smaller sheaths and narrower spines along the margins of the lamina, differently shaped scales, and broader floral bracts and petals.

**C. crassifolius** Leme (J. Bromeliad Soc. 58(1): 17–19, ill., 2008). **Type**: Brazil, Bahia (*Moreira* s.n. in *Leme* 6059 [HB]). — **Distr**: E Brazil (Bahia: near Ituaçu); rock outcrops in Campo Rupestre vegetation.

[1] Acaulescent, with stolons to 12 cm; **Ros** flattish; **L**  $\pm 10$ , spreading-recurved, sheath inconspicuous, spinulose towards the tip, **L** lamina 10–12  $\times$  1.2–1.5 cm, slightly or not narrowed at the base, sublinear-lanceolate, thickly coriaceous-succulent, to 2.5 mm thick near the middle, dark olive-grey to bronze-coloured, margins near the base slightly undulate, densely spinulose over the whole length, upper face white-lepidote but glabrescent with age, lower face densely white-lepidote; **Inf** few-flowered, with  $\pm 3$  fascicles, each 2-flowered, only staminate flowers described; primary **Bra** leaf-like; floral **Bra** sublinear-lanceolate, to 10 mm, whitish-hyaline; **Fl**  $\pm 35$  mm (with extended petals), slightly fragrant; **Sep**  $\pm 11$  mm, connate for 8 mm, symmetrical; **Pet** 23–27 mm, white, narrowly spatulate, subacute to obtuse.

**C. fosterianus** L. B. Smith (Bromeliad Soc. Bull. 2: 63, ill., 1952). **Type**: Brazil, Pernambuco (*Foster* 2431 [US]). — **Distr**: E Brazil (Pernambuco); 350 m; ecology not reported. **I**: Rauh (1990: 121, fig. 99).

[1] Acaulescent, with short stolons; **Ros** broadly funnel-shaped; **L**  $\pm 12$ , densely arranged, somewhat overlapping, sheath  $\pm$  circular, somewhat



inflated, **L** lamina linear-lanceolate, acuminate, basally narrowed but not petiolate, 30 × 4 cm, thick and fleshy, margins undulate, somewhat serrulate, upper face maroon with wavy pale cross-bands caused by grey appressed scales, lower face completely covered by grey scales; **Inf** with the outer fascicles with 3–4 hermaphrodite flowers, and the central fascicles mostly 2-flowered with male flowers; primary **Bra** leaf-like but smaller and with cordate base and longer tips; floral **Bra** broadly ovate, ± as long as the sepals, membranous; **Sep** 8 mm, connate for 5 mm, forming a narrow tube, lobes serrulate; **Pet** white.

Recently placed in the synonymy of *C. zonatus* (Visiani) Visiani (not considered succulent) by Alves & Marcucci (2015) because the distinguishing characters were variable in the studied material.

**C. glaziovii** Mez (in Martius, Fl. Bras. 3(3): 202, 1891). **Type:** Brazil, Minas Gerais (*Glaziou* 15672a [B, GH [photo], P]). — **Lit:** Leme (1992: with ill.). **Distr:** E Brazil (Minas Gerais: near Caraça); xerophytic vegetation, 1400–1600 m; known from the type locality only.

≡ *Hoplocryptanthus glaziovii* (Mez) Leme & al. (2017).

[2b] Caulescent, stem 20–40 cm, covered with leaf sheaths, usually with a single elongate offset from the inflorescence; **Ros** open; **L** 30–40, spreading-recurved, dispersed near the stem tip, **L** sheath suborbicular, outside dark red, strongly rugose, inside pale green, coarsely spiny to serrate towards the apex, **L** lamina linear-triangular, basally not contracted, 10–15 × 0.8–1.2 cm, coriaceous, channelled, green, glossy, upper face glabrous, lower face white-lepidote, margins laxly serrate with spines 1–2.5 mm long with upturned tips, reddish; **Inf** few-flowered, 2–3 cm, with ± 10 fascicles, basal fascicles 2-flowered; primary **Bra** leaf-like; floral **Bra** long-acuminate from the ovate-triangular base, almost as long as the sepals, entire or the upper laxly spinulose, almost transparent, thinly tomentose; **Fl** ± 30 mm, fragrant; **Sep** oblong-lanceolate, apiculate, 8–11.5 × 3 mm, connate for 3–4 mm, slightly asymmetrical, slightly carinate; **Pet** ± 22 mm, white, connate for 2–3 mm.

Long confused with other taxa, but finally fully described on the base of living material from the type locality by Leme (1992).

**C. incrassatus** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 2: 119, t. 49, 1950). **Type:** Brazil, Espírito Santo (*Foster* 172 [GH]). — **Distr:** E Brazil (Espírito Santo: near Vitoria); ecology not reported; known from the type collection only. **I:** Smith & Downs (1979: 1603).

[1] Acaulescent; **L** few, of 2 forms, the outer reduced to broadly ovate acute sheaths, the inner with a distinct lamina, **L** lamina linear-triangular to linear-lanceolate, to 30 × 1.5–2 cm, basally not narrowed, much thickened along the mid-vein area, upper face glabrous, lower face white-lepidote, margins laxly serrate with curved 1 mm long spines; **Inf** few-flowered; floral **Bra** lanceolate, acute, carinate, membranous, white-lepidote towards the tip; **Sep** 14 mm, connate for 10 mm, carinate, white-lepidote; **Pet** 30 mm, connate for 12 mm, white.

**C. leopoldo-horstii** Rauh (Trop. subtrop. Pfl.-welt 65: 68–71, ill., 1988). **Type:** Brazil, Minas Gerais (*Rauh & Horst* 67221 [HEID]). — **Distr:** Brazil (Minas Gerais: Diamantina area); clefts of sandstone rocks; ± 1000 m. **I:** Leme & Marigo (1993: 102).

≡ *Forzzaea leopoldo-horstii* (Rauh) Leme & al. (2017).

[2a] Acaulescent; **Ros** 15–20 × 30–40 cm Ø, with short runners; **L** 8–10, ascending-spreading becoming flatly spreading at flowering time, sheath conspicuous, to 2.5 × 3.5 cm, yellowish-white, upper face glabrous, lower face apically white-lepidote, **L** lamina narrowly long-triangular, 15–20 × 1.5 cm (at the base), somewhat canaliculate; **Inf** 2 × compound with 8–12 branches, or rarely simple; primary **Bra** leaf-like; floral **Bra** oblong-lanceolate, 10–12 × 5 mm, spine-tipped; **Fl** scented; **Sep** sharply carinate, asymmetrical, 10 mm, free almost to the base; **Pet** to 25 mm, narrowly tongue-shaped, white.

**C. microglazioui** I. Ramírez (Harvard Pap. Bot. 3(2): 219–220, ill., 1998). **Type:** Brazil, Espírito Santo (*Luther* 2965 [SEL]). — **Distr:**



**Fig. 1** *Cryptanthus microglazioui*. (Copyright: E. J. Gouda)

Brazil (Espírito Santo); ecology not described. **I:** Leme & al. (2017: 31: fig. 12G). – Fig. 1.

≡ *Rokautskyia microglazioui* (I. Ramírez) Leme & al. (2017).

[2c] Caulescent, stems to 15 cm, 1 cm Ø, erect or ascending, basally branched and offsetting; **L** dark to light green, horizontally spreading, rather soft and fleshy, sheath ovate, 8–10 mm, dark purple, apically lepidote on both surfaces and with marginal spines, **L** lamina narrowly triangular, acute and long acuminate, (3.5–) 4.5–6 × 0.4–0.6 cm, abaxially lepidote with a pattern left by the margins of the next older leaf, margins serrate with soft spines to 3 mm long, antrorsely hooked; **Inf** compound, lateral fascicles 2-flowered; primary **Bra** leaf-like but shorter, to 5 × 0.5 cm, basally dark red, abaxially with fine white lines; floral **Bra** ovate, cucullate, 15 × 6–7 mm, almost entire; **Fl** scented; **Sep** 10 × 2 mm, connate for 5 mm, central part purple, carinate, margins hyaline; **Pet** widely elliptic, white, 20 × 9 mm, basally connate for 6 mm, thicker than in other species.

Differs from *C. pseudoglaziouii* (*Rokautskyia* clade) by shorter and narrower leaves with straight

margins and longer spines, and scented flowers with larger petals. It has been successfully crossed with *Orthophytum* (see ×*Orthotanthus*).

**C. micrus** Louzada & al. (Phytotaxa 10: 13–14, figs. 2 L, 5 (pp. 6, 9), 2010). **Type:** Brazil, Minas Gerais (*Mota & al.* 1474 [BHCB, SP]). — **Distr:** E Brazil (Minas Gerais: Parque Estadual do Rio Preto); quartzite rocks, 860–1400 m.

≡ *Forzzaea micra* (Louzada & al.) Leme & al. (2017).

[2a] Shortly caulescent; **Ros** open, 3–8 cm Ø; **L** ± 30, arching-spreading, sheath deltoid, chartaceous, glabrous, **L** lamina 1.1–4.1 × 0.15–0.3 cm, linear, almost flat or channelled, somewhat succulent, green, margins with 0.5–1 mm long spines, both faces densely lepidote; **Inf** simple or with few 2-flowered fascicles; primary **Bra** erect, densely lepidote, serrulate; floral **Bra** triangular, erect, membranous, entire; **Sep** ± 6.5 mm, narrowly ovate, asymmetrical, chartaceous, whitish; **Pet** ± 11 mm, linear-spatulate, white, free.

The smallest species of the genus, and according to the protologue apart from the overall size and the shorter and narrower leaves similar to *C. leopoldo-horstii* and *C. warasii* (both from the *Forzzaea* clade) from the Diamantina Plateau.

**C. praetextus** E. Morren *ex* Baker (Handb. Bromel., 16, 1889). **Type:** K [Morren illustration, Aug. 1885]. — **Distr:** E Brazil (Espírito Santo); ecology unknown.

[1?] Shortly caulescent, with erect offsets; **L** few in an open rosette, sheath subcircular, coriaceous, **L** lamina narrowed at the base, linear-lanceolate, acuminate, 17 × 2.2 cm, margins densely serrulate and undulate, upper face glabrous with a broad paler median stripe, lower face densely white-appressed-lepidote; **Inf** few-flowered; **Fl** to 30 mm; **Sep** 11 mm, connate for ½, lobes broadly ovate, flowers not further described.

**C. schwackeanus** Mez (in Martius, Fl. Bras. 3 (3): 203, 1891). **Type:** Brazil, Minas Gerais (*Glaziou* 17823 [B, GH [photo], P]). — **Distr:** Brazil (Minas Gerais, São Paulo); rocky slopes and summits, on rocks.

≡ *Hoplocryptanthus schwackeanus* (Mez) Leme & al. (2017).

[2b] Acaulescent, rhizomatous; **Ros** dense with 15–20 recurved leaves; **L** sheaths very broadly ovate, entire or apically serrulate, **L** lamina narrowly triangular, pungent, 7–20 × 0.8–1 cm, not narrowed above the sheath, upper face green, glabrous, lower face strongly veined, with a veil of fused scales, margins laxly serrate with slender curved spines to 4 mm; **Inf** few-flowered; floral **Bra** ovate, acute to acuminate, entire or serrulate, longer than the ovary, lepidote; **Fl** to 26 mm; **Sep** 6–7 mm, connate for 3 mm, lobes ovate, rounded or emarginate, mucronate, minutely serrulate; **Pet** highly connate, white to yellowish.

**C. seidelianus** W. Weber (Feddes Repert. 97 (3–4): 119–120, ill., 1986). **Type:** Brazil, Bahia (*Seidel* 963 [Herb. Weber]). — **Distr:** Brazil (Bahia: Milagres region); ecology not described.

[1?] Acaulescent; **Ros** few-leaved, to 30 cm Ø; **L** sheath hardly differentiated, broadly ovate, 1.5 × 2 cm, grooved-lineate, margins spinose, **L** lamina to 20 cm, very narrowly triangular-linear, fleshy-succulent, canaliculate, green, lower face densely white-lepidote, margins slightly undulate, with dense brown-green spines to 2 mm long; **Inf** compound, branches 2- to 4-flowered; primary **Bra** similar to the leaves but much shorter; floral **Bra** triangular-ovate, acute, 10–13 × 7 mm, keeled, laxly lepidote near the tip; **Fl** sessile, to 37 mm; **Sep** lanceolate, acute, to 13 × 4 mm, fused for 9 mm, lepidote; **Pet** lanceolate, acute, to 25 mm, white.

Extremely xerophytic, and with similarly succulent leaves as *C. leopoldo-horstii* (*Forzzaea* clade). According to the protologue overall similar to *C. schwackeanus* (*Hoplocryptanthus* clade), from which it differs by larger, acute and more strongly fused sepals.

**C. sergipensis** I. Ramírez (Harvard Pap. Bot. 3 (2): 219–221, ill., 1998). **Type:** Brazil, Sergipe (*Jardim & al.* 489 [NY]). — **Distr:** Brazil (Sergipe: Santa Luzia do Itanhi); sandy soil in Restinga vegetation, 0–100 m; only known from the type locality.

[1] Long caulescent, stems to 35 cm tall, off-setting from axils close to the inflorescence; **L** sheaths broadly ovate, 1–2.5 × 0.6–1.3 cm, canaliculate, apically lepidote on both faces, minutely serrate, **L** lamina 25–45 × 1.5–1.6 cm, narrowly triangular, erect, recurved apically, stiffly succulent, upper face glabrous, lower face lepidote, margins serrate with antrorse spines 1–1.5 mm long and (1-) 3–5 mm apart; **Inf** compound with 1- to 3-flowered fascicles; primary **Bra** similar to the leaves, to 11 × 0.5 cm; floral **Bra** 2 per flower, triangular, obtuse, the larger 15–20 × 5 mm, slightly cucullate, the smaller 11 × 3 mm, fleshy, cucullate; **Sep** 9–11 mm, connate for 5–7 mm, lobes obtuse, cucullate, serrate; **Pet** oblong, colour not described, rounded with a small mucro, 19 × 4 mm.

According to the protologue unique by the large size, long stems and leaves and large but few seeds, and without apparent close relationships.

**C. warasii** E. Pereira (Bradea 2(36): 252, 1978). — **Distr:** Brazil (Minas Gerais: Diamantina area); humus-filled cracks in cliffs. **I:** Byer (1996); Roguenant & al. (2016: 562–563). — Fig. 2.

≡ *Forzzaea warasii* (E. Pereira) Leme & al. (2017).

[2a] Acaulescent, stoloniferous; **Ros** rather upright when sterile but flattish when flowering, to 20 cm Ø; **L** 20–30, stiffly coriaceous-succulent, lamina linear-triangular, 2–6 × 1–2 cm, slightly canaliculate, lower face slightly keeled, both faces densely white-lepidote and appearing felted, with impressions from the next inner leaf, margins with spines to 2 mm, straight or slightly retrorse near the leaf base and antrorse towards the tip; **Inf** ± 20-flowered, composed of congested 2- to 3-flowered fascicles; floral **Bra** to 11 mm, upper face glabrous, lower face lepidote, margins smooth; **Sep** 11 mm; **Pet** slightly longer than the sepals, white to off-white.

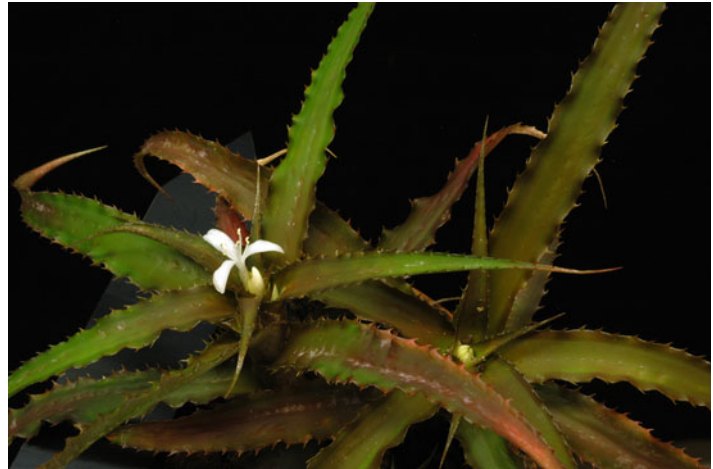
Similar to *C. micrus* from the same clade.

**C. warren-loosei** Leme (Cryptanthus Soc. J. 8 (2–3): 16–19, ill., 1993). **Type:** Brazil, Bahia (*Leme & al.* 481 [HB, RB]). — **Distr:** Brazil

**Fig. 2** *Cryptanthus warasii*. (Copyright: U. Eggli)



**Fig. 3** *Cryptanthus warren-loosei*. (Copyright: E. J. Gouda)



(Bahia: Chapada da Diamantina); dry forests. **I:** Leme & Marigo (1993: 102). –Fig. 3.

[1] Very shortly caulescent; **Ros** open, flat, with 4–8 short offsets near the inflorescence base; **L**  $\pm 15$ , spreading to arched-recurving, sheath  $\pm 2.5 \times 3.5$  cm, adaxially glabrous, abaxially rugulose, towards the tip densely spinulose, **L** lamina  $17\text{--}20 \times \pm 2$  cm, sublinear-lanceolate, long acuminate, inconspicuously narrowed at the base, canaliculate, thickly coriaceous, brown-green, margins undulate and with acicular spines to 2 mm; **Inf** many-flowered, slightly elongating to 3 cm, with  $\pm 7$  fascicles with  $\pm 3$  flowers each; primary **Bra** leaf-like; floral **Bra** membranous, those of the fascicles to

$18 \times 15$  mm, ovate-triangular and carinate, those of the centre to  $15 \times 8$  mm, ovate; **Fl** 30–40 mm; **Sep**  $12\text{--}15 \times 6$  mm, connate for 6–8 mm; **Pet**  $25\text{--}33 \times 6$  mm, white, recurved at anthesis, connate for  $\pm 10$  mm.

Related to *C. acaulis*, but differing in the production of offsets from the inflorescence base and by the more strongly coriaceous leaves with a striking, sometimes almost orange-brown colour.

## References

- Alves, M. & Marcucci, R. (2015) Nomenclatural correction in *Cryptanthus* Otto & A. Dietrich (Bromeliaceae)



- *Bromelioideae*. *Rodriguésia* 66(2): 661–664. <https://doi.org/10.1590/2175-7860201566229>
- Byer, D. (1996) *Cryptanthus warasii*. *Cact. Succ. J. (US)* 68(6): 315–316, ill.
- Cruz, G. A. S. (2013) Filogenia molecular, evolução e biogeografia do gênero *Cryptanthus* Otto & Dietr. (*Bromeliaceae*). Recife (BR): Universidade Federal de Pernambuco, unpublished Ph.D. thesis.
- Cruz, G. A. S. [& al. 2017], Zizka, G., Silvestro, D., Leme, E. M. C., Schulte, K. & Benko-Iseppon, A. M. (2017) Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (*Bromeliaceae*). *Molec. Phylog. Evol.* 107: 152–165, ills. <https://doi.org/10.1016/j.ympev.2016.10.019>
- Dias Cândido, M. de S. (1995) Chave artificial para o gênero *Cryptanthus*. Artificial key to the genus *Cryptanthus*. *Bromélia* 2(4): 15–21, ill., key.
- Evans, T. M. [& al. 2015], Jabaily, R. S., Faria, A. P. G. de, Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>
- Gitai, J. [& al. 2014], Paule, J., Zizka, G., Schulte, K. & Benko-Iseppon, A. M. (2014) Chromosome numbers and DNA content in *Bromeliaceae*: Additional data and a critical review. *Bot. J. Linn. Soc.* 176(3): 349–368, ills. <https://doi.org/10.1111/boj.12211>
- Givnish, T. J. [& al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ills., maps. <https://doi.org/10.3732/ajb.1000059>
- Hornberger, L. (1993) Botany 101: Introductory botany for the non-scientist. *Cryptanthus Soc. J.* 8(2–3): 28–31, ills.
- Krapp, F. [& al. 2013], Alves do Santos Cruz, G., Wöhrmann, T., Benko-Iseppon, A. M. & Weising, K. (2013) A set of variable plastid SSR markers for the genus *Cryptanthus* (*Bromeliaceae*). *Res. Pl. Biol.* 3(2): 18–21. <http://resplantbiol.com/article/viewFile/189/176>
- Leme, E. M. C. (1992) The true identity of *Cryptanthus glaziovii*. *J. Bromeliad Soc.* 42(6): 258–262, ills.
- Leme, E. M. C. & Marigo, L. C. (1993) Bromeliads in the Brazilian wilderness. Rio de Janeiro (BR): Marigo Comunicação Visual.
- Leme, E. M. C. [& al. 2017], Heller, S., Zizka, G. & Halbritter, H. (2017) New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (*Bromeliaceae: Bromelioideae*) based on neglected morphological traits and molecular phylogeny. *Phytotaxa* 318(1): 1–88, ills., maps, key. <https://doi.org/10.11646/phytotaxa.318.1.1>
- Louzada, R. B. [& al. 2014], Schulte, K., Wanderley, M. G. L., Silvestro, D., Zizka, G., Barfuss, M. H. & Palma-Silva, C. (2014) Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (*Bromelioideae, Bromeliaceae*) and its implications on morphological character evolution. *Molec. Phylog. Evol.* 77: 54–64. <https://doi.org/10.1016/j.ympev.2014.03.007>
- Ramírez Morillo, I. M. (1996) Systematics, phylogeny, chromosome number and evolution of *Cryptanthus* (*Bromeliaceae*). St. Louis (US): University of Missouri; unpublished Ph.D. thesis.
- Ramírez Morillo, I. M. (1998) Five new species of *Cryptanthus* (*Bromeliaceae*) and some nomenclatural novelties. *Harvard Pap. Bot.* 3(2): 215–224. <http://www.jstor.org/stable/41761570>
- Ramírez Morillo, I. M. (2000) *Cryptanthus*. In: Benzing, D. H. (ed.): *Bromeliaceae: Profile of an adaptive radiation*; pp. 551–553, map. Cambridge (GB): Cambridge University Press. <https://doi.org/10.1017/CBO9780511565175.013>
- Ramírez Morillo, I. M. & Brown, G. K. (2001) The origin of the low chromosome number in *Cryptanthus* (*Bromeliaceae*). *Syst. Bot.* 26(4): 722–726. <http://www.bioone.org/doi/abs/10.1043/0363-6445-26.4.722>
- Rauh, W. (1990) *Bromelien*. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Roguenant, A. [& al. 2016], Lecoufle, M. & Raynal-Roques, A. (2016) Les Broméliacées. Approche panoramique d’une grand famille “américaine”. Paris (FR): Belin.
- Schulte, K. [& al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromeliaceae*) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylog. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>
- Smith, L. B. (1937) *Cryptanthus glaziovii*. *Glaziou’s Cryptanthus*. *Addisonia* 20: 9–10, t. 645. <http://biodiversitylibrary.org/page/28890579>
- Smith, L. B. & Downs, R. J. (1979) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>







## Deinacanthon BROMELIACEAE

U. Eggli

**Deinacanthon** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 12, 1896). **Type:** *Rhodostachys urbaniana* Mez. — **Bromelioideae** — **Lit:** Castellanos (1954: ethnobotany). **Distr:** Paraguay, Bolivia, N Argentina. **Etym:** Gr. ‘deinos’, dreadful, terrible; and Gr. ‘akantha’, thorn, spine; for the spination.

Perennial terrestrial rosette plants with long horizontal rhizomes; **Ros** stemless, with 10–15 (rarely more) leaves; **L** to 30–40 × 1–1.5 cm, erect to spreading, sheath indistinct, narrowly ovate, lamina straight to arching, stiff, succulent, somewhat canaliculate, glabrous and often slightly shiny above, with scaly indumentum below, margin serrate, marginal **Sp** to 3 mm, ±5 mm distant, brown to black, pungent, antrorse and/or retrorse; **Inf** terminal, sessile, condensed, few-flowered, 3 cm Ø, surrounded by entire small innermost rosette leaves that grade into bracts, inner **Bra** membranous with thickened tip and hyaline margins, ovate, 18–27 × 7–10 mm; **Fl** roughly cup-shaped, dirty whitish to pale cream, ill-scented or unscented, with abundant nectar; **Sep** slightly asymmetrical, 15 mm, erect, subovate-elliptic, mucronate and spine-tipped; **Pet** 19 mm; **Fil** connate with the petals for ½; **Anth** 6 mm; **Ov** obtusely trigonous, 11 × 5–6 mm,

subclavate-cylindrical, tomentose, with numerous ovules; **Sty** columnar, massive, short; **Sti** spiral, 4 mm; **Fr** berries, dry at maturity, globose to ellipsoid, to 35 × 25 mm, yellowish-orange, basally with scaly tomentum, apically with the dry perianth remains; **Se** cuneate to semilunar, brownish to pale.

The monotypic genus differs from *Bromelia* (where its species was for long classified) by the simple sessile inflorescence and spinose-mucronate sepals. *Deinacanthon* belongs to a group of early-diverging lineages within *Bromelioideae*, and forms a weakly supported clade with *Ochagavia* + *Fascicularia* and *Greigia* (Schulte & al. 2005, Horres & al. 2007, Schulte & al. 2009, Givnish & al. 2011). Evans & al. (2015) found *Deinacanthon* imbedded in *Ochagavia*, which also includes *Fascicularia* in their tree (*Greigia* not sampled).

**D. urbanianum** (Mez) Mez (in A. & C. de Candolle, Monogr. Phan. 9: 13, 1896). **Type:** Argentina, Córdoba (*Hieronymus* s.n. [G?, B, CORD, GH, US]). — **Distr:** Gran Chaco regions of Paraguay, lowland Bolivia (Santa Cruz) and N Argentina (Chaco, Salta, Tucumán, La Rioja, Córdoba, San Juan, San Luis, Mendoza); sandy and clayey soils in chaco and monte vegetations, 500–850 m. **I:** Luther (2005); Subils (2009: 341). — Fig. 1.

≡ *Rhodostachys urbaniana* Mez (1891) ≡ *Bromelia urbaniana* (Mez) L. B. Smith (1967).

Description as for the genus.

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**Fig. 1** *Deinacanthon urbanianum*. (Copyright: U. Eggli)



The flowers are described as ill-scented by Castellanos (1954), but later authors have not repeated this observation, and cultivated plants produced unscented flowers (pers. obs.). *D. urbanianum* is one of several species from the Gran Chaco region known as “chaguar” and was used to produce fibre. Castellanos (1954) describes the method used by the Mataco (Wichí) ethnic group in N Argentina. Biurrun & al. (2007) report that the fruits are edible and were formerly eaten in La Rioja province.

## References

- Biurrun, E. [& al. 2007], Galetto, L., Anton, A. M. & Biurrun, F. (2007) Plantas silvestres comestibles utilizadas en poblaciones rurales de la provincia de la Rioja (Argentina). *Kurtziana* 33(2): 121–140.
- Castellanos, A. (1954) *Deinacanthon urbanianum* and the uses given to it by the Mataco Indians. *Bromeliad Soc. Bull.* 4: 79–81, ills.
- Evans, T. M. [& al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>
- Givnish, T. J. [& al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ills., maps. <https://doi.org/10.3732/ajb.1000059>
- Horres, R. [& al. 2007], Schulte, K., Weising, K. & Zizka, G. (2007) Systematics of *Bromelioideae* (*Bromeliaceae*) — evidence from molecular and anatomical studies. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution: Poales*. *Aliso* 23(1): 27–43, ills. <https://doi.org/10.5642/aliso.20072301.05>
- Luther, H. E. (2005) Notes on the genus *Deinacanthon*. *J. Bromeliad Soc.* 55: 125–126, ills.
- Schulte, K. [& al. 2005], Horres, R. & Zizka, G. (2005) Molecular phylogeny of *Bromelioideae* and its implications on biogeography and the evolution of CAM in the family. *Senckenberg. Biol.* 85(1): 113–125, maps.
- Schulte, K. [& al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromeliaceae*) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylogen. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>
- Subils, R. (2009) *Bromeliaceae*, Bromeliáceas. In: Kiesling, R. (ed.): *Flora de San Juan, IV*: 340–363, ills., keys. Mendoza (AR): Zeta Editores.



## × *Deuterocairnia* BROMELIACEAE

N. Schütz and F. Krapp

× ***Deuterocairnia*** D. Butcher (J. Bromeliad Soc. 52: 51, 2002). — **Distr:** Cultivated only.  
= *Deuterocohnia* × *Pitcairnia*. The only known hybrid ('Lenny') is the cross *Deuterocohnia brevifolia* (female) × *Pitcairnia* sp. It was obtained in 1999 by Len Summer, Melbourne, Australia. The plant is reminiscent of a *Deuterocohnia*, but larger than its female parent.

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## Deuterocohnia BROMELIACEAE

N. Schütz

**Deuterocohnia** Mez (in Martius, Fl. Bras. 3(3): 506, 1894). **Type:** *Dyckia longipetala* Baker. — **Pitcairnioideae** — **Lit:** Castellanos (1945: flora Argentina); Smith & Downs (1974: 231–245, Fl. Neotropica); Spencer & Smith (1992: revision); Schütz (2013: evolution, monograph). **Distr:** S America (N Peru, N Chile, S Bolivia, N Argentina, N Paraguay, E Brazil), E Andean slopes, interandean dry valleys, Atacama desert, Chaco, Pantanal, terrestrial. **Etym:** For Ferdinand Julius Cohen (1828–1898), German botanist and microbiologist from Breslau (today Wrocław, Poland); and Gr. ‘deuteros’ = second, to avoid homonymy with the name *Cohnia* (now a synonym of *Cordyline*).

**Incl.** *Abromeitiella* Mez (1927). **Type:** *Abromeitiella pulvinata* Mez.

**Incl.** *Meziothamnus* Harms (1929). **Type:** *Navia brevifolia* Grisebach.

Plants terrestrial or saxicolous, acaulescent or caulescent, often forming rings or cushions by sympodial branching, **Ros** 2–60 × 2–75 cm, to 2 m tall when flowering; **L** lamina 1.5–60 × 0.5–8 cm, recurved or incurved, adaxially plane, concave or channelled, never constricted at the

base, succulent, margin usually spinose-serrate with antrorsely or retrorsely curved spines 1–5 mm long, or margin rarely entire, surface lepidote, green to greyish, rarely reddish, adaxially and abaxially lepidote, usually more dense on the abaxial face; **Inf** terminal, sessile and annual or pedunculate and perennial, woody, with spinose-serrate bracts on the sterile part, compound or simple; primary **Bra** 3–50 × 2–15 mm, longer or shorter than the part-inflorescence or shorter than the sterile base of it, narrowly triangular to ovate; part-**Inf** 4–40 cm, spikes or racemes, simple or branched, densely to laxly flowered, axis visible or concealed; fertile **Bra** 2–15 × 2–8 mm, ±equalling the sepals or much shorter, laxly lepidote to glabrous, brownish, reddish or greenish; **Fl** 11–50 × 3–5 mm, bisexual, tubular, sessile, rarely pedicellate; **Sep** 5–20 × 3.5–6 mm, slightly asymmetric, ovate to lanceolate, glabrous, papillose or slightly lepidote, greenish, yellowish or reddish hues; **Pet** 11–45 × 4–11 mm, with slightly recurved apex or completely recurved during anthesis, erect afterwards, after anthesis more or less spirally twisted, symmetric, narrowly oblong to oblanceolate, slightly spatulate, rounded to obtuse, glabrous, greenish, yellowish or reddish, each bearing a single basal fringed appendage 2–7 mm long, base of the appendage adnate to the petal; **St** 6 in 2 whorls, antipetalous stamens adnate to the base of the petals; **Fil** 8–35 mm, free, erect; **Anth** 3–5 mm, linear, erect, recurved or coiled at anthesis, included or exserted; **Ov** 2.5–5 mm,

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superior; **Sty** 10–40 mm, terminal, filiform, whitish, greenish or reddish; **Sti** 3-lobed, conduplicate-spiral, usually exerted, rarely included; **Fr** capsules, 6–12 (–15) × 4–9 mm, ovoid to pyriform, septicidal, partially loculicidal, glabrous, brownish; **Se** 1.5–4 mm, clavate to fusiform, dorsally and apically alate.

*Deuterocohnia* belongs to the subfamily *Pitcairnioideae* (Givnish & al. 2007) and can be distinguished from its closest relatives *Dyckia* and *Encholirium* by its larger flowers, the presence of petal appendages, unwinged seeds, and its terminal, often perennial and conspicuously branched inflorescence. The woody, perennial inflorescences are an exceptional character within the family.

According to the recent revision by Schütz (2013), the genus comprises 17 species, 3 subspecies and 1 variety, including the species of the former genus *Abromeitiella* (synonymised by Spencer & Smith (1992)). The phylogenetic relationships within *Deuterocohnia* are not sufficiently resolved yet, and chloroplast DNA data analyses reflect biogeographical patterns rather than taxonomy (Schütz 2013). The recent study of Schütz & al. (2016) found *Deuterocohnia* to be paraphyletic relative to *Dyckia* and *Encholirium* in chloroplast molecular data, but monophyletic in nuclear data. The same study dates the origin of the genus at ±8.5 mybp and diversification occurred ±2–4 mybp.

All taxa are xerophytes with distinct leaf succulence and spiny leaf margins. The dense rosettes and their offsets may form dense cushions or ring-like structures. Most species have basically yellow petals, often with a greenish tip. Within *D. meiziana* different reddish and orange flower colours evolved. The plants are pollinated by insects or hummingbirds (Bernardello & al. 1991, Galetto & Bernardello 1992, Kessler 2002, Varadarajan & Brown 1988). Most of the species have a narrow distribution range, i.e. each taxon occurs in only one or few departments of a country. *D. longipetala* exhibits the most spacious distribution, especially in C and N Argentina, but also in an isolated area in N Peru. *D. haumanii* is restricted to N Argentina, where it sometimes dominates the vegetation conspicuously. While the larger-growing species of *Deuterocohnia* are less often found in

horticulture, the small ones like *D. brevifolia* or *D. lotteae* are frequently seen in botanical gardens as well as in private collections.

**D. abstrusa** (A. Castellanos) N. Schütz (Bromeliaceae 69(4): 30, 2015). **Type:** Argentina, Catamarca (*Castellanos* 29/60 [BA, US, WU]). — **Distr:** Bolivia (Tarija), Argentina (Jujuy, Salta, Tucumán, Catamarca, La Rioja); C Andean puna, Andean yungas or monte vegetations, terrestrial, saxicolous, 1500–3200 m.

≡ *Abromeitiella abstrusa* A. Castellanos (1931).

**Ros** 7–14 (–20) × 5–12 (–15) cm, in dense cushions; **L** sheath 0.5–1.3 × 1.5–2 cm, lamina 4–8 × 1–1.8 cm, recurved to straight, adaxially concave to plane, greenish-greyish, densely lepidote on both surfaces, margin spinose-serrate; **Inf** simple, annual, 1- to 3-flowered; floral **Bra** 9–13 × 3–4 mm, much shorter than the sepals, ovate, acute, mucronate, sparsely lepidote; **Fl** 26–32 (–35) mm, sessile; **Sep** 10–14 × 3–4 mm, ovate to lanceolate, obtuse, mucronulate, greenish, sparsely lepidote; **Pet** 25–32 (–35) × 4–5 mm, erect during anthesis, afterwards slightly spirally twisted, yellow-greenish, with green apex, appendage 4–5 mm; **Fil** 20–25 mm; **Anth** 4–5 mm, erect, included, greenish; **Ov** 5–6 mm; **Sty** 20–30 mm; **Fr** 10–12 (–15) mm Ø; **Se** 3–4 mm.

Morphologically close to *D. brevifolia*, but differing by larger rosettes with a laxer leaf arrangement and usually a denser indumentum. Some of the collections of *Abromeitiella lorentziana* (here treated as synonym of *D. brevifolia*) cited by Smith & Downs (1974) belong here.

**D. brevifolia** (Grisebach) M. A. Spencer & L. B. Smith (Bradea 6(16): 144, 1992). **Type:** Bolivia, Tarija (*Lorentz & Hieronymus* 947 p.p. [GOET, CORD]). — **Distr:** Bolivia (Tarija), Argentina (Jujuy, Salta, Tucumán, Catamarca); Andean Yungas and montane dry forests, terrestrial, saxicolous, 1000–3000 m. – Fig. 1.

≡ *Navia brevifolia* Grisebach (1879) ≡ *Pitcairnia brevifolia* (Grisebach) R. E. Fries (1905) ≡ *Lindmania brevifolia* (Grisebach) Hauman (1917) ≡ *Meziothamnus brevifolius* (Grisebach) Harms (1929) ≡ *Abromeitiella brevifolia* (Grisebach) A. Castellanos (1931); **incl.** *Dyckia grisebachii*

**Fig. 1** *Deuterocohnia brevifolia*. (Copyright: N. Schütz)



Baker (1889); **incl.** *Pitcairnia lorentziana* Mez (1896)  $\equiv$  *Hepetis lorentziana* (Mez) Mez (1896)  $\equiv$  *Abromeitiella lorentziana* (Mez) A. Castellanos (1944)  $\equiv$  *Deuterocohnia lorentziana* (Mez) M. A. Spencer & L. B. Smith (1992); **incl.** *Tillandsia chlorantha* Spegazzini (1899)  $\equiv$  *Lindmania chlorantha* (Spegazzini) Hauman (1917)  $\equiv$  *Pitcairnia chlorantha* (Spegazzini) A. Castellanos (1925)  $\equiv$  *Abromeitiella chlorantha* (Spegazzini) Mez (1934)  $\equiv$  *Abromeitiella brevifolia* ssp. *chlorantha* (Spegazzini) Schultze-Motel (1975); **incl.** *Abromeitiella pulvinata* Mez (1927).

**Ros** 2–10 (–15)  $\times$  2–6 cm, in dense cushions; **L** sheath 0.5–1  $\times$  1–1.5 cm, lamina 1.5–4.5  $\times$  0.5–1.5 cm, recurved to straight, adaxially concave to plane, greenish, lepidote, margin spinose-serrate or entire; **Inf** simple, annual, 1- to 3-flowered; floral **Bra** 9–13  $\times$  4–5 mm, much shorter than the sepals, ovate, acute, mucronate, entire, sparsely lepidote; **Fl** (20–) 25–30 mm, sessile; **Sep** 10–14  $\times$  3–4 mm, ovate, obtuse, mucronulate, sparsely lepidote, greenish; **Pet** (20–) 25–30  $\times$  5–6 mm, erect during anthesis, afterwards slightly spirally twisted, yellow-greenish, with green apex, appendage 4–5 mm; **Fil** 18–23 mm; **Anth** 3–4 mm, erect, included, greenish; **Ov** 4 mm; **Sty** 22–27 mm; **Fr** 8–9  $\times$  5–9 mm; **Se** 2–3 (–4) mm.

Closely related to *D. lotteae*, from which it differs by greenish flowers, and also similar to

*D. abstrusa*, but with smaller rosettes and less dense indumentum on the adaxial leaf surface. Common in cultivation and easily propagated from offsets, forming dense cushions although growth is slow. Some cushions never flower.

**D. brevispicata** Rauh & L. Hromadnik (Trop. subtrop. Pfl.-welt 65: 5–8, ills., 1988). **Type:** Bolivia, Chuquisaca (*Hromadnik & Hromadnik* 5213 [HEID]). — **Distr:** Bolivia (Chuquisaca); montane dry forest and Andean Yungas, terrestrial, saxicolous, 1200–2200 m.

**Ros** 50–60  $\times$  50–75 cm, solitary or in groups; **L** sheath 2.5–3.5  $\times$  (3–) 5–8 cm, lamina 35–60 (–70)  $\times$  (3–) 5–8 cm, recurved, adaxially concave, spinose-serrate, lepidote, greyish-green; **Inf** 100–160 (–180) cm, pedunculate, perennial, woody, main axis 8–10 mm  $\varnothing$ , fertile part 50–80 (–100) cm, compound with branches of 1. and 2. order; primary **Bra** 3–5 (–8)  $\times$  1–1.5 cm, exceeding the subtended part-inflorescence, narrowly triangular; part-**Inf** densely flowered spikes, 4–6 (–8) cm, sphaeroidal, 10- to 20-flowered, axis concealed; floral **Bra** 8–13  $\times$  5–8 mm,  $\pm$  equalling the sepals, broadly ovate, acuminate, sparsely lepidote; **Fl** 17–24 mm, sessile; **Sep** 8–14  $\times$  4–5 mm, ovate, obtuse, mucronulate, sparsely lepidote, reddish; **Pet** 16–21  $\times$  4–5 mm, erect during anthesis, afterwards slightly spirally twisted, reddish with green apex, appendage

4–5 mm; **Fil** 14–15 mm; **Anth** 3–4 mm, erect, included, greenish-yellow; **Ov** (3–) 5 mm; **Sty** 11–17 mm; **Fr** 8–9 × 5–6 mm; **Se** (1.5–) 2 (–3) mm.

Resembling *D. seramisiana* but from lower altitudes and with different flower colour. Both species have robust inflorescences and primary bracts longer than the globose part-inflorescences. Plants become probably larger in cultivation than in the natural habitat. The impressive inflorescence can flower many years.

**D. chrysantha** (Philippi) Mez (in Martius, Fl. Bras. 3(3): 507, 1894). **Type:** Chile, Atacama (Philippi s.n. [SGO]). — **Lit:** Zizka (2003). **Distr:** N Chile (Región de Antofagasta, Región de Atacama); xeric shrubland and open cactus-dominated semi-deserts, terrestrial, 20–800 m. — Fig. 2.

≡ *Pitcairnia chrysantha* Philippi (1860).

**Ros** 15–25 × 20–30 cm, in dense groups; **L** sheaths 2–2.5 × 3–6 cm, lamina (10–) 15–25 (–30) × (1.5–) 2.5–4 cm, recurved, adaxially concave, spinose-serrate, greyish-green, often reddish, lepidote; **Inf** 70–100 (–140) cm, pedunculate, perennial and woody, main axis 5–7 mm Ø, fertile part 15–40 cm, compound with branches of 1. order; primary **Bra** 10–15 × 3–4 mm, not exceeding the subtended part-inflorescence, narrowly triangular; part-**Inf** densely flowered spikes, (5–) 8–12 × 4 cm, cylindrical to spheroidal, axis concealed, (20- to) 30- to 40- (to 60-) flowered; floral **Bra** 9–15 × 5–7 mm, ± equalling the sepals,

broadly ovate, acuminate, glabrous; **Fl** (25–) 30–32 mm, sessile; **Sep** (10–) 12–13 (–15) × 4–5 mm, ovate, obtuse, mucronulate, glabrous, yellow; **Pet** 25–30 (–32) × 7–9 mm, erect during anthesis, afterwards slightly spirally twisted, yellow, with greenish tip getting yellow at the end of anthesis, appendage 5–7 mm; **Fil** (20–) 22–26 (–29) mm, **Anth** 4 mm, recurved, included or exerted, greenish-yellow; **Ov** 5–6 mm; **Sty** 24–28 mm; **Fr** 10–12 × 6–7 mm; **Se** 2 mm.

The only species in Chile, and closely related to *D. haumanii*, but with glabrous sepals, recurved anthers, fewer leaf spines and overall reddish leaves.

**D. digitata** L. B. Smith (Phytologia 18(3): 137, 1969). **Type:** Argentina, Salta (*Castellanos* s.n. [BA 46636, US]). — **Distr:** Argentina (Salta); Andean Yungas and C Andean puna, dry valleys, terrestrial on rocky hillsides, 2200–3200 (–3800) m.

**Ros** 8–12 × (8–) 10–15 cm, in dense groups or ring-forming; **L** sheath 1.5–2.5 × 3–4 cm, lamina 8–15 × 1.5–3 cm, incurved, adaxially concave, spinose-serrate, greyish, densely lepidote on both surfaces; **Inf** 15–25 cm, shortly pedunculate, perennial, woody, main axis 2–3 cm Ø, fertile part 5–15 cm, simple or compound, branches of 1. order subdigitate; primary **Bra** 2–10 × 1.5–2 mm, much shorter than the subtended part-inflorescence, narrowly triangular; part-**Inf** densely flowered simple pikes, 4–6 cm, cylindrical, axis concealed, 20- to 30-flowered; floral **Bra**

**Fig. 2** *Deuterocohnia chrysantha*. (Copyright: G. Zizka)





5–7 × 3.5–6 mm, ± equalling the sepals or shorter, broadly ovate, acute, glabrous; **Fl** (10–) 14–15 mm, sessile; **Sep** 6–7 × 3–4 mm, ovate, obtuse, glabrous, yellow-orange; **Pet** 12–15 × 4–5 mm, yellow-orange, erect during anthesis, afterwards not spirally twisted, appendage 2 mm; **Fil** 8–10 mm; **Anth** 2.5–3.5 mm, erect, included, greenish; **Ov** 3 mm; **Sty** 10 mm; **Fr** and **Se** unknown.

Morphologically and ecologically similar to *D. strobilifera* and both form hemispherical groups at the upper limit altitudinal range of the genus. *D. digitata* possesses shorter primary bracts, longer part-inflorescences, closed or only slightly opened flowers at anthesis, orange-yellow petals and erect anthers. Argentinian material cited for *D. strobilifera* by Castellanos (1945: 194, fig. 44, 126b) belongs here.

**D. gableana** R. Vásquez & Ibisch (Vidalia 1(1): 40–43, figs. 1–4, 2003). **Type:** Bolivia, Santa Cruz (Vásquez & al. 4253 [LPB, FR, Herb. Vásquez]). — **Distr:** Bolivia (Santa Cruz: Serrania Volcanes); montane dry forest, on standstone, 1100–1200 m.

**Ros** 10–15 × 15–20 cm, in dense groups; **L** sheath 2 × 3 cm, lamina 12–18 × 1.5–2 cm, recurved, adaxially concave, spinose-serrate, greenish, lepidote; **Inf** 15–20 cm, pedunculate, annual or perennial, main axis 2 mm Ø, fertile part 5–10 cm, simple, rarely branched, a spike or raceme, 5- to 15-flowered; floral **Bra** 5–15 × 2–3 mm, ± equalling the sepals, triangular to ovate, acute, abaxially with glandular trichomes; **Fl** (28–) 30–36 mm, subsessile to pedicellate; **Ped** 0.5–3 mm; **Sep** 15–18 × 3–4 mm, lanceolate, acute, abaxially with glandular trichomes, greenish; **Pet** 30–35 × 4–6 mm, erect during anthesis, afterwards slightly spirally twisted, yellow to greenish, with green apex, appendage 2–3 mm; **Fil** 21–22 mm; **Anth** 5 mm, erect, included, yellowish; **Ov** 4–5 mm; **Sty** 26–30 mm; **Fr** and **Se** unknown.

Morphologically close to *D. sanctae-crucis* and *D. scapigera*. All three species are highly similar, including colour and size, and the glandular hairs on the sepals. *D. gableana* differs in having bigger rosettes and a longer peduncle that conspicuously exceeds the rosette.

**D. glandulosa** E. Gross (Trop. subtrop. Pfl.-welt 75: 5–8, ill., 1990). **Type:** Bolivia, Tarija (*Hromadnik* 5167 [WU]). — **Distr:** Bolivia (Santa Cruz, Tarija); Andean Yungas, terrestrial, on rocks, 900–1200 m.

**Ros** 30–40 × 40–50 cm, solitary or in groups; **L** sheath 5–6 × 4–5 cm, lamina 30–45 × 2–4 cm, recurved, adaxially concave, spinose-serrate, greyish-green, lepidote; **Inf** 80–120 cm, pedunculate, perennial, woody, main axis 4–6 mm Ø, fertile part 30–50 cm, simple or compound, with branches of 1. and 2. order; primary **Bra** 10–20 × 3–4 mm, shorter than the subtended part-inflorescence, narrowly triangular; part-**Inf** spikes 5–12 × 3–4 cm, simple or branched, cylindrical, densely to laxly flowered, axis concealed, 10- to 25-flowered; floral **Bra** 4–6 × 4 mm, much shorter than the sepals, ovate, acute, abaxially with glandular trichomes; **Fl** (20–) 25–28 mm, sessile or subsessile; **Sep** 10–14 × 3.5–4 mm, narrowly ovate, acute, abaxially with glandular trichomes, greenish; **Pet** (20–) 26–28 × 5–6 mm, erect during anthesis or with slightly recurved apex, afterwards slightly spirally twisted, yellow, with greenish apex, appendage 4–5 mm; **Fil** (12–) 15–19 mm; **Anth** 4–4.5 mm, erect, included, yellowish; **Ov** 4–5 mm; **Sty** 20–21 mm; **Fr** 7 × 5 mm; **Se** 2–3 mm.

Morphologically with affinities to *D. haumanii* and *D. longipetala*.

**D. haumanii** A. Castellanos (Anales Mus. Nac. Hist. Nat. Buenos Aires, ser. 3, 36: 50, t. 13, 1929). **Type** [syn]: Argentina, Salta (*Hauman* s.n. [BA, GH, K — 1 of 2 syntypes]). — **Distr:** Argentina (S Salta, Catamarca, S Tucumán, La Rioja, Córdoba, San Juan); Andean Chaco savannas; terrestrial in thorn scrub, (500–) 1000–1900 m. **I:** Subils (2009: 343).

**Ros** 15–25 × 25–40 cm, solitary, in groups or forming rings; **L** sheath 3–4 × 4–6 cm, lamina 20–35 × (1.5–) 2–3.5 (–4.5) cm, recurved, adaxially concave, spinose-serrate, greyish-green or reddish, lepidote; **Inf** 70–120 cm, pedunculate, perennial, woody, main axis 4–7 mm Ø, fertile part 30–40 cm, simple or compound with branches of 1. order; primary **Bra** 20–40 × 4–5 mm, shorter than the subtended part-inflorescence, narrowly triangular; part-**Inf** spikes, 5–15 (–25) × 2–3



(–4.5) cm, cylindrical, densely to laxly flowered, axis concealed or visible, (5-) 10- to 40- (to 50-) flowered; floral **Bra** (4-) 6–10 (–12) × 4–5 (–8) mm, ± equalling the sepals or much shorter, broadly ovate, acute, abaxially with glandular trichomes, rarely glabrous; **Fl** (20-) 22–29 mm, sessile or subsessile; **Sep** (8-) 10–13 (–15) × 4–5 mm, ovate to lanceolate, acute, mucronulate, abaxially with glandular trichomes, rarely glabrous, greenish; **Pet** 20–29 × 4–6 mm, erect during anthesis or with slightly recurved apex, afterwards slightly spirally twisted, yellow, with greenish apex, appendage 4–6 mm; **Fil** (12-) 17–19 mm; **Anth** 4 mm, erect, included, greenish; **Ov** 3–4 mm; **Sty** 16–20 mm; **Fr** 11 × 7–8 mm; **Se** 2.5–3 mm.

With affinities to *D. longipetala* and *D. schreiteri*.

**D. longipetala** (Baker) Mez (in Martius, Fl. Bras. 3(3): 506, t. 95, 1894). **Type:** Peru, Cajamarca (*Humboldt & Bonpland* 3595 [B †?, F [photo]]). — **Distr:** Peru (Amazonas, Cajamarca, Lambayeque, La Libertad), Bolivia (Tarija), Argentina (Jujuy to Mendoza); Yungas, dry forests and monte, Chaco savannas, terrestrial, open shrub or on sandstone or granite rocks, somewhat salt-tolerant, 250–1500 m. **I:** Subils (2009: 344).

≡ *Dyckia longipetala* Baker (1889); **incl.** *Puya weberi* Schlumberger ex Lillo (1888) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Dyckia decomposita* Baker (1889); **incl.** *Puya flava* Willdenow ex Baker (1889) (*nom. inval.*, ICN Art. 36.1, 38.1); **incl.** *Deuterocohnia longipetala* fa. *uberrima* A. Castellanos (1933).

**Ros** 15–25 × 25–35 cm, solitary, in groups or forming rings; **L** sheath 3–4 × 4–6 cm, lamina (12-) 20–30 (–40) × 2–4 cm, recurved, adaxially concave, spinose-serrate, greenish, greyish or reddish, lepidote; **Inf** 80–120 cm, pedunculate, perennial, woody, main axis 4–7 mm Ø, fertile part 30–50 cm, compound, with branches of 1., 2. and 3. order; primary **Bra** 10–15 × 4–5 mm, shorter than the sterile base of the subtended part-inflorescence, narrowly triangular to ovate; part-**Inf** spikes, to 25 cm, laxly flowered, axis visible, 20- to 50-flowered; floral **Bra** 4–6 (–10) × 4–5 mm, much shorter than the sepals,

ovate, acute, mucronate, glabrous or rarely with glandular trichomes; **Fl** (20-) 22–27 mm, sessile; **Sep** (5-) 8–12 (–15) × 4–5 mm, ovate, acute to obtuse, glabrous or rarely with glandular trichomes, yellow to greenish; **Pet** 22–28 × 4–6 mm, erect during anthesis or apex slightly recurved, afterwards slightly spirally twisted, yellow, with greenish apex, appendage 3–4 mm; **Fil** 15–18 mm; **Anth** 4–6 mm, erect, included, greenish; **Ov** 4–5 mm; **Sty** 17–20 mm; **Fr** 8 × 6–7 mm; **Se** 2.5–3 (–4) mm.

*D. longipetala* has the widest range of all species of *Deuterocohnia*, and it is the only species with a conspicuously disjunct distribution area — the populations from N Peru are ±2000 km away from those in Bolivia. The species is similar to *D. haumanii*, and is closely related to *D. recurvipetala*.

**D. lotteae** (Rauh) M. A. Spencer & L. B. Smith (*Bradea* 6(16): 145, 1992). **Type:** Bolivia, Tarija (*Hromadnik* 5131 [HEID]). — **Distr:** Bolivia (Tarija); Andean Yungas and Chaco savannas, terrestrial, sometimes saxicolous, 1400–2700 m.

≡ *Abromeitiella lotteae* Rauh (1983).

**Ros** 2.5–7 × 3–6 (–8) cm, in dense cushions; **L** sheath 0.5 × 0.5–1 cm, lamina 2–6 × 1–1.5 cm, recurved to straight, adaxially concave to plane, spinose-serrate, greenish, lepidote; **Inf** simple, annual, 1- to 3-flowered; floral **Bra** 11–14 × 3–4 mm, ± equalling the sepals, broadly ovate, acuminate, mucronate to aristate, sparsely lepidote; **Fl** 25–35 mm, sessile; **Sep** 10–14 × 3–4 mm, ovate, obtuse, mucronulate, sparsely lepidote, greenish-reddish; **Pet** 25–35 × 4–5 mm, erect during anthesis, afterwards slightly spirally twisted, reddish-brownish, with green apex, appendage 4–5 mm; **Fil** 18–25 mm; **Anth** 3–4 mm, erect, included, greenish; **Ov** 4–5 mm; **Sty** 20–30 mm; **Fr** 8–9 × 5–7 mm; **Se** 2–3 mm.

Morphologically close to *D. brevifolia* (differing by reddish-greenish petals) and also similar to *D. abstrusa* (differing by smaller rosettes and more greenish leaves).

**D. meziana** Kuntze ex Mez (in A. & C. de Candolle, Monogr. Phan. 9: 465, 1896). **Type:** Brazil, Mato Grosso (*Kuntze* s.n. [NY,

B]). — **Lit:** Schütz (2014: with key to ssp.). **Distr:** Bolivia, Paraguay, Brazil.

**D. meziana** ssp. **carmineoviridiflora** (Rauh) N. Schütz (Phytotaxa 162(1): 23, fig. 3 (p. 24), 2014). **Type:** Bolivia, Santa Cruz (Rauh 40642 [HEID [lecto, 3 sheets]]). — **Lit:** Schröder & al. (2016: typification). **Distr:** Bolivia (Cochabamba, Santa Cruz); montane dry forests, terrestrial or saxicolous, 1300–2200 m.

≡ *Deuterocohnia meziana* var. *carmineoviridiflora* Rauh (1985) ≡ *Deuterocohnia carmineoviridiflora* (Rauh) Gouda (2012).

Differs from ssp. *meziana*: **L** lamina 40–70 cm; **Sep** magenta to carmine; **Pet** carmine.

**D. meziana** ssp. **meziana** — **Distr:** Bolivia (Santa Cruz, Tarija), Brazil (Mato Grosso do Sul), Paraguay (Amambay, Concepción); Chaco savannas and humid Chaco, Chiquitania dry forests,

terrestrial or saxicolous on limestone, laterite or granite outcrops, or on sandstone, or in seasonally inundated forests, 150–1400 m. **I:** Schütz (2014: 21); Roguenant & al. (2016: 130). — Fig. 3.

**Incl.** *Deuterocohnia paraguariensis* Hassler (1919); **incl.** *Deuterocohnia divaricata* Mez (1919) (*nom. illeg.*, Art. 52.1).

**Ros** 20–70 × 25–100 cm, solitary or in groups; **L** sheath 3–5 × 6–10 cm, lamina 25–80 (–100) × 4–9 cm, recurved, adaxially concave, spinose-serrate, greenish or greyish, lepidote; **Inf** 100–180 cm, pedunculate, perennial, woody, main axis 5–10 mm Ø, fertile part 40–70 cm, compound, with branches of 1. to 4. order; primary **Bra** 3–4 × 2–3 mm, shorter than the sterile base of the subtended part-inflorescence, triangular to ovate; part-**Inf** to 40 cm, laxly flowered spikes, axis visible, 10- to 40-flowered; floral **Bra** 1–2 (–5) × 3–4 mm, much shorter than the sepals, broadly ovate, acute, mucronate, glabrous; **Fl** (20–



**Fig. 3** *Deuterocohnia meziana* ssp. *meziana*. (Copyright: N. Schütz)

30–50 mm, sessile to distinctly pedicellate; **Ped** 0.5–15 mm; **Sep** 10–20 × 5–6 mm, ovate to lanceolate, obtuse, mucronulate, glabrous, greenish, orange or reddish; **Pet** (20–) 30–45 × 7–10 mm, erect during anthesis, afterwards conspicuously spirally twisted, yellowish, orange or reddish, with greenish apex, appendage 4–6 mm; **Fil** (15–) 25–35 mm; **Anth** 4–5 mm, erect, included, greenish; **Ov** 3–5 mm; **Sty** (15–) 25–40 mm; **Fr** 10–12 × 6–8 mm; **Se** 3–4 mm.

The typical subspecies differs from the other subspecies by orange sepals and yellow to orange petals (with a greenish apex as in other subspecies). The rosettes are large, with broad, robust leaves.

**D. meziana** ssp. **pedicellata** (W. Till) N. Schütz (Phytotaxa 162(1): 25, fig. 4 (p. 26), 2014). **Type:** Bolivia, Chuquisaca (*Vargas* 6285 [WU, LPB, MO]). — **Distr:** Bolivia (Chuquisaca); montane dry forest in Inter-Andean valleys, terrestrial, 900–1400 m.

≡ *Deuterocohnia pedicellata* W. Till (2004).

Differs from ssp. *meziana*: **L** lamina 50–80 cm; **Fl** usually conspicuously (to 15 mm) pedicellate; **Sep** greenish; **Pet** yellow.

Morphologically closely similar to *D. longipetala* but with larger rosettes, shorter floral bracts, more laxly flowered inflorescences, and distinct pedicels.

**D. meziana** ssp. **vogtii** N. Schütz (Phytotaxa 162(1): 27, fig. 5 (p. 28), 2014). **Type:** Paraguay, Presidente Hayes (*Vogt* 970 [FCQ, FACEN]). — **Distr:** Paraguay (Alto Paraguay, Boquerón, Presidente Hayes); Chaco savannas, terrestrial, 100–300 m.

Differs from ssp. *meziana*: **L** lamina 30–60 cm; **Inf** few-flowered; floral **Bra** inconspicuous; **Fl** 35–45 mm; **Pet** rose to magenta.

**D. recurvipetala** E. Gross (Trop. subtrop. Pfl.-welt 79: 5–7, ill., 1991). **Type:** Argentina, Córdoba (*Rauh* 64236 [HEID]). — **Distr:** Argentina (Córdoba); ecology unknown, 500–600 m.

**Ros** 30–40 × 40–50 cm, solitary or in groups; **L** sheath 3–5 × 6–10 cm, lamina 25–35 × 3–4 cm, recurved, adaxially concave, spinose-serrate, greyish-green, densely lepidote on both faces; **Inf** 100–120 cm, pedunculate, perennial, woody,

main axis 6–10 mm Ø, fertile part 30–50 cm, simple or compound, with branches of 1., 2. and 3. order; primary **Bra** 5 × 3.5 mm, shorter than the sterile base of the subtended part-inflorescence, triangular; part-**Inf** to 30 cm, laxly flowered spikes, axis visible, 10- to 50-flowered; floral **Bra** 3–4 × 3 mm, much shorter than the sepals, broadly ovate, obtuse, mucronulate, glabrous; **Fl** 10–11 mm in outline, sessile; **Sep** 6–8 × 4 mm, ovate, obtuse, glabrous, yellow-greenish; **Pet** (12–) 14–15 × 4 mm, recurved during anthesis, afterwards erect, not becoming spirally twisted, yellow, appendage 4–5 mm; **Fil** 9–10 mm; **Anth** 4 mm, recurved, exserted, yellowish; **Ov** 2.5 mm; **Sty** 10 mm; **Fr** 7–8 × 5–6 mm; **Se** 1.5–2 mm.

Morphologically closely similar to *D. longipetala*, but with shorter flowers, recurved petals during anthesis and recurved anthers.

**D. sanctae-crucis** (R. Vásquez & Ibisch) N. Schütz (in press). **Type:** Bolivia, Santa Cruz (*Müller* 259 [LPB, USZ]). — **Distr:** Bolivia (Cochabamba, Santa Cruz, Chuquisaca); montane dry forest and Andean Yungas, saxicolous, 1200–2500 m.

≡ *Deuterocohnia scapigera* ssp. *sanctae-crucis* R. Vásquez & Ibisch (2003).

**Ros** 10–12 × 6–12 cm, in dense groups or cushions, the inflorescence slightly exceeding the rosette; **L** sheath 1.5 × 2 cm, lamina 5–10 × 1–2 cm, recurved to straight, adaxially concave to plane, spinose-serrate, greenish, lepidote; **Inf** 6–7 cm, shortly pedunculate, occasionally perennial, main axis 1–2 mm Ø, fertile part 4–5 cm, simple or branched, a spike or a raceme, 2- to 5-flowered; floral **Bra** 5–10 × 2–3 mm, ± equalling the sepals or much shorter, triangular to ovate, acute, aristate, abaxially with glandular trichomes; **Fl** 30–35 mm, sessile or subsessile; **Sep** 10–15 × 3–4 mm, ovate to lanceolate, obtuse, abaxially with glandular trichomes, yellow-greenish; **Pet** 30–35 × 4–6 mm, erect during anthesis, afterwards slightly spirally twisted, yellow, with green apex, appendage 2–3 mm; **Fil** 20–25 mm; **Anth** 4–5 mm, erect, included, yellow-greenish; **Ov** 4–5 mm; **Sty** 25–30 mm; **Fr** and **Se** unknown.

Similar to *D. scapigera* and *D. gableana*, but with smaller rosettes, less robust inflorescences,

and shorter floral bracts. The inflorescences can be branched conspicuously and then have more flowers.

**D. scapigera** (Rauh & L. Hromadnik) M. A. Spencer & L. B. Smith (Bradea 6(16): 145, 1992). **Type:** Bolivia, Potosí (*Hromadnik* 5275 [HEID]). — **Distr:** Bolivia (Potosí, Chuquisaca); montane dry forest and C Andean puna, terrestrial or saxicolous, 2400–3300 m.

≡ *Abromeitiella scapigera* Rauh & L. Hromadnik (1987).

**Ros** 12–18 × 10–15 cm, in dense groups or cushions, the inflorescence slightly exceeding the rosette; **L** sheath 2 × 2–3 cm, lamina 7–12 × 1–2 cm, recurved to straight, adaxially concave to plane, spinose-serrate, greenish, lepidote; **Inf** 6–8 cm, shortly pedunculate, occasionally perennial, main axis 1–2 mm Ø, fertile part 4–5 cm, simple, rarely branched, a spike or raceme, 3- to 10-flowered; floral **Bra** 10–16 × 2–4 mm, ± equalling the sepals or much shorter, triangular to ovate, acute, aristate, abaxially with glandular trichomes; **Fl** (28–) 30–38 mm, sessile or subsessile; **Sep** 10–15 × 3–4 mm, ovate to lanceolate, obtuse, rounded or mucronulate, abaxially glabrous or with glandular trichomes, yellow-greenish; **Pet** 30–35 × 4–6 mm, erect during anthesis, afterwards slightly spirally twisted, yellow, with green apex, appendage 2–4 mm; **Fil** 21–26 mm; **Anth** 4–5 mm, erect, included, yellowish; **Ov** 5 mm; **Sty** 25–30 mm; **Fr** and **Se** unknown.

Closely similar to *D. sanctae-crucis* and *D. gableana*, and taking an intermediate position between the two, but also somewhat similar to *D. abstrusa*.

**D. schreiteri** A. Castellanos (Anales Mus. Nac. Hist. Nat. Buenos Aires, ser. 3, 36: 51, t. 1, 1929). **Type:** Argentina, Tucumán (*Schreiter* 1098 [LIL, BA, US [fragment]]). — **Distr:** Argentina (Salta, Tucumán, Catamarca, La Rioja, San Luis, Córdoba, San Juan); monte, C Andean puna and Andean Yungas, terrestrial or on sandstone slopes or weathered granite, (850–) 1000–2500 (–2900) m. **I:** Subils (2009: 344–345).

**Ros** 15–25 × 20–30 cm, solitary, in groups or forming rings; **L** sheath (2–) 3–4 × (3–) 5–6 cm,

lamina 15–25 (–35) × 2.5–3.5 cm, recurved, adaxially concave, spinose-serrate, greyish-green, lepidote; **Inf** 50–80 cm, pedunculate, perennial, woody, main axis 5–7 mm Ø, fertile part 20–50 cm, simple or compound with branches of 1. order; primary **Bra** (5–) 10–20 × 0.5 cm, shorter than the subtended part-inflorescence, narrowly triangular; part-**Inf** spikes, cylindrical, (3–) 5–12 (–18) × 1.5–3 cm, densely to laxly flowered, axis concealed, (10-) 25- to 50- (to 80-) flowered; floral **Bra** 3–6 × 3–4 mm, ± equalling the sepals, ovate, acute, mucronate, glabrous; **Fl** 11–16 (–21) mm, sessile; **Sep** 5–6 × 4–5 mm, broadly ovate, obtuse, glabrous, greenish-brownish; **Pet** 11–16 × 4–5 mm, erect during anthesis, afterwards not spirally twisted, yellow, appendage 2.5 mm; **Fil** 9–12 (–14) mm; **Anth** 3 mm, erect, included, yellow; **Ov** 2.5–3.5 mm; **Sty** 10–13 (–15) mm; **Fr** 6–7 × 5 mm; **Se** 1.5–2 mm.

Resembles *D. haumanii*, but differs in noticeably smaller floral bracts, smaller flowers and laxly spinose leaves. From *D. digitata* it can be distinguished by its longer peduncle and inflorescence and the yellow flowers.

**D. seramisiana** R. Vásquez & al. (Bromelie 2002(1): 4–10, figs. 1–6, 2002). **Type:** Bolivia, Chuquisaca (*Vásquez & Ric* 4093 [LPB]). — **Distr:** Bolivia (Chuquisaca); montane dry forest, terrestrial or saxicolous, 2000–2400 m.

**Ros** 20–30 × 40–50 cm, solitary or in groups; **L** sheath 1–3 × (3–) 5–7 cm, lamina 30–45 × 5–6 cm, recurved, adaxially concave, spinose-serrate, greyish-green, lepidote; **Inf** 70–120 cm, pedunculate, perennial, woody, main axis 6–10 mm Ø, fertile part 30–50 cm, compound, with branches of 1. and 2. order; primary **Bra** 3–5 × 1 cm, exceeding the subtended part-inflorescence, narrowly triangular; part-**Inf** spikes, 3–4 cm, densely flowered, spheroidal, axis concealed, 3- to 4-flowered; floral **Bra** 13–15 × 6–8 mm, ± equalling the sepals, broadly ovate, acuminate, sparsely lepidote; **Fl** 18–20 mm, sessile; **Sep** 10–11 × 4–5 mm, ovate, obtuse, mucronulate, sparsely lepidote, yellow-brownish; **Pet** 17–18 × 4–5 mm, erect during anthesis, afterwards not or slightly spirally twisted, yellow, with greenish apex, appendage 3–4 mm; **Fil** 14–15 mm; **Anth** 2.5 mm, erect,



included or exerted, greenish; **Ov** 3–5 mm; **Sty** 14–16 mm; **Fr** 8–9 × 5–6 mm; **Se** 2 mm.

Morphologically close to *D. brevispicata*, but differing by the yellow-greenish flowers, and occurring at higher altitudes.

**D. strobilifera** Mez (Repert. Spec. Nov. Regni Veg. 3: 15, 1906). **Type:** Bolivia, Chuquisaca (Fiebrig 2933 [B]). — **Distr:** Bolivia.

Morphologically as well as ecologically similar to *D. digitata*, and both grow at high altitudes, but distinguished by longer primary bracts, shorter part-inflorescences, conspicuously open flowers, yellow petals and recurved anthers. Cultivated plants have greenish and recurved leaves, rather than incurved and reddish-yellowish leaves as in habitat.

**D. strobilifera** var. **inermis** L. B. Smith (Contr. US Nation. Herb. 29: 535, 1954). **Type:** Bolivia, Chuquisaca (Cárdenas 4094 [US, LIL]). — **Distr:** Bolivia (Chuquisaca, Potosí); ecology as for the typical subspecies.

Differs from var. *strobiliformis*: **L** margin without spines.

**D. strobilifera** var. **strobilifera** — **Distr:** Bolivia (Chuquisaca, Potosí, Tarija), Argentina (Jujuy); montane dry forest and prepuna, terrestrial on rocky slopes and places with sparse vegetation, 2300–3900 m.

**Incl.** *Deuterocohnia bracteosa* W. Till & L. Hromadnik (1997).

**Ros** 10–20 (–25) × 10–20 cm, in dense groups or forming rings; **L** sheath 1.7–3 (–4) × 3.5–5.5 cm, lamina 7.5–25 (–28) × 1.5–4 cm, incurved, channelled, spinose-serrate or entire, abaxially greyish, adaxially greenish to reddish, densely lepidote on both surfaces; **Inf** 20–40 cm, pedunculate, perennial, woody, main axis 3–4 (–7) mm Ø, fertile part 0–20 cm, compound, with branches of 1. order; primary **Bra** 6–9 × 0.6–1.5 cm, shorter than the subtended part-inflorescence, narrowly triangular; part-**Inf** 2–4 cm, densely flowered spikes, spheroidal, axis concealed, 10- to 25-flowered; floral **Bra** 6–8 × 0.5–0.8 mm, ± equalling the sepals, broadly ovate, acuminate, sparsely lepidote; **Fl**

12–16 mm, sessile; **Sep** (4.5–) 6–9 × 3–5 (–6) mm, ovate, obtuse, mucronulate, glabrous, yellow-brownish; **Pet** (8–) 11–15 × (2–) 3–5 mm, glabrous or adaxially with some glandular trichomes, recurved during anthesis, afterwards not spirally twisted, yellow, appendage 3–5 mm; **Fl** (5.5–) 10–12 mm; **Anth** (1.5–) 2–3.5 mm, recurved, exerted, yellow; **Ov** (2–) 3 mm; **Sty** (4–) 7–9 mm; **Fr** 8–9 × 4–5 mm; **Se** 3 mm.

## References

- Bernardello, L. M. [et al. 1991], Galetto, L. & Juliani, H. R. (1991) Floral nectar, nectary structure and pollinators in some Argentinean *Bromeliaceae*. *Ann. Bot. (Oxford)*, n.s. 67(4): 401–411. <https://doi.org/10.1093/oxford-journals.aob.a088174>
- Castellanos, A. (1945) *Bromeliaceae*. In: Descole, H. R. (ed.): *Genera et Species Plantarum Argentinae*. Tomus III; pp. 105–378, tt. 22–133. Buenos Aires (AR): Guillermo Kraft Ltda., Fundación Lillo.
- Galetto, L. & Bernardello, L. M. (1992) Nectar secretion pattern and removal effects in six Argentinean *Pitcairnioideae* (*Bromeliaceae*). *Bot. Acta* 105: 292–299.
- Givnish, T. J. [et al. 2007], Millan, K. C., Berry, P. E. & Sytsma, K. J. (2007) Phylogeny, adaptive radiation, and historical biogeography of *Bromeliaceae* inferred from *ndhF* sequence data. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution: Poales*. *Aliso* 23: 3–26. <https://doi.org/10.5642/aliso.20072301.04>
- Kessler, M. (2002) Environmental patterns and ecological correlates of range size among Bromeliad communities of Andean forests in Bolivia. *Bot. Rev. (Lancaster)* 68(1): 100–127. [https://doi.org/10.1663/0006-8101\(2002\)068\[0100:EPAECO\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2002)068[0100:EPAECO]2.0.CO;2)
- Roguenant, A. [et al. 2016], Lecoufle, M. & Raynal-Roques, A. (2016) Les Broméliacées. Approche panoramique d'une grande famille "américaine". Paris (FR): Belin.
- Schröder, C. N. [et al. 2016], Sack, P. & Koch, M. A. (2016) Some notes on original material and locus classicus of *Deuterocohnia meziana* Kuntze ex Mez var. *carmineo-viridiflora* Rauh (*Bromeliaceae*). *Pl. Diversity Evol.* 131(4): 223–237, ills. <https://doi.org/10.1127/pde/2015/0131-0083>.
- Schütz, N. (2013) Systematics and evolution of the genus *Deuterocohnia* Mez (*Bromeliaceae*). Kassel (DE): University Kassel. <https://d-nb.info/1037768965/34>
- Schütz, N. (2014) *Deuterocohnia meziana* (*Bromeliaceae*): Subspecies classification and the description of the new subspecies *D. meziana* subsp. *vogtii* from northern Paraguay. *Phytotaxa* 162(1): 18–30, map, ills., key. <https://doi.org/10.11646/phytotaxa.162.1.2>
- Schütz, N. [et al. 2016], Krapp, F., Wagner, N. & Weising, K. (2016) Phylogenetics of *Pitcairnioideae* s.s.



- (*Bromeliaceae*): Evidence from nuclear and plastid DNA sequence data. *Bot. J. Linn. Soc.* 181(3): 323–342, maps, ills. <https://doi.org/10.1111/boj.12403>.
- Smith, L. B. & Downs, R. J. (1974) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 1: *Pitcairnioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4393694>
- Spencer, M. A. & Smith, L. B. (1992) A revision of the genus *Deuterocohnia* Mez (*Bromeliaceae: Pitcairnioideae*). *Bradea* 6: 141–146.
- Subils, R. (2009) *Bromeliaceae*, Bromeliáceas. In: Kiesling, R. (ed.): *Flora de San Juan*, IV: 340–363, ills., keys. Mendoza (AR): Zeta Editores.
- Varadarajan, G. S. & Brown, G. K. (1988) Morphological variation of some floral features of the subfamily *Pitcairnioideae* (*Bromeliaceae*) and their significance in pollination. *Bot. Gaz.* 149(1): 82–91. <http://www.jstor.org/stable/2995424>
- Zizka, G. (2003) *Deuterocohnia chrysantha*: An interesting Chilean endemic. *J. Bromeliad Soc.* 53(4): 147–150, ills., map.





## × *Dyckcohnia* BROMELIACEAE

N. Schütz and F. Krapp

× ***Dyckcohnia*** G. H. Anderson *ex* J. Grant (Selbyana 19: 116, 1998). — **Distr:** Cultivated only.

= *Dyckia* × *Deuterocohnia*. First reported by Anderson (1986: 103). He reported an unnamed hybrid *Deuterocohnia schreiteri* × *Dyckia fosteriana* and described it as variable in colour, and with spines more similar to *Dyckia fosteriana*. Currently, 5 additional cultivars are known:

‘Bones Mahagony’ (= *Deuterocohnia brevispicata* (female) × *Dyckia reitzii* ‘Rubra’), ‘Cherry Bomb’ (= *Deuterocohnia brevispicata*

(female) × *Dyckia estevesii*), ‘Conrad Morton’ (= *Dyckia macedoi* (female) × *Deuterocohnia meziana*), ‘July’ (= *Deuterocohnia lorentziana* cf. (female) crossed with a *Dyckia marnier-lapostollei*-hybrid), and ‘June’ (= (*Deuterocohnia lorentziana* × *Dyckia* sp.) (female) × *Dyckia* sp.).

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### References

Anderson, G. H. (1986) Hybrids by design and by chance. *J. Bromeliad Soc.* 36(3): 99–103, 109, ill.

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## Dyckia BROMELIACEAE

F. Krapp and U. Eggli

**Dyckia** Schultes *fil.* (in Roemer & Schultes, Syst. Veg. 7(2): lxx, 1194, 1830). **Type:** *Dyckia densiflora* Schultes *fil.* [lectotype, designated by L. B. Smith, ING card 00365, 1955]. — **Pitcairnioideae** — **Lit:** Smith & Downs (1974: 500–577, Fl. Neotropica); Krapp (2013: phylogeny); Krapp & al. (2014: phylogeny); Santos-Silva & al. (2015: fruit dehiscence); Pinangé & al. (2017: phylogeny, evolution & biogeography). **Distr:** Brazil, E Bolivia, Paraguay, Uruguay, N Argentina. **Etym:** For Fürst Joseph Salm-Reifferscheid-Dyck (1773–1861), German (Prussian) botanist, botanical artist, horticulturist and succulent plant collector.

**Incl.** *Garrelia* Gaudichaud (1851). **Type:** *Garrelia encholirioides* Gaudichaud.

**Incl.** *Prionophyllum* K. Koch (1874). **Type:** *Prionophyllum selloum* K. Koch.

Perennial terrestrial rosette plants, usually with thick and often repent rhizomes or short branches and often forming groups, leaves, inflorescences, bracts and sepals glabrous or variously to completely covered with cinereous scales; **L** in

open to dense rosettes, typically tough and stiff, coriaceous to succulent, with well developed marginal spines; **Inf** lateral, simple to 3 orders of branching, often with extrafloral nectaries, axis sometimes with brilliant colours similar to the flowers; **Fl** sessile or pedicellate, unscented or slightly fragrant, usually hermaphrodite and uniform within the inflorescence or sometimes (species of the “*Prionophyllum* complex”) plants gynomonocious with larger hermaphrodite flowers and smaller female flowers in the same inflorescence (female flowers usually confined to the distal parts of the inflorescence axes); **Per** typically orange, red or yellow, rarely greenish or green, brown or black, tubular or campanulate; **Pet** centrally attached to the **Fil** tube (referred to as “common tube”); **Anth** frequently recurved; **Ov** superior; **Sti** conduplicate-spiral; **Fr** 3-locular septicial xerochastic capsules with additional delayed loculicidal dehiscence resulting in 6 apical teeth; **Se** typically asymmetrical, alate, broad, in some species (“*Prionophyllum* complex”) oblong.

The large genus currently contains 168 species, many of them recently described narrow endemics. Delimitation and identification of *Dyckia* species is extremely difficult due to highly variable and overlapping morphological features. Many of the older names are based exclusively on herbarium material, whereas more recent taxa are based on ample collections, often also including living plants. No modern revision is available, and the key supplied by Smith & Downs (1974) is not reliable.

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*Dyckia* species are typically strongly xeromorphic plants of the azonal rock vegetation of Neotropical savannas. They are notable for their consistent lateral inflorescence position. It appears that inflorescence origin has not been studied in detail yet, and it is unknown whether inflorescence position is truly lateral, or whether conditions are similar to the species of *Hechtia* with seemingly lateral inflorescences that are, in fact (see Espejo-Serna & al., for the genus *Hechtia* in this volume) terminal, with the flowering rosette becoming pushed in a lateral position before incipient inflorescence growth is noticeable.

The diversity centre of the genus is located in the Brazilian Campos Rupestres, esp. in Minas Gerais (Serra do Espinhaço) and Bahia (Chapada Diamantina). Many species are narrow endemics with small populations. Some species grow in riverbeds with alternating seasons of submergence and desiccation, but the term “rheophyte”, as used in some publications, is hardly justified.

Succulence can be pronounced, and the water storage tissue, devoid of chlorophyll, can account for the major part of the leaf volume (Voltolini & al. 2009). Plants show some plasticity in size, depending on water and nutrient availability. Under optimal cultivation conditions, plants are therefore often larger and the inflorescences may be more branched than under natural conditions.

**Fruit Morphology:** Fruits are rather uniform throughout the genus, differing only in size among the species. Fruits of 3 species were studied in detail by Santos-Silva & al. (2015): The carpels are incompletely fused with 3 suture lines remaining clearly visible. Opening of the capsules is first septicial, followed by delayed loculicidal dehiscence so that the open fruit presents 6 apical teeth. Santos-Silva & al. (2015) call the capsules “denticidal”, while Fagundes & Mariath (2010) use the term “bicial”. The capsules are xerochastic, i.e. they open when drying out, caused by “lignified sclerenchymatous walls that are oriented in different directions” (Santos-Silva & al. 2015).

**Evolution and Phylogeny:** Molecular data derived from chloroplast DNA sequences suggest

that the genus is monophyletic and arose from within a paraphyletic genus *Encholirium* (Krapp 2013, Krapp & al. 2014). The phylogeny based on combined chloroplast and nuclear data of Schütz & al. (2016) supports this position. The close relationship between the two genera is also supported by the shared presence of winged seeds (see Fig. 1 in Schütz & al. (2016)).

The impressive species diversity is the result of a recent explosive radiation during the last three million years. Within the genus the genetic diversity is disappointingly low and the resolution of the available phylogenetic trees is limited. The chloroplast DNA sequence data shows a geographic pattern, rather than a clear assignment to particular morphospecies, probably resulting from poor seed dispersal ability. Severe incongruencies between morphologically defined species and nuclear and chloroplast data suggest frequent exchange of genetic material across species borders. Although most morphospecies seem to be cohesive and stable, hybridization and introgression are common events. This may be the primary reason for the pronounced difficulties to reliably delimit and identify *Dyckia* species. In addition, some degree of intercompatibility and introgression between species of *Dyckia* and *Encholirium* appears to exist, explaining the apparent paraphyly of the latter in the molecular studies (Krapp & al. 2014). A subsequent phylogenetic study based on AFLP data and morphological aspects (Pinangé & al. 2017) corroborated the poor resolution along the backbone of the phylogeny, and the likely importance of hybridization and introgression. Character reconstructions supported the geographical structuring found amongst some major clades.

Here, we follow the traditional morphology-based species concept. The taxonomy of Smith & Downs (1974) is largely followed, and subsequently described taxa have been added, recognizing that some appear to differ in minor characters only and are thus candidates for future synonymizations. Moreover, many of the species described in the nineteenth century are still only poorly known and have not been recollected in recent years. Unfortunately, no infrageneric classification is available. Instead, we use a simple

artificial grouping based on inflorescence branching and filament characters:

- [1] Inflorescence compound with up to 3 orders of branching, primary branches spreading.
- [2] Inflorescence compound with 1 order of branching, branches erect.
- [3] Inflorescence simple or pseudosimple:
  - [a] Filaments free above the common tube (= species of subkey 3 of Smith & Downs (1974)).
  - [b] Filaments connate above the common tube (= species of subkey 4 of Smith & Downs (1974)).

Some of the species assigned to subgen. *Prionophyllum* by Smith & Downs (1974), i.e. *D. maritima* and *D. selloa*, are notable for the presence of gynomonocy, with some pistillate flowers (smaller in sepal and petal size than the hermaphrodite flowers) in part of their inflorescences. Unisexual flowers are otherwise rare in the family, but some species of *Cryptanthus* are andromonoecious, and *Hechtia* is completely dioecious. In the course of the years, additional species have been assigned to an informal “*Prionophyllum* complex”, most of them with hermaphrodite flowers, however. It remains to be investigated whether gynomonocy is a diagnostic character for some species, or a group of species, or whether it occurs sporadically in just some populations.

**Ecology:** Only few studies have investigated the pollination of *Dyckia* flowers. The conspicuous bright orange flowers conform to the ornithophily syndrome, and for *D. floribunda*, *D. ragonesei* and *D. velascana* Bernardello & al. (1991) indeed observed pollination by hummingbirds in Argentina. These authors also observed a butterfly foraging for nectar on *D. floribunda*, and European honey bees to collect pollen on the same species. In view of the size spectrum of flower size and morphology, other pollinators are to be expected for some species, and indeed, Hmeljevski & al. (2011) found a carpenter bee of the genus *Xylocopa* as pollinator of *D. ibiramensis*, together with hummingbirds.

**Horticulture:** Species of *Dyckia* in general have little horticultural potential, mainly due to the usually long-elongate inflorescences with generally not very showy flowers, and despite the variability in leaf shapes, colours and armature. An exception is *D. marnier-lapostollei*, which is fairly commonly encountered in the horticultural trade. Hobby growers have produced a considerable number of hybrids and cultivars.

Formally named hybrids are known with *Deuterocohnia* (= ×*Dyckcohnia*), *Hechtia* (= ×*Dycktia*), and *Puya* (= ×*Pukia*), all of which have separate entries in this handbook.

The following names are of unresolved application but are referred to this genus: *Dyckia acrosoma* Rojas (1897); *Dyckia altissima* Lindley (1841); *Dyckia laxiflora* Martius ex Baker (1889) (*nom. inval.*, ICN Art. 36.1c); *Dyckia lemaireana* hort. (1874) (*nom. inval.*, ICN Art. 38.1a); *Dyckia lindaiana* hort. (s.a.) (*nom. inval.*, ICN Art. 29.1); *Dyckia ramosa* hort. ex K. Koch (1874) (*nom. inval.*, ICN Art. 38.1a); *Dyckia schreiteri* Hort. Heidelberg (s.a.) (*nom. inval.*, ICN Art. 29.1); *Puya edulis* E. Morren (1878).

**D. acutiflora** Leme & Z. J. G. Miranda (Phytotaxa 67: 10–13, ills., 2012). **Type:** Brazil, Goiás (*Miranda* s.n. in Leme 6806 [RB]). — **Dist:** Brazil (Goiás); rock outcrops in Campo Rupestre vegetation.

[2] **Ros** offsetting, densely leaved; **L** 25–30 × 1.1–1.4 cm, thinly coriaceous, sheath wider than the lamina, **L** lamina narrowly triangular, nearly flat, arcuate, apex long acuminate-caudate, acicular, pungent, yellowish-green, veined, subdensely to densely white-lepidote on both faces, margins glabrescent, subdensely spinose, **Sp** 0.5–2 mm, acicular, spreading or nearly so, pale-coloured with yellowish-castaneous tip, glabrous, 3–8 mm apart; **Inf** 90–100 cm; peduncle erect, ±60 cm, green towards the base and orange near the apex, with subdense to sparse glandulose trichomes; peduncular **Bra** narrowly triangular-lanceolate, erect, acuminate, spinescent, 20–45 × 5–7 mm, longer than the internodes except the upper, green to stramineous, veined, inconspicuously white-lepidote to glabrous, densely and inconspicuously

spinulose; fertile **Inf** part simple and 35–46 cm, or with 1–4 **Br**,  $\pm 60$ -flowered, subdense to dense, straight, subangulose, orange, densely covered by white glandular trichomes; **Br** suberect, 4–6 cm, densely 5- to 10-flowered; primary **Bra** like the peduncular bracts, distinctly exceeding the sterile branch base; floral **Bra** narrowly triangular to triangular-ovate, acuminate to caudate, ecarinate, spreading to suberect, 8–18  $\times$  5 mm, from slightly shorter than the sepals to equalling the flowers, thin-textured, soon stramineous, with dense, white, glandular trichomes, densely and remotely denticulate; **Fl** subspreading at anthesis to erect afterwards,  $\pm 15$  mm, somewhat tubular, fragrant already at bud-stage; **Ped** 2–3 mm, stout; **Sep** subovate-triangular, acute, 9–10  $\times$  5 mm, orange; **Pet** spatulate, acute, slenderly apiculate, ecarinate,  $\pm 11 \times 6$  mm, orange, glabrous or glabrescent; **St** just included; **Fil** free above the 2 mm high common tube, complanate, 7–8 mm, yellowish; **Anth** subtriangular, strongly recurved at anthesis,  $\pm 2$  mm, base obtuse-bilobed, acute; **Ov** ovoid,  $\pm 4 \times 2.5$  mm, yellowish; **Sty**  $\pm 4$  mm, orange, **Sti** scalloped-lacerate; **Fr** and **Se** unknown.

**D. affinis** Baker (Handb. Bromel., 133–134, 1889). **Type:** Paraguay, Paraguari (*Balansa* 534 [G [status?], F [photo]]). — **Distr:** Paraguay (Paraguari); ecology not reported.

[2] **Ros** not described; **L** to 50  $\times$  1.5 cm, sheath not described, **L** lamina sublinear, long-attenuate to an acicular apex, subdensely ferruginous-lepidote abaxially, serrate, **Sp** 2.5–3 mm; **Inf**  $\pm 1$  m, peduncle glabrous at maturity; peduncular **Bra** ovate, linear-laminate (lower) to long-acuminate (upper), shorter than the internodes (upper), fimbriate-serrulate; **Inf** paniculate with few ascending branches, **Br** mostly elongate, laxly many-flowered, cinereous-furfuraceous; primary **Bra** like the upper peduncular bracts; floral **Bra** spreading or reflexed, triangular-ovate, acute to acuminate, reaching the middle of the sepals; **Fl** spreading or suberect at anthesis, to 18 mm, orange; **Ped** 3 mm, obconical; **Sep** ovate-elliptic, 7 mm, abruptly acute, carinate, furfuraceous towards the base; **Pet** elliptic-rhombic, 14 mm, obtuse and inflexed, undulate, carinate, suberect;

**St** distinctly shorter than the petals; **Fil** free above the common tube; **Anth** sagittate, sublinear, apex recurved; **Sty** very short.

Insufficiently known, never illustrated, and not recently recollected.

**D. agudensis** Irgang & Sobral (Napaea 3: 5–7, figs. 1–3, 1987). **Type:** Brazil, Rio Grande do Sul (Sobral & al. 5581 [ICN, MBM]). — **Lit:** Silva & al. (2007: conservation, propagation). **Distr:** Brazil (Rio Grande do Sul: Agudo); on basalt rocks, very local.

[1] **Ros** 70 cm  $\varnothing$ ; **L** 40–50  $\times$  1–2 cm, succulent, sheath not described, **L** lamina lanceolate, glabrous, densely or sparsely bright-lepidote on both faces, **Sp** antroretrorely curved or straight, 4–6 mm, dark,  $\pm 10$  mm apart; **Inf** to 90 cm; peduncle  $\pm 60$  cm; peduncular **Bra** to 50  $\times$  10 mm, except the lowest shorter than the internodes, glabrous, margins glabrous or brown-floccose, entire, the lower ones soon dry; fertile **Inf** part compound, glabrous, sometimes grey-lepidote; **Br** 1- to 12-flowered, sterile base 5–8 cm, rachis 4–9 cm, terminal part of the main axis longer than the branches; floral **Bra** acuminate, carinate or ecarinate, to 10  $\times$  8 mm, glabrous, entire; **Ped** absent; **Sep** obtuse, 10  $\times$  4–5 mm, abaxially dark brown-lanate, floccose, adaxially glabrous; **Pet** rounded or obovate, 13–15  $\times$  3–5 mm, yellow; **St** 7–8 mm; **Fil** free for 4–6.5 mm above the 8 mm high common tube; **Anth** ovate-lanceolate, to 3  $\times$  1 mm; **Ov** 4–5 mm; **Sty** 4 mm, shortly fimbriate; **Fr** ovate, apex rostrate, to 12  $\times$  8 mm, dark brown or black; **Se** with thick regular yellowish-brown margins, unwinged, trigonous to tetragonous, ovoid, asymmetrical, 2.5–3  $\times$  1–1.2 mm, castaneous.

Growing only on a single hill, and threatened with extinction. Similar to *D. encholirioides*.

**D. alba** S. Winkler (Doc. Nat. 3: 33–34, Fig. 2, 1982). **Type:** Brazil, Rio Grande do Sul (Winkler 747 [ICN]). — **Distr:** Brazil (Rio Grande do Sul); dry sandstone rocks. – Fig. 1.

[1] **Ros** to 100 cm  $\varnothing$ , acaulescent; **L** very numerous, to 60  $\times$  4 cm, lamina white-tomentose on both faces, strongly spinose, **Sp** to 6 mm; **Inf** to 1.5 m; peduncle glabrous; peduncular **Bra** leaf-

**Fig. 1** *Dyckia alba* (Eggl  
2470: Brazil; Rio Grande do  
Sul; Pedras de Segredo).  
(Copyright: U. Eggl)



like, with dark brown pungent tip, longer (lower) or shorter (upper) than the internodes, spinose; fertile **Inf** part 3× branched, glabrous; **Br** shortly white-tomentose, densely many-flowered; floral **Bra** small, to 2 mm; **Fl** sessile, widely opening; **Sep** broadly triangular, acute, subcarinate, to 4 mm, abaxially white-tomentose; **Pet** broadly ovate, to 8 mm, yellow; **St** equalling the petals, exerted at anthesis; **Fil** free above the 0.5 mm high common tube; **Sty** exerted for 3 mm; **Fr** and **Se** not described.

**D. arenicola** Leme (Phytotaxa 67: 13–15, *ills.*, 2012). **Type:** Brazil, Mato Grosso (*Leme & Gonzalez* 6964 [RB, HB]). — **Distr:** Brazil (Mato Grosso); sandstone outcrops.

[3a?] **Ros** solitary or group-forming, densely 30- to 40-leaved; **L** 15–22 × 1–1.3 cm, 2–3 mm thick, coriaceous, sheath wider than the lamina, **L** lamina narrowly triangular, slightly canaliculate towards the apex, arcuate, green to dark reddish, finely veined and obscurely white-lepidote abaxially, less densely lepidote adaxially, apex long-acuminate-caudate, acicular, pungent, margins coarsely white-lepidote to glabrous, subdensely spinose, **Sp** 2.5–4 mm, acicular, spreading to retrorse, pale with yellowish-castaneous tip, glabrous, 3–12 mm apart; **Inf** 30–38 cm, simple; peduncle erect, 20–25 cm, dark reddish to greenish, glabrous, distally sulcate; peduncular **Bra** broadly ovate at the base,

apex narrowly sublinear-triangular to acuminate-caudate, rigid, erect, 8–30 × 3–5 mm, exceeding to equalling (lowest) or shorter (upper) than the internodes, stramineous, veined, glabrous, entire (upper) or remotely spinulose (lowest); fertile **Inf** part 15- to 28-flowered, subdense to dense, suberect, 6–14 cm, rachis straight to flexuous towards the apex, dark to wine-red, glabrous; floral **Bra** like the upper peduncular bracts (lowest) to suborbicular and acute and apiculate (upper), distinctly shorter than the sepals (lowest) or exceeding the pedicel (upper); **Fl** subspreading to suberect at anthesis, 15–16 mm, tubular; **Ped** ±2 mm, stout; **Sep** ovate to suborbicular, convex, apex obtuse to acute and sometimes narrowly emarginate, slightly cucullate, 7–8 × 5–8 mm, red or orange-red, glabrous; **Pet** spatulate from a narrowed base, acute to emarginate, ecarinate, 11–13 × 6–10 mm, orange to reddish-orange; **St** slightly exerted; **Fil** free above the 2–2.5 mm high common tube (data from the protologue, completely connate according to fig. 3 in Pinangé & al. (2017)), 8–10 × 1.5–2 mm, yellowish; **Anth** sublinear, slightly to distinctly recurved, 4–4.5 mm, base bilobed, acuminate; **Ov** suboblong-ovate, ±5 × 2 mm, yellowish; **Sty** ±1 mm, yellowish, **Sti** scalloped-lacerate, orange; **Fr** and **Se** unknown.

Closely related to *D. pumila* according to the protologue, but with broader leaves, longer spines, glabrous inflorescences and more numerous flowers, etc. — [F. Krapp]



**D. atratiflora** P. J. Braun & al. (Bromeliaceae 2009 (2–3): 83–88, ills.; 2010(1): 46 [erratum], 2009). **Type:** Brazil, Goiás (*Esteves Pereira* 446 [UFG]). — **Distr:** Brazil (Goiás); sandy-loamy soil. **I:** Braun (2018: 77).

[2/3b] **Ros** ±1.25 m Ø, with a stem to 17 × 9 cm in very old plants, solitary or in small groups; **L** ±80 × 5.8 cm, sheath ±3.6 × 9.5 cm, whitish-green, **L** lamina suberect or recurved, coriaceous, soft and flexible, spreading radially, narrowly triangular to lanceolate, green or chocolate-brown to brownish-red, both faces strongly veined, adaxially brilliantly glossy, abaxially white-lepidote, margins minutely laxly serrate, **Sp** not pungent, antrorse, ±1 mm, brown, 3–7 mm apart; **Inf** to 1.75 m, usually simple or with 1 (–9) **Br** to 19 cm; peduncle erect, terete, glossy, green, silky light-grey-lepidote; peduncular **Bra** subfoliaceous, linear-lanceolate, suberect or sinuous, ± amplexicaul, 8–14 × 9 mm (uppermost), green at the base, soon brownish-green, withering stramineous, densely veined, tip hard but not pungent, margins minutely serrate with teeth <1 mm; fertile **Inf** part sparsely flowered at the base, rachis 29–37 cm, green, silky light-grey-lepidote; primary **Bra** like the upper peduncular bracts but shorter; floral **Bra** triangular to lanceolate, base succulent, ±12 × 3.5 mm (lowest) to 2.5–4 mm long (uppermost), very dark pink, densely light grey-lepidote; **Fl** horizontally ± spreading, 17–21 mm; **Ped** ±6 mm; **Sep** lanceolate, ±10 × 5.2 mm, sometimes obtuse, succulent, rose to blackish-green or pink, densely light grey-lepidote (less dense near the margins); **Pet** obtuse, ±15 × 11 mm, blackish to very dark orange or pink, apical margins rosy; **Fil** ±10.5 mm, apical 0.8–1.7 mm free, yellowish-orange; **Anth** ±3 × 1.6 mm, yellow, recurved; **Ov** narrowly subpyramidal, ±7–19 × 3–4.5 mm, yellow with a slight green hue; **Sty** 2.6 mm, very dark pink; **Sti** yellow, hidden at anthesis; **Fr** ellipsoid to ovoid, acuminate, 16–18 × 11–14 mm, dark brown, lustrous.

**D. aurea** L. B. Smith (Phytologia 14: 488, t. 1, figs. 46–49, 1967). **Type:** Brazil, Goiás (*Irwin & al.* 13613 [US, NY]). — **Distr:** Brazil (Goiás); ecology not described, ±1200 m. **I:** Smith & Downs (1974: 575).

[3b] **Ros** not described; **L** to 23 × 3 cm, sheath suborbicular, 2–3 cm, stramineous, **L** lamina strongly recurved, narrowly triangular, attenuate to an abruptly acute pungent apex, adaxially glabrous, finely lepidote in the narrow grooves abaxially, margins laxly serrate, **Sp** recurved, 1.5 mm; **Inf** to ±1 m, simple; peduncle sparsely white-lepidote; peduncular **Bra** broadly ovate, acuminate, <½ as long as the internodes (upper), entire; fertile **Inf** part laxly many-flowered, 30 cm, sparsely and fugaciously white-lepidote; floral **Bra** broadly ovate, acuminate, exceeding the sepals (lowest), entire; **Ped** 4 mm, subcylindrical, stout; **Sep** ovate, broadly subacute, 8 mm; **Pet** obovate, 12 mm, colour not described but presumably yellow; **St** equalling the petals; **Fil** completely connate above the common tube; **Sty** <1 mm.

Insufficiently known, though apparently recently recollected as material is included in the study of Pinangé & al. (2017).

**D. barthlottii** R. Vásquez & Ibisch (Bromeliaceae 2012(3): 123–124, ills. (pp. 124–126), 2012). **Type:** Bolivia, Santa Cruz (*Vásquez & Coimbra* 2010 [LPB, NY, SEL, USZ]). — **Distr:** Bolivia (Santa Cruz); lowland Chaco dry forest; only known from a small region.

[3b] **Ros** 30–40 cm Ø, with a short stem to 5 mm Ø, offsetting; **L** curved, coriaceous, greyish-green, sheath suborbicular, 3 cm wide, **L** lamina narrowly triangular, 15–20 cm, abaxially finely lepidote, margins serrate, **Sp** black with white base, retrorse, 2–4 mm, ±4–6 mm apart; **Inf** to 45 cm, erect, simple; peduncle 23 cm, cinereously lepidote; peduncular **Bra** shorter than the internodes, 10 mm, acuminate; fertile **Inf** part 16 cm, ±10-flowered, slightly twisted, rather densely grey-tomentose; floral **Bra** broadly ovate, apiculate, shorter than the sepals, erect and appressed to the axis, rather densely grey-tomentose; **Fl** 10 mm, sessile, diverging-ascending, tubular and narrowed towards the tip, with lemon-like scent; **Ped** none; **Sep** elliptic, 6 × 3 mm, greenish-brown, convex, grey-tomentose, tip slightly incised; **Pet** rhomboid, 10 × 8 mm, greenish-yellow, carinate, marginally infolded towards the apex, glabrous; **St** included;



**Fil** shortly connate above the common tube; **Anth** linear, recurved at anthesis; **Ov** oblong-pyramidal, 3 mm; **Sty** and **Sti** not described; **Fr** dark brown, 20 × 10 mm; **Se** 4 × 5 mm, brownish, winged.

First confused with the long-lost *D. gracilis*, from which it differs by the recurved somewhat greyish leaves, tomentose peduncles, tomentose sepals and greenish-yellow petals. The flower colour is described as sulphur-yellow in the protologue text, but the photographs illustrate distinctly greenish flowers. — [U. Egli]

**D. beateae** E. Gross & Rauh (Trop. subtrop. Pfl.-welt 79: 7–10, Fig. 2, 1991). **Type:** Brazil, Mato Grosso (*Braun* 560 [HEID]). — **Distr:** Brazil (Matto Grosso); flat sandstone rocks, Cerrado vegetation. **I:** Braun (2018: 73).

[1/2] **Ros** flat, ±60–70 cm Ø, acaulescent; **L** numerous, 43–48 × 2 cm, sheath broadly ovate, 2.5 × 3 cm, pale, lustrous, glabrous, **L** lamina narrowly triangular, acuminate, succulent, becoming reddish-green in the sun, both faces white-lepidote, adaxially soon glabrous, margins serrate, **Sp** predominantly retrorse, to 8 mm, light green, ±10 mm apart; **Inf** ±80 cm, 2× or rarely 3× branched; peduncle erect, terete, 50 cm, green, sparsely white-floccose (denser near the flowering part), soon glabrous; peduncular **Bra** membranous, lanceolate, acuminate, 20 mm, shorter than the internodes, light brown, sparsely lepidote, veined; fertile **Inf** part dense, polystichous; **Br** shortly cylindrical to sessile and globose, terminal part of the inflorescence to 9 cm, narrowly conical to cylindrical in outline; primary **Bra** like the peduncular bracts; lower floral **Bra** shallowly bowl-shaped, long-acuminate, membranous, 15 mm, exceeding the flowers, light brown, upper ones triangular-acuminate, erect, thin, 10 × 5 mm, shorter than the sepals, abaxially white-lanate, veined, with a strong midvein, crenate; **Fl** erect-spreading, 15 mm, subsessile; **Sep** oblong-ovate, 10 × 6 mm, obtuse, carinate, slightly crenate at the tip, light orange-yellow, glabrous to sparsely white-lanate; **Pet** rhombic, 14 × 10 mm, erect, ecarinate, crenate, obtuse, brilliant orange, glabrous; **St** exerted; **Fil** free above the common tube, light orange-yellow; **Anth** curved outwards, golden-

yellow; **Ov** not described; **Sty** 3 mm; **Sti** branches free, papillate, orange, equalling the anthers; **Fr** and **Se** not described.

According to the protologue closely related to *D. microcalyx*. The flowers produce abundant nectar.

**D. brachyphylla** L. B. Smith (Phytologia 19: 282, t. 1, figs. 1–3, 1970). **Type:** Brazil, Minas Gerais (*Irwin & al.* 22383 [US, NY]). — **Distr:** Brazil (Minas Gerais); quartzite outcrops with Cerrado vegetation, 1300 m. **I:** Smith & Downs (1974: 568).

[3a] **Ros** symmetrical, 8.4 cm Ø, densely leaved; **L** ±9 × 1.2 cm, sheath broad, wholly covered, 15 mm, **L** lamina recurved, broadly canaliculate, soon glabrous adaxially, appressedly whitish-lepidote abaxially, margins very laxly serrate, **Sp** nearly straight to antrorse-uncinate, slender, 0.8–1.1 mm, yellow, 3–10 mm apart; **Inf** to 50 cm, simple; peduncle straight, white-lepidote, soon glabrous; peduncular **Bra** ovate, acuminate, much shorter than the internodes, entire; fertile **Inf** part 7 cm, few-flowered, lax at the base, sparsely white-lepidote when young; floral **Bra** ovate, acuminate, shorter than the sepals, entire; **Fl** subsessile; **Sep** broadly ovate, 4 mm, rounded at the apex and cucullate, ecarinate; **Pet** erect, elliptic, 8 mm, ecarinate, orange; **St** included; **Fil** free above the common tube; **Anth** linear; **Ov** not described; **Sty** 0.7 mm; **Sti** sessile; **Fr** and **Se** not described.

Similar to *D. elongata*, and often confused with *D. macedoi*. The species belongs into the *D. saxatilis* complex (Guarçoni & al. 2014).

**D. brachystachya** Rauh & E. Gross (Trop. subtrop. Pfl.-welt 65: 8–10, figs. 3 and 4, 1988). **Type:** Brazil, Bahia (*Rauh* 56443a [HEID]). — **Distr:** Brazil (Bahia); quartzitic rocks.

[3b] **Ros** ±7-leaved, with a short stem surrounded by old leaf sheaths; **L** to 17 × 1 cm, sheath broadly ovate, to 2 × 1.8 cm, glabrous adaxially, densely lepidote abaxially, **L** lamina erect (younger) to reflexed (older), sturdy, strongly canaliculate, with pungent tip, reddish-green, adaxially sparsely white-lepidote, abaxially veined and denser white-lepidote, serrate, **Sp**

retorse, 2 mm, brownish; **Inf** to 12 cm, simple, erect; peduncle 6 cm, much shorter than the leaves, olive-green, floccose; peduncular **Bra** triangular, slightly longer (lower) or shorter (upper) than the internodes, appressed, soon drying; fertile **Inf** part 4- to 7-flowered, 2–3 cm; floral **Bra** narrowly-lanceolate from a broad sheath, small, much shorter than the sepals, olive-green, lanate; **Fl** spreading, hardly opening, subsessile; **Sep** free, broadly ovate,  $5 \times 5$  mm, obtuse, ecarinate, brilliant orange, abaxially sparsely lanate; **Pet** erect, spatulate,  $10 \times 5$  mm, obtuse, brilliant orange; **Fil** high-connate and forming a tube 5 mm long, yellowish; **Ov** 5 mm, white; **Sty** erect,  $\pm 2$  mm; **Sti** surpassed by the anthers; **Fr** and **Se** not described.

Compared with *D. oligantha* (here treated as synonym of *D. saxatilis*) in the protologue, but with shorter inflorescences and subsessile flowers.

**D. bracteata** (Wittmack) Mez (in Martius, Fl. Bras. 3(3): 470, 1894). **Type:** Brazil, Minas Gerais (*Schenck* 3510 [B]). — **Distr:** Brazil (Minas Gerais); high-altitude grassland, rocky fields, >1900 m. **I:** Machado & al. (2016: 138).

≡ *Dyckia dissitiflora* var. *bracteata* Wittmack (1891).

[3b] **Ros** solitary or with few offsets; **L**  $50 \times \pm 1.5$  cm, sheath not described, lamina narrowly triangular, densely cinereous-lepidote abaxially, **Sp** 1.5–2 mm; **Inf** to 50 cm and more, often appearing simple and spicate but usually paniculately branched from near the base; peduncle ferruginous-tomentulose; peduncular **Bra** ovate, long-attenuate, exceeding the internodes, laxly lacinate-spinulose; fertile **Inf** part densely ferruginous-tomentulose; floral **Bra** spreading, lanceolate-ovate, acuminate, to 25 mm, exceeding the flowers, spinulose-serrate; **Ped** short; **Sep** obtuse, convex, 12 mm, fimbriate; **Pet** lamina large, suborbicular, obtuse, slightly undulate, ecarinate, apparently erect, 16 mm, orange; **St** included, **Fil** 2–6 mm connate above the common tube; **Anth** oblong, acute, recurved; **Sty**  $\frac{1}{3}$  as long as the ovary.

Similar to and sometimes misidentified as *D. minarum* or *D. reitzii*. Insufficiently known.

**D. brasiliiana** L. B. Smith (Phytologia 14: 481, t. 1, figs. 13–15, 1967). **Type:** Brazil, Distrito

Federal (*Irwin & al.* 10268 [US, NY]). — **Distr:** Brazil (Distrito Federal); open Cerrado vegetation. **I:** Smith & Downs (1974: 539).

[3b] **Ros** densely many-leaved; **L**  $> 30 \times 2$ –3 cm, sheath suborbicular, castaneous, **L** lamina linear-triangular and filiform-attenuate, appressedly white-lepidote abaxially, laxly serrate, **Sp** slender, retrorsely curved, 2.5 mm; **Inf** to 1.5 m, simple; peduncle sparsely and finely white-lepidote, soon glabrous; peduncular **Bra** lanceolate-ovate, acuminate, very irregularly longer and shorter than the internodes, serrulate; fertile **Inf** part elongate, laxly many-flowered, finely and fugaciously white-lepidote; floral **Bra** ovate, acuminate, broad, exceeding the flowers (lowest), serrulate; **Ped** 5–7 mm, subterete; **Sep** suborbicular, 9 mm, cucullate; **Pet** broadly obovate, 15 mm, suberect to spreading, orange; **St** included; **Fil** connate above the common tube; **Sty** very short.

Similar to *D. pseudococcinea*. — [F. Krapp]

**D. braunii** Rauh (J. Bromeliad Soc. 40(1): 25–26, ill., 1990). **Type:** Brazil, Goiás (*Braun & Esteves* P. 690 [HEID]). — **Distr:** Brazil (N Goiás); rocky exposed areas. **I:** Braun & Esteves Pereira (1991); Braun & al. (2008).

[3a] **Ros** solitary or rarely branched, with 10–15 leaves, to  $9 \times 20$  cm  $\varnothing$ ; **L** to  $10 \times 4$  cm, 2 mm thick, lamina stiff, adaxially shiny silvery to white-lepidote with the scales arranged in conspicuous rows, marginal **Sp** black to brown, glabrous; **Inf** to 1.2 m but usually less, simple or compound; peduncle to 50 cm, reddish-brown, glabrous; fertile **Inf** part slender, laxly spirally 8- to 12-flowered, 15–30 (–70) cm; floral **Bra** to  $4 \times 3$  mm, frequently much reduced or absent; **Fl** sessile, erect to suberect, tubular to tubular-urceolate and narrowed towards the throat,  $\pm 10 \times 5$  mm, yellow to light orange, unscented; **Sep** thin, hyaline, tough, ovate,  $\pm 7 \times 3$  mm, yellowish-orange, glabrous, occasionally with some nectar drops; **Pet** 10–11  $\times$  7–8 mm, orange; **St** almost included at anthesis; **Fil** 8 mm, free above the common tube; **Sty**  $\pm 1.7$  mm; **Fr** sessile, 6–9  $\times$   $\pm 8$  mm, brown; **Se** 1.5–3 mm  $\varnothing$ , light brown, chartaceous, thin.

Closely related to *D. joanae-marcoi* with more open flowers. The species is self-fertile according to Braun & al. (2008).

**D. brevifolia** Baker (Refug. Bot. 4: t. 236 + text, 1871). **Type:** [icono]: l.c. t. 236. — **Lit:** Rogalski & al. (2009: pollination ecology, with ill.). **Distr:** Brazil (Minas Gerais, Rio de Janeiro, São Paulo, Santa Catarina, Rio Grande do Sul), Uruguay (Rivera)?; ledges along streams and rock islands, seasonally inundated. **I:** Smith & Downs (1974: 539); Reitz (1983: t. 44).

**Incl.** *Dyckia sulphurea* K. Koch (1874); **incl.** *Dyckia gemellaria* E. Morren ex Mez (1894).

[3a] **Ros** dense, many-leaved, in dense groups of 2–5 and more; **L** 10–20 × 2.5–3.5 cm, very thick when living, sheaths suborbicular or reniform, scarcely wider than the lamina, **L** lamina lanceolate-triangular, acute, glabrous adaxially, minutely pale-lepidote between the prominent veins abaxially, evenly laxly serrate, **Sp** hooked, 2 mm; **Inf** 40–110 cm, simple; peduncle stout, soon glabrous; peduncular **Bra** leaf-like and densely imbricate (lower) or much shorter (upper), longer than the internodes, serrulate or sometimes entire (upper); fertile **Inf** part lax or rather dense at anthesis, many-flowered, soon glabrous; floral **Bra** spreading or reflexed, narrowly lanceolate-triangular, entire, the lowest usually exceeding the flowers; **Fl** spreading at anthesis, afterwards erect; **Ped** 2–4 mm at anthesis, elongating in fruit; **Sep** ovate, acute or obtuse, to 8 mm, glabrous; **Pet** lamina spreading, suborbicular, ±10 mm, obtuse or apiculate, ± carinate towards the apex, not undulate, bright yellow; **St** included; **Fil** free above the very short common tube; **Anth** narrowly triangular, acute, recurved; **Sty** ± ½ as long as the ovary.

Winkler (1982: 34) reports the taxon for N-most Rio Grande do Sul from rocks in the river bed of the Rio Uruguay, and it likely also occurs in neighbouring Argentina (Formosa). Whether superficially similar broad-leaved plants from N Uruguay are this species has not yet been clarified. — The main pollinator is the hummingbird *Amazilia versicolor* (Rogalski & al. 2009).

**D. burchellii** Baker (Handb. Bromel., 131, 1889). **Type:** Brazil, Goiás (*Burchell* 8178 [K, GH [photo]]). — **Distr:** Brazil (Goiás); rocky terrain, 400–800 m.

[3a] **Ros** not described; **L** >40 cm, sheaths broadly ovate, thick, dark, **L** lamina very narrowly triangular, becoming involute, with pungent tip, sharply carinate and appressedly pale-lepidote abaxially, entire (inner) or basally minutely spinose (outer), **Sp** brown, hooked; **Inf** to 50 cm, simple; peduncle ±16 cm, slender, lepidote or glabrous; peduncular **Bra** suborbicular with long linear lamina, slightly shorter than the internodes, entire; fertile **Inf** part lax, 2- to 6-flowered, axis very slender, ± glabrous; floral **Bra** spreading, broadly ovate with 10–13 mm long acuminate tips (lower), exceeding the flowers; **Fl** suberect, subsecund, 9 mm or longer, glabrous, subsessile; **Sep** subelliptic with a minute recurved mucro at the apex; **Pet** erect, lamina large, suborbicular, obtuse, colour not described; **St** included; **Fil** free above the common tube; **Anth** elliptic, acute, straight or slightly recurved; **Sty** very short; **Fr** and **Se** not described.

Insufficiently known and not recently collected.

**D. burle-marxii** L. B. Smith & Read (Phytologia 38: 137–138, t. 5, 1977). **Type:** Brazil, Bahia (*Burle Marx* s.n. [HB, US [photo]]). — **Distr:** Brazil (Bahia: Chapada Diamantina); ecology not recorded.

[1?] **Ros** not described; **L** >30 × 1.5 cm, sheath not described, **L** lamina very narrowly triangular, between the veins finely pale-lepidote abaxially, soon glabrous and lustrous adaxially except on the spines, laxly spinose-serrate, **Sp** curved, 9 mm; **Inf** 1.7 m or more, compound; peduncle glabrous at least with age; peduncular **Bra** ovate, lamina narrowly triangular (lower) to attenuate (upper), exceeding the internodes but not imbricate, serrulate (lower) or entire (upper); fertile **Inf** part finely cinereous-tomentose; **Br** suberect, slender, ±30 cm; primary **Bra** lanceolate-ovate, attenuate, to 5 cm, serrulate or entire; floral **Bra** broadly ovate, acuminate, nearly equalling the sepals; **Ped** 3 mm, obconical; **Sep** broadly subelliptic, 6 mm, broadly rounded at the apex, ecarinate, cucullate at anthesis; **Pet** lamina spreading, elliptic, 8 mm, broadly rounded, ecarinate, orange; **St** ± equalling the petals; **Fil** high-connate above the common tube; **Ov** broadly ovoid; **Sty** very short.

Probably related to *D. encholirioides*. — [F. Krapp]

**D. cabrerae** L. B. Smith & Reitz (Sellowia 14: 101, fig. 2, 1962). **Type:** Brazil, Santa Catarina (Smith & al. 9262 [US, HBR]). — **Distr:** Brazil (Santa Catarina); dry open ground and rocks. **I:** Smith & Downs (1974: 523).

[1/2?] **Ros** dense, many-leaved; **L** 31–40 × 1.5 cm, rigid, slightly curved, sheath ovate, 3 × 2–4 cm, glabrous and sublustrous adaxially, densely cinereous-lepidote towards the apex abaxially, **L** lamina linear, canaliculate, acute, abruptly acute and mucronulate, appressedly cinereous-lepidote, soon glabrous adaxially, laxly serrate, **Sp** slender, retrorsely curved, 3 mm, brown; **Inf** to 1.2 m, branched; peduncle ± flattened, ±70 cm, glabrous; peduncular **Bra** broadly ovate, acuminate or the lowest leaf-like, the uppermost remote, cinereous-lepidote towards the apex, glabrous elsewhere; fertile **Inf** part with 1–2 long-stipitate racemes at the base, lax, 38–54 cm, diffusely cinereous-lepidote, soon glabrous; **Br** few-flowered; primary **Bra** like the upper peduncular bracts, to 2 cm, much exceeded by the sterile branch bases; floral **Bra** acuminate from a broadly ovate base, ascending, reaching ± the middle of the sepals, minutely serrulate; **Fil** suberect, to 17 mm, orange; **Ped** 5 mm, slender; **Sep** broadly ovate, 8–13 mm, acute, strongly incurved, subeven, the posterior ones strongly carinate; **Pet** distinctly unguiculate, curved-spreading towards the apex, lamina rhombic, obtuse; **St** slightly shorter than the petals; **Fil** short-connate above the common tube; **Anth** narrowly triangular, 3 mm, recurved towards the apex; **Ov** ovoid; **Sty** short; **Fr** stout-ovoid, acute, 18 mm, dark castaneous, lustrous; **Se** subovate, 4 mm, strongly complanate, wing asymmetrical and circumferential.

**D. cangaphila** P. J. Braun & al. (Bromeliac 2010(3): 107, ill. (pp. 105–110), 2010). **Type:** Brazil, Goiás (Esteves Pereira 392 [UFG]). — **Distr:** Brazil (SW Goiás); iron-rich gravel deposits (“pedra canga”) on and between sandstone. **I:** Esteves Pereira & Gouda (2017: 180).

[2/3a] **Ros** with up to 70 living leaves, to 35 cm Ø, with a stem to 11 × 4.7 cm; **L** to 19 × 2.6 cm,

sheaths broadly ovate, to 1.8 × 2.8 cm, whitish, glabrous adaxially, **L** lamina arching, very rigid, concave, triangular-lanceolate, brownish-red to purple, sometimes green basally, veined, adaxially glossy and sparsely lepidote basally, abaxially densely light grey-lepidote, serrate, **Sp** strong and claw-like, pungent, brownish; **Inf** to 1.3 m, simple or with up to 3 branches; peduncle ± erect, 85–107 cm, pale green to pale brownish, densely grey-lepidote; peduncular **Bra** leaf-like, triangular-lanceolate, to 65 × 5.5 mm (uppermost only to 17 mm), green to brownish-green (lower) or dull pale green (upper), later stramineous; fertile **Inf** part to 41 cm, 37- to 52-flowered, basally lax, above much denser, rachis initially pale green, towards the apex changing to greenish-orange or orange, grey- or orange-lepidote; **Br** slender, ±15 cm; floral **Bra** ±19 mm, sometimes equalling the petals, smaller higher up, brownish-green, soon stramineous, strongly veined; **Fil** slightly ascending, ±16 × 8 mm; **Ped** absent in bud, to 7 mm at anthesis; **Sep** ±7.7 × 6.5 mm, orange-yellowish, creamish-yellow-lepidote, base succulent; **Pet** obtuse, ±11 × 7.6 mm, emarginate (V-like), orange-yellowish; **St** included at anthesis; **Fil** 7.6 mm, apical 1.4 mm free, yellow; **Anth** yellow, ±3.5 mm, apex curved; **Ov** narrowly pyramidal, ±5.5 × 2.8 mm, yellow to light yellow; **Sty** ±4 mm; **Sti** lobes linear, yellow; **Fr** conically ovoid, to 15 × 12 mm, chestnut-brown to blackish-wine-coloured.

Closely related to *D. pumila*.

**D. choristaminea** Mez (Repert. Spec. Nov. Regni Veg. 16: 71, 1919). **Type:** Brazil, Rio Grande do Sul (Malme s.n. [B]). — **Distr:** S Brazil (Rio Grande do Sul); open rocky places. **I:** Smith & Downs (1974: 528). — Fig. 2.

[3a] **Ros** solitary or with some congested off-sets, to 15 cm Ø; **L** 7–12 × 0.5 cm, sheath suborbicular, 2 cm, pale, glabrous, **L** lamina linear, deeply canaliculate, both faces cinereous-lepidote, margins laxly serrate, **Sp** slender, curved, 2.5 mm; **Inf** 15–25 cm, simple; peduncle slender, glabrous; peduncular **Bra** densely imbricate, broadly ovate, abruptly acute, somewhat inflated, minutely lepidote; fertile **Inf** part few-flowered, 3–5 cm, rachis densely white-



**Fig. 2** *Dyckia choristaminea* (Kirschnek s.n.: Brazil; Rio Grande do Sul, sine loco). (Copyright: U. Eggli)



villous, subterete; floral **Bra** like the peduncular bracts, carinate towards the apex, 15 mm, equaling the sepals, entire; **Ped** short, stout; **Fl** 18–24 mm,  $\pm$  funnel-shaped; **Sep** very broadly ovate, acute, 10–11 mm; **Pet** lobes spreading to recurved at anthesis, yellow; **St** included to slightly exserted; **Fil** free above the very short common tube; **Ov** 8 mm; **Sty** very stout, 8 mm.

**D. cinerea** Mez (in Martius, Fl. Bras. 3(3): 469, 1894). **Type:** Brazil, sine loco (*Glaziou* 18570 [B, K, F [photo]]). — **Distr:** Brazil (Minas Gerais); high-altitude grasslands, rocky fields, on rocks.

[2] **Ros** acaulescent; **L** very numerous,  $\pm 50 \times >3$  cm, very rigid, sheath not described, **L** lamina narrowly triangular, densely cinereous-lepidote, laxly serrate, **Sp** stout, curved, 2.5 mm; **Inf** 1 m or more, compound or pseudo-racemose with reduced branches or buds only in the axils of the lower bracts; peduncle stout, cinereous-tomentulose or glabrescent; peduncular **Bra** broadly ovate with narrowly triangular lamina, exceeding the internodes, serrulate; fertile **Inf** part cinereous-tomentulose; floral **Bra** broadly ovate, apiculate, reflexed (upper), equaling the flowers or shorter (lower), serrulate; **Ped** short, stout; **Fl** erect to spreading, 17–18 mm, orange; **Sep** 11 mm, abruptly obtuse, cucullate, obtusely carinate towards the apex, subglabrous, minutely fimbriate; **Pet** erect, elliptical-oblong, 16 mm,

subacute or obtuse, orange; **St** much shorter than the petals; **Fil** 2 mm connate above the common tube; **Anth** sublinear, stout,  $\pm$  recurved; **Sty**  $\pm$  none.

**D. commixta** Hassler (Annuaire Conserv. Jard. Bot. Genève 20: 305, 1919). **Type:** Paraguay, Cordillera (*Chodat & Vischer* 97 p.p. [G, F [photo]]). — **Distr:** Brazil (Paraná), Paraguay; ecology not reported.

[3a] Known only from fragments; inner **L** 6  $\times$  0.5 cm, sheaths triangular-elliptic, 3  $\times$  1.5 cm, membranous, glabrous adaxially, striate abaxially with whitish scales between the veins, margins entire and hyaline, **L** lamina linear-triangular, attenuate, pungent,  $\pm$  glabrate adaxially, like the sheaths abaxially, serrate, **Sp** antroretorsely curved or straight, 1–1.5 mm; **Inf** size unknown, pseudosimple; peduncle flexuous, long, glabrous; peduncular **Bra** broadly ovate, acuminate (lower), much shorter than the internodes, 6–20 mm (lowest), striately immersed-lepidote (lowest), with hyaline margin and  $\pm$  finely fimbriate (uppermost); fertile **Inf** part with undeveloped buds in the axils of the lowest bracts, laxly flowered, rachis flexuous, subquadrangular, glabrous; floral **Bra** erect to spreading, broadly ovate, acute and mucronulate, convex, 5–6 mm,  $\pm$   $\frac{1}{2}$  as long as the sepals, glabrous; **Fl** 14–15 mm; **Ped** 1–2 mm, rather stout; **Sep** ovate-elliptic, 10  $\times$  7 mm, subacute, thin, with hyaline margin, glabrous,



rugulose when dry; **Pet** erect, ovate-elliptic, 14 mm, ecarinate, inflexed at the apex, colour not described; **St** included; **Fil** free above the 2 mm high common tube; **Anth** linear-triangular, sagittate at the base, 6 mm; **Ov** trigonous, 10 mm; **Sty** 1 mm.

**D. concepcionensis** O. B. C. Ribeiro & Leme (J. Bromeliad Soc. 65(1): 15–19, ill., 2015). **Type:** Brazil, Minas Gerais (*Ribeiro* 267 [BHCB]). — **Distr:** Brazil (Minas Gerais: Conceição do Mato Dentro); on iron-rich rock (“pedra canga”) outcrops,  $\pm 1000$  m.

[3a] **Ros**  $\pm 20$  cm  $\varnothing$ ; **L**  $\pm 20$ , erect to spreading, straight to arcuate, coriaceous, sheath 1.7–1.9  $\times$  2–2.2 cm, whitish, glabrous and glossy on both faces, **L** lamina narrowly triangular, 9–10  $\times$  1.5 cm, canaliculate, dark red to bronze-coloured towards the tip, adaxially glabrous and glossy, abaxially distinctly veined and between the veins rather densely white-lepidote, tip acuminate spine-tipped, pungent, margins laxly spinose, **Sp** retrorse-uncinate, 2.5–3 mm, subtriangular,  $\pm 15$  mm apart; **Inf**  $\pm 50$  cm, simple, erect; peduncle 30–35 cm, glabrescent, reddish-green; peduncular **Bra** ovate-acuminate, 9–11  $\times$  5–6 mm, much shorter than the internodes, greenish near the base to ochraceous near the tip, veined and with prominent midvein near the tip, sparsely white-lepidote, margins minutely denticulate to subentire; fertile **Inf** part 18–20 cm, laxly 6- to 20-flowered, rachis reddish, sparsely lepidote; floral **Bra** broadly ovate, 9–10  $\times$  5–6 mm, acute, remotely denticulate, somewhat spreading; **Fl** 14–15 mm, porrect-spreading, tubular, sessile; **Sep** broadly ovate, 6–7  $\times$  5–6 mm, orange-red, obtuse-emarginate, convex, sparsely white-lepidote; **Pet** broadly spatulate, 10–11  $\times$  9 mm, erect, orange, ecarinate, broadly obtuse-emarginate; **St** included; **Fil** yellow, free above the common tube; **Anth** suboblong-lanceolate, straight, base bilobed; **Ov**  $\pm 6$  mm, suboblong, yellow; **Sty**  $\pm 1$  mm, distinct, orange; **Sti** conduplicate-spiral; **Fr** and **Se** unknown.

A member of the *D. saxatilis* complex, and compared with the similar *D. brachyphylla* in the protologue. — [U. Eggli]

**D. consimilis** Mez (in Martius, Fl. Bras. 3(3): 479, t. 90, 1894). **Type:** Brazil, Minas Gerais (*Weddell* 1407 [P, GH [photo]]). — **Distr:** Brazil (Minas Gerais); rocky fields, on rocks. **I:** Smith & Downs (1974: 575).

[3b] **Ros** acaulescent, with a basal bulbous part and a short thick rhizome; **L** numerous, densely arranged,  $\pm 5 \times 0.7$  cm, sheath broad and conspicuous, depressedly semicircular, glabrous and glossy, abaxially brownish, **L** lamina narrowly triangular, glabrous adaxially, appressedly ferruginous- or canescent-lepidote abaxially, laxly serrate, **Sp** stout, 3 mm; **Inf**  $< 50$  cm, simple; peduncle slender, completely glabrous; peduncular **Bra** ovate, acuminate, much shorter than the internodes, obscurely serrulate; fertile **Inf** part subdense, few-flowered, glabrous or sparsely lepidote; floral **Bra** broadly ovate, long-apiculate, 5 mm, slightly shorter than the sepals; **Fl** spreading or reflexed,  $\pm 8$  mm; **Ped** very short; **Sep** broadly ovate, 4 mm or longer, subacute; **Pet** lamina erect, suborbicular, colour not described; **St** included; **Fil** high-connate above the common tube; **Anth** narrowly subtriangular, recurved; **Sty** very short.

Insufficiently known and apparently not recently recollected. Nonetheless, it is compared with *D. nana* in the protologue of the latter, and Guarçoni & al. (2014) place it in the *D. saxatilis* complex.

**D. coximensis** L. B. Smith & Reitz (Phytologia 19: 282, t. 1, figs. 4–6, 1970). **Type:** Brazil, Mato Grosso (*Reitz* 7365 [HBR, US [photo]]). — **Distr:** Brazil (Mato Grosso); on rocks. **I:** Smith & Downs (1974: 565).

[3a] **Ros** symmetrical; **L** incompletely known, recurved,  $> 10 \times 1.5$  cm, sheath suborbicular, 1.5 cm, brown, **L** lamina narrowly triangular, pungent, appressedly cinereous-lepidote on both faces, margins very laxly serrate, **Sp** flat, mostly retrorse, 1 mm; **Inf** 30 cm, simple; peduncle erect, very sparsely and minutely white-lepidote; peduncular **Bra** ovate, acuminate, pungent, small, remote; fertile **Inf** part laxly  $\pm 7$ -flowered, rachis slender, 4 cm, very sparsely and minutely lepidote; floral **Bra** broadly ovate, acuminate, the lower  $\pm$  equaling the sepals; **Fl** spreading; **Ped** 1 mm, obconical;

**Sep** triangular-ovate, 5 mm, obtuse, the posterior carinate; **Pet** suborbicular, 10 mm, slightly carinate, orange; **St** slightly exerted; **Fil** free above the short common tube; **Sty** very short.

Similar to *D. pumila*. The recently described *D. secundifolia* is also compared with *D. coximensis* in its protologue.

**D. crassifolia** Rauh (Trop. subtrop. Pfl.-welt 79: 10–11, fig. 4, 1991). **Type:** Bolivia, Santa Cruz (*Rauh* 40670 [HEID]). — **Distr:** Bolivia (Santa Cruz); dry forest, 1200 m.

[3a] **Ros** few-leaved, to 16 cm Ø, ±8 cm high, acaulescent; **L** 10–16 × 1.2 cm, strongly succulent, sheath 1.5 × 1.3 cm, white, glabrous adaxially, lepidote abaxially, **L** lamina narrowly triangular, with a long pungent tip, pale green to reddish adaxially, densely white-lepidote abaxially, margins spinose, **Sp** strong, retrorse, to 5 mm, dark brown, lepidote, ±10 mm apart; **Inf** to 45 cm, simple; peduncle slender, 30–40 cm, green to reddish, sparsely white-lepidote; peduncular **Bra** oblong-ovate, acuminate, 5 mm, shorter than the internodes, veined, indistinctly serrulate; fertile **Inf** part lax, 10 cm, ±10-flowered, rachis green to reddish, sparsely white-lepidote, slender; floral **Bra** broadly ovate, short-acuminate, very small, 2 mm, brownish, membranous, appressed; **Fl** spreading, 17 mm, narrowly tubular and narrowed towards the throat; **Ped** very short, stout; **Sep** oblong, 7 mm, obtuse, succulent, slightly carinate, orange-red, darker at the tip, sparsely white-lepidote, margins membranous, indistinctly serrulate; **Pet** 15 mm, obtuse, erect, orange-red, margins smooth; **St** slightly exerted; **Fil** free above the very short common tube; **Anth** curved outwards; **Sty** much shorter than the conspicuous **Sti** branches; **Fr** and **Se** not described.

Similar to *D. leptostachya*. Sometimes treated as synonym of *D. pulquinensis*. — [F. Krapp]

**D. crocea** L. B. Smith (Phytologia 19: 282, t. 1, figs. 7 and 8, 1970). **Type:** Brazil, Paraná (*Hatschbach* 17391 [US]). — **Distr:** Brazil (Paraná); open fields; **I:** Smith & Downs (1974: 575).

[3b] **Ros** many-leaved; **L** to 25 × 0.8–1.3 cm, sheath suborbicular, 3 cm, yellow, glabrous and

lustrous adaxially, **L** lamina very narrowly triangular, soon glabrous adaxially, appressedly pale-lepidote abaxially, laxly serrate, **Sp** recurved or spreading, 1–2.5 mm; **Inf** 60–120 cm, usually simple; peduncle straight or nearly so, glabrous; peduncular **Bra** ovate, acuminate, shorter than most of the internodes, entire or inconspicuously serrulate; fertile **Inf** part laxly many-flowered, 17–32 cm, soon glabrous; floral **Bra** spreading, ovate, acuminate, shorter than the sepals, entire; **Sep** ovate, acute, ± carinate, 8–9 mm; **Pet** lamina elliptic, cucullate, 15 mm, orange; **St** included; **Fil** connate above the common tube; **Sty** ± none.

Similar to *D. aurea*. — [F. Krapp]

**D. dawsonii** L. B. Smith (Contr. Sci. Nat. Hist. Mus. Los Angeles County 17: 2, figs. 2–4, 1957). **Type:** Brazil, Goiás (*Dawson* 15236 [R, LAM, US]). — **Distr:** Brazil (Goiás); rock outcrops along a canyon, Cerrado vegetation. — Fig. 3.

[3b] **Ros** acaulescent, 30–40 cm Ø, slowly offsetting and forming a dense clump; **L** to 22 × 0.7 cm, mostly spreading, sheath suborbicular, >2 cm wide, stramineous, lustrous, glabrous, **L** lamina linear, appressedly cinereous-lepidote on both faces, laxly serrate, **Sp** slender, curved, 5–7 mm, mostly subopposite; **Inf** ±70 cm, simple; peduncle glabrous; peduncular **Bra** broadly ovate with a linear lamina, thin, all but the lowest much shorter than the internodes, entire; fertile **Inf** part lax, 25–30 cm, glabrous; floral **Bra** suborbicular, apiculate, thin, 4 mm, erose; **Ped** 3 mm, stoutly obconical; **Sep** broadly elliptic, obtuse, thin, ecarinate, 5–6 mm; **Pet** ecarinate, lamina broadly obovate, 9 mm, yellow; **St** exerted; **Fil** 2 mm connate above the 1 mm high common tube; **Sty** ± none.

The protologue description is incomplete; rosette characters have been added from offspring of the type collection cultivated at the Sukkulentens-Sammlung Zürich. The species has recently used for hybridization, with *Dyckia* 'Brittle Star' (likely = *D. fosteriana* × *D. platyphylla*) as second parent, yielding very attractive plants (Saul 2018).

**D. delicata** Larocca & Sobral (Novon 12(2): 234–236, ill., 2002). **Type:** Brazil, Rio Grande

**Fig. 3** *Dyckia dawsonii* (Dawson 15236: Brazil; Goiás, E of Formoso, type collection.). (Copyright: U. Eggli)



do Sul (*Larocca & al.* 96/001 [ICN, MBM, US, ZSS]). — **Lit:** Sachs (2011: with ills.). **Distr:** Brazil (Rio Grande do Sul); basalt outcrops.

[1?] **Ros** 20–60 cm Ø; **L** lamina 5–20 × 0.7–2 cm, succulent, eventually recurved in solitary individuals, cinereous to reddish-cinereous, densely pale-lepidote on both faces, sheath broadly triangular, **L** lamina linear-triangular, apex forming a rigid spine, margins undulate, **Sp** soft, straight, antrorretorse, flexible, 5–7 mm, 3–5 mm apart near the leaf tip; **Inf** ±120 cm, simple or with up to 9 branches to 35 cm long; peduncular **Bra** linear-lanceolate, papyraceous, 30–55 × 6–16 mm, exceeding the internodes (lower) or shorter (upper), with 10–20 parallel veins, glabrous, with teeth to 3 mm (upper); fertile **Inf** part 80- to 150-flowered, erect, rachis softly ridged, glabrous; floral **Bra** elliptic-ovate, rounded or acute, 5.5–8 × 5–6 mm, glabrous; **Sep** ovate-oblong, rounded, 6–7 × 3.5–4 mm, green, margins hyaline for ±1 mm; **Pet** lanceolate-spatulate to oblanceolate, 10–13 × 3–4 mm, yellow; **St** 9–10 mm; **Fil** somewhat unequally fused with the petals, free above the common tube; **Anth** lanceolate-ovate, ±2 × 1 mm; **Ov** triquetrous, oblong-acute, ±7 × 2.5–3 mm; **Sty** 7–10 mm, **Sti** lobes papillose; **Fr** ellipsoid, 9–12 × 3–5 mm; **Se** triangular, with a reduced wing along the longitudinal axis, 1.2–1.7 × 0.5–1 mm.

Similar to *D. hebbingii*. — [F. Krapp]

**D. deltoidea** (L. B. Smith) L. B. Smith (*Phytologia* 14: 485, 1967). **Type:** Brazil, Paraná (*Dusén* 17357 [GH, S]). — **Distr:** Brazil (Paraná); campo, 740 m.

≡ *Dyckia coccinea* var. *deltoidea* L. B. Smith (1943) ≡ *Dyckia tuberosa* var. *deltoidea* (L. B. Smith) L. B. Smith (1950).

[3a] **Ros** not described; **L** >40 × 1.4 cm, sheath suborbicular, 4 cm, brown, **L** lamina linear, attenuate to a finely subulate rigid apex, flat, glabrous adaxially, closely appressedly brownish-lepidote abaxially, very laxly serrate, **Sp** slender, curved, 2 mm; **Inf** to 80 cm, simple; peduncle soon glabrous; peduncular **Bra** erect, subfoliaceous and imbricate (lowest) to ovate and acuminate, shorter than the internodes, densely lepidote abaxially; fertile **Inf** part lax, 23–28 cm, rachis soon glabrous; floral **Bra** narrowly triangular, to 22 mm, exceeding the lowest flowers, densely appressed-lepidote abaxially, minutely serrulate; **Fl** spreading; **Ped** 5 mm, subcylindrical, stout; **Sep** broadly ovate or elliptic, 10 mm, acuminate, mucronate, smooth except for the strong midvein, slightly if at all carinate, minutely serrulate, white-lepidote, glabrescent; **Pet** lamina suberect to spreading, subrhombic, 17 mm, carinate-complicate, orange-yellow; **St** included; **Fil** free above the common tube; **Sty** ± none. — [F. Krapp]

**D. densiflora** Schultes *fil.* (in Roemer & Schultes, Syst. Veg. 7(2): 1194, 1830). **Type:** Brazil, Minas Gerais (*Martius* s.n. [M, US [photo]]). — **Distr:** Brazil (Minas Gerais: Diamantina region: Morro de Vila Rica); rocky slopes, 1070–1200 m; only known from the region of the type locality. **I:** Smith & Downs (1974: 535).

[3b] **Ros** not described; **L** to 5 × 0.7 cm, sheath 2 cm wide, dark brown, glabrous, **L** lamina narrowly triangular, soon glabrous adaxially, cinereous-lepidote abaxially, laxly serrate, **Sp** 2 mm; **Inf** to 40 cm, simple; peduncle densely ferruginous-lepidote; peduncular **Bra** ovate, acuminate, equalling the internodes, densely serrulate; fertile **Inf** part subdensely few-flowered, densely tomentose-lepidote; floral **Bra** spreading or reflexed, ovate, acuminate, equalling the sepals (lower) or shorter (upper), serrulate; **Fl** spreading at anthesis and then erect, 10 mm; **Ped** 2 mm; **Sep** ovate, 8 mm, apiculate, fimbriate-serrulate; **Pet** lamina suberect, broadly elliptic, obtusely undulate, barely carinate, orange; **St** slightly shorter than the petals; **Fil** high-connate (to completely connate) above the common tube; **Anth** stout, subacute, ± recurved; **Sty** very short. — [F. Krapp]

**D. dissitiflora** Schultes *fil.* (in Roemer & Schultes, Syst. Veg. 7(2): 1194, 1830). **Type:** Brazil, Bahia (*Martius* s.n. [M, F [photo]]). — **Distr:** Brazil (Bahia, Minas Gerais, Piauí); on rocks in dense Caatinga vegetation or savanna.

[3b] **Ros** not described; **L** ±20 × ±1 cm, sheath not described, **L** lamina narrowly triangular, densely appressed-lepidote abaxially, serrate, **Sp** slightly >1 mm; **Inf** 50–100 cm, simple; peduncle glabrous; peduncular **Bra** ovate with long-attenuate pungent lamina, much shorter than the internodes, entire; fertile **Inf** part lax, elongate, lepidote; floral **Bra** spreading, lanceolate and acuminate (lower) or broadly ovate and apiculate (upper), equalling or exceeding the sepals (lower) or much shorter (upper); **Fl** 12–13 mm; **Ped** 3–4 mm; **Sep** elliptic, broadly acute and apiculate, straight or nearly so, 7 (–9) mm, furfuraceous esp. towards the base; **Pet** suberect, lamina suborbicular, carinate, when dry brownish-yellow; **St** included; **Fil** completely

connate above the common tube; **Anth** narrowly triangular, acute, nearly or quite straight; **Sty** ⅓ as long as the ovary. — [F. Krapp]

**D. distachya** Hassler (Annuaire Conserv. Jard. Bot. Genève 20: 308, 1919). **Type:** Paraguay (*Fiebrig* 5648 [G, F [photo]]). — **Lit:** Pompelli & Guerra (2004: conservation); Wiesbauer (2008: biology, conservation); Voltolini & al. (2009: leaf anatomy). **Distr:** Brazil (Santa Catarina), Paraguay; ledges by streams and rock islands, seasonally inundated. **I:** Smith & Downs (1974: 542); Reitz (1983: t. 45).

≡ *Dyckia interrupta* Mez (1919) (*nom. illeg.*, Art. 52.1); **incl.** *Dyckia distachya* fa. *induta* Hassler (1919).

[2] **Ros** acaulescent, ±50-leaved; **L** 14–20 × 2–3.5 cm, thick, rigid, sheath suborbicular, **L** lamina narrowly triangular, pungent, glabrous adaxially, minutely white-lepidote between the prominent veins abaxially, very laxly serrate, **Sp** minute, curved; **Inf** to 1.3 m, simple or few-branched; peduncle soon glabrous; lowest peduncular **Bra** leaf-like, all others much smaller, to 10 mm, shorter than the internodes, entire; fertile **Inf** part to 50 cm, white-furfuraceous, **Br** laxly flowered, divergent; primary **Bra** shorter than the sterile branch base; floral **Bra** broadly ovate, apiculate, shorter than or ± equalling the sepals (lowest), entire; **Ped** 1–1.5 mm; **Sep** elliptic, 6–8 mm, obtuse, ecarinate; **Pet** suborbicular, 12–15 mm, orange or yellow; **St** included; **Fil** free above the common tube; **Sty** ± equalling the ovary; **Fr** trigonous, dark brown, glossy, 17 × 8 mm; **Se** 3 mm.

The disjunct distribution is notable. Reitz (1983) compares the species with *D. brevifolia*. The species appears severely threatened by dam construction, and micropropagation possibilities have been developed (Pompelli & Guerra 2004, Pompelli & Guerra 2005).

**D. divaricata** Leme & H. Büneker (J. Bromeliad Soc. 65(2): 129–134, ill., 2015). **Type:** Brazil, Mato Grosso do Sul (*Kranz & al.* 426 [RB, HB]). — **Distr:** Brazil (Mato Grosso do Sul: region of Antônio João); on horizontal rock outcrop with disturbed semi-deciduous tropical forest, ±480 m.



[1] **Ros** offsetting and forming large colonies; **L** 20–25, densely rosulate, coriaceous-succulent, suberect to arching, sheath suborbicular,  $\pm 5 \times 6$  cm, densely white-lepidote at the apex, glabrous below, at least near the apex castaneous and glossy, **L** lamina narrowly triangular, attenuate,  $40\text{--}45 \times 2\text{--}2.3$  cm, vividly green, shallowly canaliculate towards the tip, adaxially densely white-lepidote towards the base but glabrous above, adaxially subdensely white-lepidote along the veins, tip a pungent spine, margins spinose, **Sp** narrowly triangular, 3–6 mm, antrorse-uncinate, 5–20 mm apart; **Inf**  $\pm 1.7$  m, ascending-spreading, broadly paniculate; peduncle to 75 cm, erect, glabrescent, densely covered with white wax, pale greenish-bronze-coloured; peduncular **Bra** narrowly triangular,  $60\text{--}80 \times 15\text{--}20$  mm, acuminate, spinescent, subdensely white-lepidote; **Br**  $\pm 11$ , spreading, 35–47 cm, densely 50- to 85-flowered, rachis straight, densely white-floccose; primary **Bra** similar to the upper peduncular bracts,  $40\text{--}45 \times 10$  mm, as long as or shorter than the sterile branch base; floral **Bra** triangular-ovate to broadly ovate,  $3\text{--}10 \times 2\text{--}4$  mm, stramineous, densely white-floccose, irregularly dentate to entire; **Fl** 15–17 mm, 16 mm  $\varnothing$ , subverticillately arranged, broadly campanulate to substellate, spreading; **Ped**  $\pm 3$  mm, stout but inconspicuous, densely white-floccose; **Sep**

broadly elliptic to orbicular,  $5\text{--}6 \times 4.5\text{--}5$  mm, green with yellowish apex, strongly convex, densely white-floccose; **Pet** elliptic to obovate, spreading, obtuse-emarginate,  $11\text{--}12 \times 7\text{--}7.5$  mm, yellow, ecarinate, basally connate for 2 mm, glabrous; **St**  $\pm$  as long as the petals, exposed, erect; **Fil** free above the common tube, yellow; **Anth** sublinear,  $\pm 4$  mm, straight, base deeply bilobed; **Ov** slenderly ovoid,  $\pm 6 \times 2.5$  mm, yellow; **Sty** 4 mm, yellow; **Sti** conduplicate-spiral, yellow,  $\pm 2$  mm; **Fr** subglobose, dark brown, glossy, size not described; **Se** unknown.

Compared with *D. walteriana*, *D. microcalyx* and *D. exserta* in the protologue. The species occurs within 10 km of the border with Paraguay and probably occurs in that country as well. — [U. Eggli]

**D. domfelicianensis** Strehl (Vidalia 2(2): 30–32, figs. 5–8, 2004). **Type:** Brazil, Rio Grande do Sul (Strehl & Silva 1283 [HAS]). — **Distr:** S Brazil (Rio Grande do Sul); rocky outcrops between grasses. — Fig. 4.

[1] **Ros** very many-leaved (100–300 leaves), 50 cm  $\varnothing$ , with a short stem; **L** sheath  $\pm 3.5 \times 5.5$  cm, dark brown, glossy on both faces, **L** lamina  $23\text{--}25 \times \pm 3.5$  cm, tough and succulent, acuminate, acute, clear green, cinereously white-lepidote, with pungent tip, margin spinose, **Sp** hooked, antrorse, brown; **Inf** to 120 cm,  $1\text{--}2 \times$

**Fig. 4** *Dyckia domfelicianensis* (Sachs s.n.: Brazil; Rio Grande do Sul; Arroio dos Ratos). (Copyright: U. Eggli)





branched, paniculate; peduncle  $\pm 50$  cm, green to brownish, with fine white tomentum; peduncular **Bra** leaf-like (lowest), long-triangular, acuminate, to  $\pm 50$  mm, sparsely serrate, laxly arranged; fertile **Inf** part 60–80 cm, lax, white-lepidote; **Br** to 45 cm, rachis slightly angular, white-lepidote; floral **Bra** broadly triangular, acute,  $\pm 2 \times \pm 3$  mm, green to brown, abaxially puberulous; **Fl** sessile, narrowly tubular; **Sep** ovate-acuminate,  $5\text{--}6 \times 3$  mm, carinate, connate for  $\frac{1}{3}$  of their length, abaxially white-lepidote, tip  $\pm$  bifid; **Pet** ovate,  $9 \times 3\text{--}4$  mm, clear yellow, abaxially white-lepidote; **St** exerted; **Fil** free,  $\pm 6$  mm; **Ov** green,  $\pm 3\text{--}4$  mm; **Sty**  $\pm 6$  mm, yellow; **Fr** and **Se** not described.

Similar to *D. hebdingii*.

**D. duckei** L. B. Smith (Bol. Mus. Paraense “Emilio Goeldi”, n.s., Bot. 1: 3, fig. k–o, 1958). **Type:** Brazil, Pará (*Ducke* s.n. [US, MG 14856]). — **Distr:** Brazil (Maranhão, Pará); iron-rich rocky (“pedra canga”) fields. **I:** Smith & Downs (1974: 558).

[3a] **Ros** acaulescent, very dense, very many-leaved; **L** to  $26\text{--}40 \times 1.5\text{--}2$  cm, arching-recurved, sheath broadly elliptic, 2–3 cm, **L** lamina very narrowly triangular, with pungent tip, soon glabrous adaxially, appressedly cinereous-lepidote abaxially, margins laxly serrate, **Sp** slender, spreading, 2 mm; **Inf** 40–130 cm, simple or subsimple; peduncle very slender, glabrous; peduncular **Bra** ovate, acuminate, very small, entire (except the lowest), remote; fertile **Inf** part lax, 5–26 cm, soon glabrous; floral **Bra** broadly ovate, apiculate, shorter than the pedicels, entire; **Fl** divergent or spreading; **Ped** to 3 mm, slender; **Sep** elliptic, 5.5 mm, obtuse, ecarinate, erose; **Pet** lamina rhomboid, 10 mm, carinate, orange; **St** slightly but distinctly exerted; **Fil** free above the 1 mm high common tube, 10 mm, orange; **Sty** 1 mm; **Fr** subglobose, 10–12 mm, dark castaneous.

Monteiro & Forzza (2016, 1260) describe and illustrate material under this name with rosettes with few erect to spreading leaves only 10–13 cm long, and much smaller inflorescences, but with similar flowers.

**D. dusenii** L. B. Smith (Contr. Gray Herb. 98: 6, t. 2, 1932). **Type:** Brazil, Paraná (*Dusén* 18081

[S, GH [photo]]). — **Distr:** Brazil (Paraná, Santa Catarina, Rio Grande do Sul); cliffs and dry fields. **I:** Smith & Downs (1974: 539).

[3b] Plants stout; **L**  $30\text{--}40 \times 1.5\text{--}2$  cm, sheath broad, suborbicular, dark castaneous, **L** lamina narrowly triangular, attenuate, yellow-green, glabrous adaxially, densely pale-lepidote abaxially, laxly serrate, **Sp** curved, 2–3 mm; **Inf** to 70 cm, simple; peduncle stout, soon glabrous; peduncular **Bra** broadly ovate, acuminate, large, much exceeding the internodes, densely pale-lepidote, entire or minutely denticulate; fertile **Inf** part subdense, many-flowered, 20–30 cm; floral **Bra** broadly ovate, acuminate, exceeding the sepals (all) and the petals (lowest); **Fl** subspreading, soon glabrous; **Ped** 5 mm, stout; **Sep** ovate, 16 mm, acute, strongly alate-carinate, frequently denticulate; **Pet** lamina broadly elliptic, 15–20 mm, obtuse, ecarinate, suberect, yellow; **St** much shorter than the petals; **Fil** shortly connate above the common tube; **Anth** sublinear, acuminate; **Sty** very short.

**D. edwardii** P. J. Braun & al. (Bromelie 2008 (3): 116–123, ills., 2008). **Type:** Brazil, Goiás (*Esteves Pereira* 467 [UFG]). — **Lit:** Braun & Esteves Pereira (2009a). **Distr:** Brazil (Goiás); granitic rocks and granite-derived soils in very dry Cerrado vegetation. **I:** Braun (2018: 75).

[2] **Ros** with  $>50$  living leaves, to 1 m  $\emptyset$ , usually solitary, sometimes forming small groups, with a stem to  $50 \times \pm 17$  cm in very old plants, compactly covered by old leaves; **L**  $\pm 56 \times$  to 4.3 cm, sheath  $\pm 3.2 \times 4.3$  cm, white, apically densely yellowish-lepidote, **L** lamina erect to slightly arching, narrowly triangular to lanceolate, apex a flat brownish pungent tip to 35 mm long, light-green to chocolate-brown, adaxially lustrous, abaxially white-lepidote, strongly veined, sparsely serrate, **Sp** pungent, uncinatate, usually antrorse, retrorse towards the leaf tip, to 5.5 mm, 6–18 mm apart; **Inf** to 1.8 m, compound; peduncle hard and strong, terete, slightly sinuous and sulcate,  $\pm 50$  cm, green to reddish-green; peduncular **Bra** linear to lanceolate, acuminate, pungent, exceeding or equalling the internodes,  $3.1\text{--}4.4 \times 1$  cm, pale green, soon stramineous, serrate; fertile **Inf** part lax,  $\pm 1.4$  m, ascending, below the first

branch with 1–2 dormant buds; **Br** 7–15, ascending, spreading, flexible, 26–53 cm, dark rose, sparsely white-lepidote; primary **Bra** like the upper peduncular bracts but shorter; floral **Bra** narrowly triangular to lanceolate,  $\pm 22 \times 7$  mm (lower) to 6 mm (upper), brownish-green, soon stramineous, densely white-lepidote, serrate; **Fl** ascending,  $18\text{--}20 \times 7\text{--}9$  mm; **Ped** 0–2 mm; **Sep** lanceolate,  $\pm 11 \times 5.9$  mm, yellowish to reddish-orange, scatteredly white-lepidote; **Pet** obtuse,  $\pm 11 \times 8$  mm, orange but more yellowish than the sepals, basally light orange to yellow; **Fil** 9 mm, apical 1.8 mm free above the 7 mm high common tube, pale yellow; **Anth** to  $2.6 \times 1.2$  mm, yellow, recurved at anthesis; **Ov** narrowly subpyramidal,  $\pm 5$  mm; **Sty**  $\pm 1.3$  mm, yellow, **Sti**  $\pm 2.5$  mm, yellowish-orange, hidden at anthesis; **Fr** ellipsoid-ovate, apex acuminate,  $15\text{--}16 \times 8\text{--}10$  mm, dark brown, lustrous.

Similar to *D. goiana* and *D. uleana*, but forming extraordinary stems to 50 cm long in old plants.

**D. elata** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 508, 1896). **Type:** Brazil, Minas Gerais (*Schwacke* 8739 [B, F [photo]]). — **Distr:** Brazil (Minas Gerais); rocky fields.

[2?] Insufficiently described; **L** to  $40 \times 1.7$  cm, sheath suborbicular, large, **L** lamina narrowly triangular, green, subglabrous adaxially, laxly serrate, **Sp** 4 mm; **Inf** probably  $>1$  m, laxly paniculate; peduncle stout, 50 cm, soon glabrous; peduncular **Bra** subfoliaceous, equalling or exceeding the internodes, sparsely serrulate; fertile **Inf** part many-flowered, narrow, rachis tomentulose but soon glabrous; **Br** elongate, laxly flowered; primary **Bra** much shorter than the sterile branch bases; floral **Bra** reflexed, broadly ovate, acute, shorter than the flowers or equalling the sepals (lowest), finely serrate; **Fl** spreading or reflexed, 12 mm; **Ped** short; **Sep** elliptic, 7 mm, broadly rounded, glabrous; **Pet** erect, lamina large, suborbicular, neither carinate nor undulate when dry, orange; **St** included; **Fil** free above the common tube; **Anth** short, subtriangular, apiculate, scarcely recurved; **Sty** to  $\frac{1}{2}$  as long as the ovary. — [F. Krapp]

**D. elisabethae** S. Winkler (Doc. Nat. 3: 36–37, fig. 3, 1982). **Type:** Brazil, Rio Grande do Sul (*Winkler* 741 [ICN]). — **Distr:** Brazil (E Rio Grande do Sul); barren granite rocks in moist ground.

[1?] **Ros** to 30 cm  $\emptyset$ ; **L**  $35 \times 3$  cm, sheath dark, **L** lamina adaxially light green, abaxially white-lepidote, margins conspicuously serrate, **Sp** curved, to 5 mm, irregularly arranged; **Inf** to 1.7 m, usually branched or rarely simple, branches not further described; peduncle reddish to red (younger parts), white-pubescent; peduncular **Bra** serrate; floral **Bra** elliptic, acuminate, pubescent, to 8 mm; **Fl** sessile; **Sep** lanceolate-ovate, to 12 mm, yellow, white-pubescent, tip rounded; **Pet** orbicular, to 18 mm, light yellow, finely lepidote, ecarinate, margins shortly ciliate; **St** included or equalling the petals; **Fil** free above the common tube; **Ov** 3 mm; **Sty** 3 mm.

The incomplete description from the protologue was expanded on the base of the comparison with *D. pontesii* in the protologue of the latter. The flowers are described as sessile in the protologue, but as pedicellate in the comparison with *D. pontesii*.

**D. elongata** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 529, 1896). **Type:** Brazil, sine loco (*Sellow* Brom. Paris 58 [P, GH [photo]]). — **Distr:** Brazil (Bahia); on rocks. **I:** Smith & Downs (1974: 568).

[3a] **Ros** not described; **L** to  $40 \times \pm 1.5$  cm, sheath broadly ovate, **L** lamina narrowly triangular, appressedly pale-lepidote abaxially, serrate, **Sp** stout, straight or curved, 6 mm; **Inf** almost 1 m, simple; peduncle slender, soon glabrous; peduncular **Bra** ovate-triangular (upper), much shorter than the internodes,  $\pm 10$  mm; fertile **Inf** part very laxly few-flowered, soon glabrous; floral **Bra** spreading or subreflexed, ovate-triangular, shorter than the sepals; **Fl** suberect, 11 mm, subsessile; **Sep** broadly ovate, 7–8 mm, obtuse; **Pet** lamina suberect, broadly obovate, obscurely carinate, colour not described; **St** included; **Fil** free above the common tube; **Anth** triangular, acute, straight or slightly recurved; **Sty** very short. — [F. Krapp]

**D. eminens** Mez (Bot. Jahrb. Syst. 30 (Beiblatt 67): 5, 1901). **Type:** Brazil, Goiás (*Glaziou* 22192-A [B, K, P]). — **Distr:** Brazil (Goiás); ecology not reported.

[3a?] **Ros** not described; **L**  $\pm 30 \times > 2$  cm, sheath not described, **L** lamina narrowly triangular, with a strongly pointed hard tip, sparsely appressed-lepidote abaxially, laxly serrate, **Sp** 1 mm, far apart; **Inf** 1 m or more, simple; peduncle stout, soon glabrous; peduncular **Bra** broad with narrowly triangular pungent lamina, exceeding the internodes, serrulate; fertile **Inf** part lax, densely furfuraceous; floral **Bra** reflexed, broadly ovate, acuminate (lower), 20 mm; **Fl** spreading or subreflexed,  $\pm 14$  mm; **Ped**  $< 5$  mm; **Sep** broadly elliptic,  $\pm 9$  mm obtuse; **Pet** suberect, trapeziform, carinate, slightly undulate, colour not described; **St** much shorter than the petals; **Fil** free or shortly connate above the common tube; **Anth** 3 mm, strongly spirally reflexed; **Sty** very short. — [F. Krapp]

**D. encholirioides** (Gaudichaud) Mez (in A. & C. de Candolle, Monogr. Phan. 9: 507, 1896). **Type:** Brazil, Santa Catarina (*Gaudichaud* 130 [P, GH [photo]]). — **Lit:** Kriek (2008: pollination ecology, with ill.). **Distr:** Brazil (São Paulo, Paraná, Santa Catarina, Rio Grande do Sul); on rocks and sand, along the coast. **I:** Smith & Downs (1974: 521).

≡ *Garrelia encholirioides* Gaudichaud (1851); **incl.** *Encholirium garrelii* Beer (1857) (*nom. illeg.*, Art. 52.1).

[1] **Ros** to 1.5 m  $\emptyset$ , with prostrate branching stems to 2 m  $\times$  10–15 cm; **L** 30–100  $\times$  to 4 cm, sheath not described, **L** lamina narrowly triangular, glabrous adaxially, densely pale-lepidote abaxially, area between the veins broad and shallow, margins laxly serrate, **Sp** coarse, curved, 3–5 mm; **Inf** very variable, to 2 m, simple to paniculate with many long branches; peduncle stout, ferruginous-puberulous; peduncular **Bra** broadly ovate with narrowly triangular lamina, longer than the internodes or sometimes the uppermost slightly shorter, serrulate; fertile **Inf** part many-flowered with 50–100 flowers, ferruginous-tomentulose; primary **Bra** like the peduncular bracts, much shorter than the sterile branch bases; floral **Bra**

ovate or lanceolate, acuminate, varying from shorter than the sepals to longer than the flowers, minutely serrulate; **Fl** spreading; **Ped** 1–2 mm, rather slender; **Sep** broadly ovate, 8 mm, acute and mucronulate, fimbriate; **Pet** lamina elliptic to obovate, 12 mm, apiculate, undulate, carinate, red or yellow; **St** included; **Fil** free to shortly connate above the common tube; **Anth** narrowly triangular, apiculate, recurved; **Sty**  $\frac{1}{3}$  as long as the ovary.

As expected for a plant from coastal habitats, seed viability is not reduced by high-salt conditions, but germination only occurs when salt concentrations are low or nil (Pompelli & al. 2006). Flowers are visited by native Brazilian bees of the genera *Xylocopa* and *Trigona*, the introduced honey bee, as well as by hummingbirds (Kriek 2008). The measurements given by these authors indicate that the flowers can be much larger than in the description above (sepals  $\pm 15$  mm, petals 15–19 mm).

**D. encholirioides** var. **encholirioides** — **Distr:** Brazil (São Paulo, Paraná, Santa Catarina, Rio Grande do Sul); on rocks and sand, along the coast. **I:** Reitz (1983: t. 46).

**Incl.** *Dyckia catharinensis* K. Koch (1874) (*nom. illeg.*, Art. 52.1?) ≡ *Encholirium catharinense* (K. Koch) Benth & Hooker *fil. ex* Mez (1934); **incl.** *Dyckia catharinensis* var. *dentata* Wittmack (1891).

[1] Axes of the **Inf** and the **Sep** yellow. — [F. Krapp]

**D. encholirioides** var. **rubra** (Wittmack) Reitz (Anais Bot. Herb. “Barbosa Rodrigues” 3: 108, 1951). **Type:** Brazil, Santa Catarina (*Schenck* 619 [not located]). — **Distr:** Brazil (Santa Catarina); on rocks and sand, along the coast.

≡ *Dyckia rubra* Wittmack (1891).

[1] Axes of the **Inf** and the **Sep** red. — [F. Krapp]

**D. espiritosantensis** Leme & al. (Rodriguésia 61(1): 34–36, figs. 4E–F and 5A–G, 2010). **Type:** Brazil, Espírito Santo (*Leme & al.* 6930 [RB, MBML, VIC]). — **Distr:** Brazil (Espírito Santo); shallow soils.

[3a] **Ros** dense,  $\pm 25$ -leaved, with short basal shoots; **L** 23–26  $\times$  1.5–1.7 cm, strongly coriaceous, slightly succulent, sheath  $\pm 2.5 \times 3$  cm, whitish towards the base,  $\pm$  glabrous, **L** lamina narrowly triangular, flat, suberect, green to reddish, acuminate, pungent with a nearly subulate tip, adaxially subdensely white-lepidote, abaxially finely veined and densely white-lepidote, margins white-lepidote, laxly spinose, **Sp** triangular, pre-vaillingly antrorse-uncinate, 2–3 mm, subdensely white-lepidote, pale, 8–20 mm apart; **Inf**  $\pm 1$  m, erect, simple; peduncle  $\pm 50$  cm, greenish to bronze, subdensely white-lepidote to glabrous; peduncular **Bra** subfoliaceous (lowest), erect, narrowly triangular, acuminate, 10–20  $\times$  4–6 mm, distinctly shorter than the internodes, stramineous at anthesis, subdensely white-lepidote, veined, inconspicuously denticulate to subentire; fertile **Inf** part  $\pm 45$ -flowered, lax to subdense, erect,  $\pm 37$  cm, rachis  $\pm$  straight, pale orange, subdensely pale ferruginous-lepidote to glabrescent; floral **Bra** spreading to reflexed at anthesis, narrowly subtriangular-ovate (lower) or broadly ovate to suborbicular (upper), acuminate, carinate, 7–10  $\times$  4–5 mm (lower) to  $\pm 4 \times 3$  mm (upper), stramineous at anthesis, distinctly veined, densely pale ferruginous-lepidote, remotely denticulate to entire; **Fl** spreading to reflexed at anthesis,  $\pm 15$  mm, narrowly campanulate, unscented;

**Ped** 2.5–3 mm, orange; **Sep** broadly ovate, 5–6  $\times$   $\pm 5$  mm, rounded, ecarinate, convex, orange, densely pale ferruginous-lepidote, entire; **Pet** obovate-spatulate,  $\pm 11 \times 7.5$  mm, obtuse-emarginate, ecarinate, orange,  $\pm$  glabrous, entire; **St** just included; **Fil** free above the 1 mm high common tube, complanate,  $\pm 8$  mm, pale orange towards the apex; **Anth** narrowly subtriangular,  $\pm 2.5$  mm, straight at anthesis, base truncate, acute; **Ov** narrowly suboblong,  $\pm 6.5$  mm, pale yellow; **Sty** 1–1.5 mm, **Sti**  $\pm 1$  mm, orange, margins minutely crenulate.

Closely similar to *D. mello-barretoii*, but also somewhat similar to *D. martinellii*.

**D. estevesii** Rauh (Trop. subtrop. Pfl.-welt 60: 16–20, ill., 1987). **Type:** Brazil, Goiás (*Esteves Pereira* s.n. in *BG Heidelberg* 67420 [HEID]). — **Distr:** Brazil (Goiás); ecology not recorded. **I:** Braun (2018: 70). — Fig. 5.

[2] **Ros** fan-like, clump-forming, stem to 10 cm  $\varnothing$ , thickened towards the base, densely covered by leaf sheaths, branching at the base; **L** numerous, distichous, spreading-recurved, sheath distinct, densely imbricate, to 5  $\times$  10 cm, green with brown base, soon stramineous, glabrous, upper margins with wing-like scales, sulcate abaxially, persistent, **L** lamina erect (younger) to spreading (older), to  $\pm 30 \times 3.5$  cm,

**Fig. 5** *Dyckia estevesii*.  
(Copyright: U. Eggli)





slightly succulent, narrowly lanceolate, long-attenuate with pungent tip, distinctly sulcate, adaxially dark green to brownish, abaxially greyish-green, sparsely lepidote, margins dentate especially basally, **Sp** hard, retrorse, 5 mm, 10–30 mm apart; **Inf** to 1.2 m, very laxly branched; peduncle slender, erect, to 50 cm, greyish-green, glabrous; peduncular **Bra** narrowly lanceolate (lower) to triangular (upper), to 5 mm, much shorter than the internodes, entire; fertile **Inf** part laxly flowered, rachis very slender, slightly flexuous, greyish-green; **Br** 2–3, 15–25 cm with 2–4 densely rosulate and scale-like bracts; primary **Bra** scale-like, small; floral **Bra** broadly ovate, 2–3 mm, shortly apiculate, reddish-brown, glabrous; **Fl** partially secund, erect to divergent,  $\pm 15$  mm; **Ped**  $\pm 5$  mm; **Sep** ovoid,  $5 \times 2\text{--}3$  mm, obtuse, subcarinate, free, glabrous; **Pet** erect, obtuse,  $13\text{--}15 \times 5$  mm, indistinctly carinate, little diverging at the tips, described as reddish-brown but orange in cultivated material; **St** slightly exerted; **Fil** free above the common tube; **Anth** outcurved; **Ov**  $\pm 10$  mm; **Sty** short; **Sti** roundly capitate-lobate; **Fr** oblong-globose, 17 mm, blackish-brown.

The leaves are usually arranged distichously, but can also form a regular rosette, and the feature varies even within offsets of a single specimen. Butcher (2010) concluded that the distichous arrangement is an anomaly.

**D. excelsa** Leme (Pabstia 4(4): 6–7, ills., 1993). **Type:** Brazil, Mato Grosso? (*Burle Marx* s.n. [HB, RB]). — **Lit:** Paggi & al. (2015: with ills.). **Distr:** Brazil (W Mato Grosso do Sul: region of Corumbá and Ladário); granitic and iron-rich rock outcrops.

[3a] **Ros** dense; **L**  $\pm 70 \times 4$  cm, rigid, lamina canaliculate, suberect-arcuate, narrowly triangular, long acuminate, apex caudate, green, both faces white-lepidote, margins subdensely spinose, **Sp** 5–9 mm, uncinat, pale brown; **Inf**  $\pm 2$  m, erect, simple; peduncle  $\pm 70$  cm, lepidote but glabrescent; peduncular **Bra** subfoliaceous; fertile **Inf** part lax (basally) to subdense (apically) at anthesis,  $\pm 120$  cm, rachis notably brown-lepidote, towards the apex densely pale brown-sublanate; floral **Bra** spreading or uppermost

recurved, subtriangular and shortly acuminate (lower) or broadly ovate-elliptic and acute (upper),  $\pm$  equalling the sepals (lower) to equalling the pedicels (upper), densely pale-lanate, entire; **Fl** suberect,  $\pm 50$  mm, vary narrowly urceolate and narrowing towards the throat; **Ped** 6–10 mm, pale brown-lanate; **Sep** suborbicular,  $\pm 14 \times 13$  mm, obtuse, when dry distinctly corrugately veined, thick, reddish-orange, pale brown-sublanate; **Pet** narrowly ovate,  $\pm 32 \times 16$  mm, rounded, slightly thick, erect at anthesis, reddish-orange, densely pale brown-lanate; **St** barely exerted; **Fil**  $\pm$  free above the common tube,  $\pm 33$  mm, yellow; **Anth** narrowly triangular,  $\pm 5$  mm, recurved; **Ov** subpyramidal, sulcate,  $\pm 20$  mm, pale green; **Sty**  $\pm 17$  mm, slightly surpassing the anthers, yellow; **Sti** yellow,  $\pm 3$  mm; **Fr** and **Se** not described.

Similar to *D. ferruginea*. While the type is said to have been collected in the State of Mato Grosso (but without known locality), Paggi & al. (2015) record the taxon only from Mato Grosso do Sul.

**D. exserta** L. B. Smith (Revista Argent. Agron. 8: 192, figs. 1–5, 1941). **Type:** Paraguay, Amambay (*Rojas* 7563 [GH]). — **Distr:** Paraguay (Amambay); ecology not recorded.

[1?] **Ros** stout; **L**  $> 70 \times 4.5$  cm, lamina narrowly triangular, punctulate and sublustrous adaxially, finely appressedly white-lepidote and striate abaxially, **Sp** slightly curved, to 9 mm, 20–30 mm apart; **Inf** probably 1 m or more, few-branched; peduncle stout, glabrous; peduncular **Bra** broadly ovate, acute, 15–20 mm, upper much shorter than the internodes; fertile **Inf** part lax, glabrous, terminal part to 60 cm; **Br** densely flowered, subspreading, to 16 cm; primary **Bra** like the peduncular bracts, distinctly shorter than the sterile branch bases; floral **Bra** broadly ovate, acute, except for the lowest shorter than the sepals; **Fl** yellowish, subsessile; **Sep** suborbicular or broadly ovate, 6 mm, apiculate; **Pet** elliptic, 11–13 mm, obtuse, not unguiculate, pale-margined when dry, yellowish; **St** long-exserted, slightly exceeding the style; **Fil** free above the 1 mm high common tube; **Anth** straight, 3.5 mm; **Sty** slender, elongate, longer than the ovary; **Se** narrowly winged. — [F. Krapp]



**D. ferox** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 511, 1896). **Type:** Paraguay (*Kuntze* s.n. [NY]). — **Distr:** Brazil (Mato Grosso), Paraguay, Bolivia (Santa Cruz), Argentina (Chaco, Corrientes, Entre Ríos, Formosa); dry fields and woods. **I:** Smith & Downs (1974: 544).

**Incl.** *Dyckia meziana* Kuntze (1898); **incl.** *Dyckia hamosa* Mez (1906)  $\equiv$  *Dyckia ferox* ssp. *hamosa* (Mez) Hassler (1919)  $\equiv$  *Dyckia ferox* fa. *hamosa* (Mez) Castellanos (1933); **incl.** *Dyckia ferox* fa. *vulgaris* Hassler (1919); **incl.** *Dyckia ferox* fa. *australis* Hassler (1919) (*nom. inval.*, Art. 26.2).

[1] **Ros** slowly offsetting and clump-forming; **L** 20–50  $\times$  0.8–2 cm or longer, sheath suborbicular,  $\pm$ 3 cm, **L** lamina narrowly triangular, closely appressedly pale-lepidote abaxially, **Sp** acicular, antroretrorely curved, 4–6 mm; **Inf** 60 cm, simple or few-branched with short branches; peduncle slender, cinereous-tomentose, soon glabrous; peduncular **Bra** very broadly ovate, abruptly acute, shorter than the internodes, entire; fertile **Inf** part lax, cinereous-tomentose to glabrous; primary **Bra** scarcely larger than the floral bracts; floral **Bra** spreading or reflexed, suborbicular-ovate, obtuse or apiculate, much shorter than the sepals, subglabrous; **Fl** subsessile, narrowly funnel-shaped; **Sep** very broadly elliptic, 5–7 mm, very broadly rounded at the apex, subglabrous; **Pet** lamina suberect, subrhombic, to 12 mm, rounded, scarcely undulate, little if at all carinate, yellow; **St** shorter than the petals; **Fil** free above the common tube; **Anth** triangular, subacute, strongly recurved at the apex; **Sty** very short. — [F. Krapp]

**D. ferrisicola** O. B. C. Ribeiro & Leme (J. Bromeliad Soc. 65(1): 19–22, ill. (incl. p. 18), 2015). **Type:** Brazil, Minas Gerais (*Ribeiro* 249 [BHCB]). — **Distr:** Brazil (C Minas Gerais: Sarzedo); white iron-rich rock outcrop (“canga couraçada”), in full sun,  $\pm$ 1200 m; known from the type area only.

[3b] **Ros**  $\pm$ 40 cm  $\varnothing$ , offsetting; **L** 11–14, suberect to arching-spreading, coriaceous, sheath 3.5–4  $\times$  4.5–5 cm, distinct from the lamina, whitish, both faces glabrous and glossy, **L** lamina

narrowly triangular, 20–22  $\times$  2.5–3 cm, strongly canaliculate, mostly wine-red or sometimes green, adaxially glabrous and glossy, abaxially white-lepidote at the base but glabrous further up, distinctly veined, tip acuminate, pungent, margins laxly spinose, **Sp** narrowly subtriangular, spreading to retrorse, 3.5–4 mm,  $\pm$ 20 mm apart; **Inf** 60–80 cm, erect, simple; peduncle 35–40 cm, reddish-green, densely white-hairy; peduncular **Bra** broadly triangular with a long lanceolate acuminate-caudate lamina, 15–17  $\times$  6–8 mm, erect, with prominent midvein and appearing carinate, densely white-lanate; fertile **Inf** part 30–40 cm, laxly 15- to 40-flowered, rachis red, densely white-lanate; floral **Bra** subtriangular, acuminate, 10–11  $\times$  5–6 mm, with prominent midvein and appearing carinate, stramineous towards the tip, minutely denticulate; **Fl** 15–16 mm, porrect-spreading, tubular, unscented; **Ped** 4–5 mm, white-lanate; **Sep** broadly ovate to suborbicular, 6–7  $\times$  5–6 mm, convex, ecarinate, reddish, sparsely white-lanate, margins with recurved fimbriate trichomes; **Pet** broadly spatulate, emarginate, 11–12  $\times$  9–10 mm, orange, basally connate for 2.5 mm, ecarinate; **St** included and distinctly shorter than the petals; **Fil** yellow, connate for  $\pm$ 2 mm above the common tube; **Anth** oblong-lanceolate,  $\pm$ 2 mm, straight, base bilobed; **Ov** suboblong,  $\pm$ 6  $\times$  2 mm, yellow; **Sty**  $\pm$ 2 mm, distinct, orange; **Sti** conduplicate-spiral, yellow, lobes shortly lacerate; **Fr** and **Se** unknown.

A member of the *D. saxatilis* complex, and compared with *D. saxatilis* in the protologue. — [U. Eggli]

**D. ferruginea** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 533, 1896). **Type:** Brazil, Mato Grosso (*Kuntze* s.n. [NY]). — **Distr:** Brazil (Mato Grosso); vertical walls of red sandstone. **I:** Smith & Downs (1974: 535).

[3a] **Ros** not described; **L** to 80  $\times$  2.5 cm, sheath suborbicular, 5 cm, castaneous, glabrous, **L** lamina narrowly triangular, soon glabrous adaxially, subappressedly white-lepidote abaxially, margins densely and coarsely serrate, **Sp** curved, 10 mm; **Inf** 1 m or more, simple; peduncle stout, ferruginous-tomentulose or glabrous with age;

peduncular **Bra** leaf-like, imbricate, the upper ones linear-lanceolate, entire; fertile **Inf** part dense or  $\pm$  interrupted, many-flowered, rachis stout, densely ferruginous-tomentulose; floral **Bra** divergent to spreading, narrowly triangular, to 7 mm, shorter than the sepals; **Fl** suberect to spreading, to 15 mm; **Ped** very short; **Sep** ovate, 7–8.5 mm, broadly rounded; **Pet** lamina broadly elliptic, 10–14 mm, obtuse, ecarinate, suberect, yellowish-green, ferruginous-tomentulose outside; **St** exserted ( $\pm$  equalling the petals according to the protologue); **Fil** free above the common tube; **Anth** linear, obtuse, scarcely recurved; **Ov** sparsely lepidote; **Sty** as long as the ovary.

The protologue is based on immature flowers according to Smith & Downs (1974), and in fresh material, the stamens are exserted.

**D. floribunda** Grisebach (Gött. Abh. 24: 331, 1879). **Type:** Argentina, Córdoba (*Hieronymus* 566 p.p. [GOET]). — **Lit:** Vesprini & al. (2003: ecology). **Distr:** Argentina (Catamarca, Córdoba, La Rioja, San Lu s, San Juan, Jujuy, Salta); dry rocky slopes. **I:** Smith & Downs (1974: 549); Subils (2009: 349, 423).

**Incl.** *Dyckia gilliesii* Baker (1889); **incl.** *Dyckia chaguar* A. Castellanos (1931).

[1] **Ros** densely many-leaved, acaulescent, with  $\pm$  sessile offsets; **L** 20–100  $\times$  2.5 cm, sheath suborbicular, 3–6 cm, pale, glabrous, **L** lamina attenuate to a pungent tip, white- or cinereous-lepidote esp. abaxially, laxly serrate, **Sp** curved, 4–6 mm; **Inf** 60–100 cm, paniculate; peduncle elongate, glabrescent; peduncular **Bra** broadly triangular-ovate, acuminate, thin, shorter than the internodes; fertile **Inf** part laxly branched, lepidote at least at anthesis, **Br** subspreading, slightly flexuous, laxly to densely flowered; primary **Bra** ovate, apiculate, small; floral **Bra** ovate-triangular, acute or apiculate, much exceeded by the sepals; **Fl** divergent to spreading, orange; **Ped** very short at anthesis, to 4 mm in fruit; **Sep** broad, 7 mm, rounded, obtuse or apiculate, strongly convex; **Pet** obovate-elliptic, 10–14 mm, broadly rounded and emarginate, undulate, carinate; **St** slightly exserted; **Fil** free above the very short common tube; **Anth** sub-linear, acute,  $\pm$  recurved; **Sty** free, very short.

**D. formosensis** Leme & Z. J. G. Miranda (Phytotaxa 67: 15–17, ills., 2012). **Type:** Brazil, Goi s (Leme & Miranda 6451 [RB, HB]). — **Distr:** Brazil (Goi s); open Cerrado vegetation.

[3b] **Ros** solitary, subdense,  $\pm$ 18-leaved; **L** 60–65  $\times$  3.5–4 cm, rigid, thickly coriaceous, sheath wider than the lamina, **L** lamina narrowly triangular, canaliculate, suberect, straight, acuminate and with spinescent tip, green to reddish-ferruginous, veined, adaxially inconspicuously white-lepidote, abaxially densely non-obscuringly white-lepidote, margins glabrescent and laxly spinose, **Sp** shortly acicular, retrorse-uncinate, 1.5–5 mm, pale castaneous, glabrous, 10–20 mm apart; **Inf** 1.9–2 m, simple, erect; peduncle 95–100 cm, reddish-ferruginous, densely white-sublanate; peduncular **Bra** subfoliaceous (lowest) to narrowly triangular-lanceolate (upper), acuminate, with spinescent tip, erect, distinctly shorter than the internodes, stramineous, inconspicuously white-sublanate, veined, densely spinulose, uppermost like the floral bracts; fertile **Inf** part 70- to 75-flowered, lax basally, subdense apically, 90–100 cm,  $\pm$  straight, reddish-ferruginous towards the base and orange towards the apex, densely white-sublanate; floral **Bra** suberect to slightly reflexed, ovate-triangular to lanceolate, acuminate-caudate, 15–35  $\times$  6–15 mm, stramineous, inconspicuously white-sublanate abaxially, veined, densely spinulose; **Fl** spreading to slightly reflexed at anthesis,  $\pm$  erect afterwards, 18–22 mm, campanulate, slightly fragrant; **Ped** stout, 3–5 mm; **Sep** broadly ovate, 8–10  $\times$  7–8 mm, apex obtuse, ecarinate, convex, orange, densely and coarsely white-lepidote, margins with fimbriate trichomes, remotely and densely spinulose-crenulate; **Pet** broadly spatulate, 13–14  $\times$  8–12 mm, obtuse and emarginate, the base narrower, ecarinate, orange, glabrous; **St** included; **Fil** 5–6 mm connate above the 2–4 mm high common tube, complanate, 9–10 mm, orange; **Anth** subtriangular, 3–5 mm, strongly recurved at anthesis, acute and apiculate, base bilobed; **Ov** narrowly oblong-subpyramidal, yellowish; **Sty** slender, 3–3.5 mm, orange; **Sti** slightly exceeding the anthers after anthesis,  $\pm$ 1.5 mm, orange, margins crenulate-lacerate.

Closely related to *D. brasiliensis*, and also similar to *D. goiana*. — [F. Krapp]

**D. fosteriana** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 107, t. 106, 1943). **Type:** Brazil, Paraná (*Foster* 1154 [GH]). — **Distr:** Brazil (Paraná).

[3b] **Ros** dense, flat, clustering; **L** numerous, 9–17 × 0.8–1.2 cm, arching-recurved, sheath suborbicular, **L** lamina narrowly triangular, covered with a cinereous membrane of fused scales, **Sp** antroretroretrorsely curved, 2–4 mm; **Inf** 10–45 cm, simple; peduncle sparsely flocculose; peduncular **Bra** lanceolate, acuminate, exceeding the internodes or the upper slightly shorter, densely lepidote, serrulate; fertile **Inf** part 3.5–13 cm, densely lepidote; floral **Bra** like the peduncular bracts, carinate towards the apex, lowest ± equalling the flowers, serrulate; **Fl** suberect or spreading; **Ped** ± 2 mm; **Sep** ovate, 6–9 mm, acute, carinate, ferruginous-lepidote; **Pet** lamina spreading, rhombic, 8–10 mm, orange; **St** included; **Fil** short-connate above the common tube; **Sty** very short. — [F. Krapp]

**D. fosteriana** var. **fosteriana** — **Distr:** Brazil (Paraná); sandstone outcrops. **I:** Smith & Downs (1974: 531).

[3b] **L** lamina 0.8–1 cm wide, repand-serrate with recurved **Sp** 2–3 mm long; **Inf** peduncle slender; **Fl** dense to lax; **Sep** 6 mm. — [F. Krapp]

**D. fosteriana** var. **robustior** L. B. Smith (Phytologia 19: 283, 1970). **Type:** Brazil, Paraná (*Hatschbach* 17310 [US]). — **Distr:** Brazil (Paraná); in soil.

[3b] **L** lamina 1.2 cm wide, laxly serrate but scarcely repand, the mostly antrorse **Sp** to 4 mm; **Inf** peduncle stout, 6 mm Ø; **Fl** dense; **Sep** to 9 mm. — [F. Krapp]

**D. frigida** Hooker *fil.* (Curtis's Bot. Mag. 103: t. 6294 + text, 1877). **Type:** Brazil (*Anonymus ex Hort. Linden* s.n. [K, LG [status?]]). — **Distr:** Brazil (Paraná); on rocks. **I:** Smith & Downs (1974: 519).

**Incl.** *Dyckia regalis* Linden & Morren *ex Baker* (1889) (*nom. inval.*, Art. 34.1a).

[1] **Ros** robust, acaulescent; **L** ± 100 × 3.5 cm, sheath reniform, 9 cm wide, dark castaneous, **L** lamina narrowly triangular, with pungent tip,

pale or glaucescent, densely appressed-lepidote abaxially, **Sp** 2–5 mm; **Inf** ± 1 m, amply paniculate; peduncle ascending, stout, lepidote when young; peduncular **Bra** sparse, acute from a broadly ovate base, exceeding the internodes or the upper shorter, minutely serrulate; fertile **Inf** part many-flowered, subferruginous-tomentellous, **Br** spreading, subdense towards the apex, to 30 cm; primary **Bra** like the upper peduncular bracts, usually shorter than the sterile branch bases; floral **Bra** broadly ovate, abruptly acute, shorter than the flowers, the lower serrulate; **Fl** spreading-ascending, 11–18 mm, narrowly funnel-shaped; **Ped** to 3 mm; **Sep** ovate, 5–8 mm, acute, carinate, fimbriate; **Pet** subovate, rounded, undulate, strongly carinate, spreading-recurved, yellow or pale yellow; **St** much shorter than the petals but well visible in the throat; **Fil** free above the common tube; **Anth** broadly truncate at the base, attenuate, strongly recurved; **Ov** narrowly ovoid; **Sty** very short.

**D. glabrifolia** Leme & O. B. C. Ribeiro (Phytotaxa 67: 18–20, ill., 2012). **Type:** Brazil, Minas Gerais (*Leme & al.* 7273 [RB, HB]). — **Distr:** Brazil (Minas Gerais); on rocky quartzite outcrops, Campo Rupestre vegetation.

[2] **Ros** solitary or in small groups, 17- to 25-leaved; **L** 25–42 × 2–4 cm, distinctly succulent mainly towards the base, sheath subreniform, ± 3.5 × 7.5 cm, whitish towards the base, green to reddish at the apex, lustrous, glabrous, **L** lamina narrowly triangular, attenuate, flat, suberect-arcuate, acuminate-caudate, with pungent tip, green to reddish, lustrous and veined adaxially, opaque abaxially, glabrous on both faces except adaxially at the base, margins laxly spinose, **Sp** straight to slightly antrorse, narrowly triangular, 1–2 mm, tip castaneous, 7–17 mm apart; **Inf** 90–150 cm, erect, usually simple or sometimes with a short branch near the base; peduncle 36–81 cm, greenish, sparsely white-sublanate, soon glabrous; peduncular **Bra** subfoliaceous (lowest), erect, narrowly ovate-triangular, acuminate, 15–30 × 6–10 mm, from equalling to distinctly shorter than the internodes, green or reddish, stramineous at anthesis, subdensely white-sublanate basally, glabrous apically, veined,

densely and minutely denticulate; fertile **Inf** part  $\pm 50$ - to 110-flowered, 33–77 cm, rachis straight, greenish to pale orange, subdensely to densely pale-lanate; floral **Bra** spreading to suberect, narrowly subovate-triangular (lowest), acuminate-caudate,  $10\text{--}25 \times 4\text{--}8$  mm, stramineous towards the apex at anthesis, pale-lanate, veined, denticulate to subentire; **Fl** spreading at anthesis, erect afterwards, 16–19 mm, broadly tubular with narrowed throat, unscented; **Ped** 2–4 mm, orange, densely white-sublanate; **Sep** ovate to broadly ovate,  $6\text{--}8 \times 6$  mm, convex, apex subacute and apiculate, ecarinate, orange, subdensely white-lanate, fimbriate; **Pet** broadly obovate-spatulate,  $12\text{--}13 \times 10\text{--}11$  mm, apex obtuse to subacute and inconspicuously apiculate, ecarinate, orange, glabrous, entire or sometimes irregularly crenulate near the apex; **St** included; **Fil** 9–10 mm, 3–4 mm connate above the 1 mm high common tube (according to the protologue, completely connate according to Fig. 3 in Pinangé & al. (2017)), yellowish towards the apex; **Anth** narrowly subtriangular,  $\pm 4$  mm and straight before anthesis, after anthesis distinctly smaller and strongly recurved, base bilobed, acute; **Ov** narrowly suboblong,  $\pm 6.5$  mm, pale yellow; **Sty**  $\pm 1$  mm, **Sti**  $\pm 1.5$  mm, yellow, margins minutely crenulate-lacerate; **Fr** broadly ovoid, beaked,  $\pm 15 \times 11$  mm, dark castaneous, lustrous; **Se** flat, asymmetrical, subcuneate,  $3\text{--}4 \times 2\text{--}2.5$  mm.

Closely related to *D. trichostachya*, and also similar to *D. weddelliana*.

**D. glandulosa** L. B. Smith & Reitz (Phytologia 14: 484, t. 1, figs. 20–24, 1967). **Type:** Brazil, Minas Gerais (*Magalhães* 18959 [HB, NY, US [photo]]). — **Distr:** Brazil (Minas Gerais: Diamantina Plateau); among rocks in Campo Rupestre vegetation, 1400–1800 m. **I:** Smith & Downs (1974: 565).

[3a] **Ros** not described; **L** to  $23 \times 2.3$  cm, sheath suborbicular, 2 cm, **L** lamina narrowly triangular, attenuate to an abruptly acute pungent apex, smooth and glabrous adaxially, appressedly cinereous-lepidote abaxially, laxly serrate, **Sp** antrorsely uncinata, 2 mm; **Inf** 70 cm, simple; peduncle laxly glandular-lepidote with yellow trichomes; peduncular **Bra** triangular to linear-

lamine (lowest), small, shorter than the internodes (uppermost), peltate-lepidote (lower) to vestite with glandular trichomes alone, entire; fertile **Inf** part laxly many-flowered, to 27 cm, all parts incl. pedicels and sepals laxly glandular-tomentose; floral **Bra** triangular-ovate, acuminate, the lowest exceeding the sepals, entire; **Fl** spreading; **Ped** 5 mm, subcylindrical; **Sep** ovate, 7 mm, obtuse, cucullate, ecarinate, rugose when dry as if initially fleshy; **Pet** lamina rhombic, 12 mm, obtuse, carinate, orange; **St** included; **Fil** free above the common tube; **Sty** 1 mm. — [F. Krapp]

**D. goehringii** E. Gross & Rauh (Trop. subtrop. Pfl.-welt 79: 12–14, ill., 1991). **Type:** Brazil, Goiás (*Esteves Pereira* s.n. in *Rauh* 67622 [HB, HEID]). — **Distr:** Brazil (Minas Gerais); rocky fields, on rocks or quartz sand. **I:** Braun & Esteves Pereira (2006b). — Fig. 6.

[3b] **Ros** many-leaved,  $\pm 50$  cm  $\varnothing$ ,  $\pm 30$  cm high, with a short stem; **L** to  $23 \times 2$  cm, reflexed, succulent, sheath broadly ovate, appressed to the stem,  $3 \times 3.5$  cm, whitish adaxially, castaneous and lustrous abaxially, glabrous, **L** lamina triangular, with pungent tip, both faces appressedly white-lepidote, adaxially with conspicuous imprint from neighbouring leaves, abaxially veined, trichomes arranged in distinct rows, margins spinose, **Sp** strong, antroretorse, white-lepidote,  $\pm 10$  mm apart; **Inf**  $\pm 80$  cm, usually simple; peduncle  $\pm 50$  cm, green, glabrous at the base, upper part white-lepidote; peduncular **Bra** broadly lanceolate, acuminate, 10 mm and much shorter than the internodes (upper), the lowest longer than the internodes, sparsely lepidote, veined, indistinctly serrulate; fertile **Inf** part  $\pm 25$ -flowered, lax, 35 cm, rachis green, densely white-lanate, terete; floral **Bra** broadly ovate, acuminate, much shorter than the sepals,  $\pm 5 \times 6$  mm, densely white-lanate, indistinctly serrulate; **Fl** spreading, 15 mm, subsessile; **Sep** oblong-ovate, 7 mm, obtuse, ecarinate, slightly succulent, greenish-orange-red, white-floccose, margins hyaline, indistinctly serrulate; **Pet** erect, rhombic,  $10 \times 10$  mm, obtuse, ecarinate, forming a narrow tube, orange-red, margins indistinctly serrulate; **St** slightly exerted; **Fil** short-connate above the common tube



**Fig. 6** *Dyckia goehringii* (Esteves Pereira s.n. in Rauh 67622: Brazil; Goiás, near Portelândia; type collection). (Copyright: U. Eggli)



(or completely free according to Fig. 3 in Pinangé & al. (2017)), basally broadly complanate, attenuate; **Anth** golden-yellow, sagittate; **Sty** very short, **Sti** papillate.

Related to *D. crassifolia* and *D. leptostachya*. — [F. Krapp]

**D. goiana** L. B. Smith (Phytologia 14: 479, t. 1, figs. 1–5, 1967). **Type:** Brazil, Goiás (Irwin & al. 15163 [US, NY]). — **Distr:** Brazil (Goiás); Cerrado vegetation, 800 m. **I:** Smith & Downs (1974: 528); Esteves Pereira & Gouda (2017: 181).

[1] **Ros** 1.5–1.8 m Ø; **L** 80–100 cm long, adaxially lepidote, margins serrate but apical  $\frac{1}{3}$  entire; **Inf** to 2.5 m, laxly compound with up to 8 suberect branches; peduncle stout, soon glabrous; peduncular **Bra** presumably foliaceous (lower) to ovate with a long narrowly triangular apex (upper), exceeding the internodes, serrulate; fertile **Inf** part 100 cm, initially finely cinereous-lepidote, sublax; **Br** slender, slightly flexuous, to 50 cm; primary **Bra** like the upper peduncular bracts, to 70 mm; floral **Bra** broadly ovate, long-acuminate (lower) to apiculate (upper), exceeding the flowers (lower) or shorter than the sepals (upper), serrulate; **Fl** spreading and slightly descending; **Ped** to 4 mm in fruit, stout; **Sep** broadly deltoid-ovate, to 6 mm, ecarinate,

persistently brown-black-lepidote; **Pet** spreading, elliptic, 10–12 mm, rounded, carinate, reddish-orange; **St** ± equalling the petals; **Fil** shortly connate above the common tube; **Sty** 1 mm.

Similar to *D. elata* and compared with *D. edwardii* in the protologue of the latter.

**D. gouveiana** Leme & O. B. C. Ribeiro (Phytotaxa 67: 21–23, ills., 2012). **Type:** Brazil, Minas Gerais (Leme & al. 8485 [RB]). — **Distr:** Brazil (Minas Gerais: Diamantina Plateau); rock outcrops in Campo Rupestre vegetation, in shallow humus on rocks; only known from the type locality.

[3b] **Ros** dense, 12- to 18-leaved; **L** 12–18 × 2–2.6 cm, strongly coriaceous, sheath inconspicuous, **L** lamina narrowly triangular, strongly canaliculate, suberect to nearly erect and unilaterally curved, acuminate and spine-tipped, light green, obscurely white-lepidote on both faces, veined mainly adaxially, subdensely to densely spinose, **Sp** narrowly triangular, straight to prevailingly antrorse-uncinate, 1–2.5 mm, with pale castaneous tip, 2–7 mm apart; **Inf** 35–60 cm, simple, erect; peduncle 18–30 cm, dark reddish-green, sparsely to subdensely white-lepidote, glabrescent; peduncular **Bra** base suborbicular to subreniform and slightly gibbose, lamina long narrowly triangular and acuminate-spinescent,



ecarinate, to 18–45 × 3–6 mm, longer (lowest) to shorter (uppermost) than the internodes, stramineous towards the apex, veined, subdensely white-lepidote, densely spinulose; fertile **Inf** part 8- to 26-flowered, lax, 13–24 cm, straight, dark reddish, (sub-) densely non-obscuringly white-sublanate; floral **Bra** ovate-triangular, acuminate-caudate, spreading at anthesis, ecarinate with raised midvein, the upper ones convex at the base, 13–19 × 7–10 mm, soon becoming stramineous towards the apex, (sub-) densely white-lepidote, finely veined, densely spinulose to inconspicuously denticulate; **Fl** spreading, 16–17 mm, subtubular, unscented; **Ped** 3–4 mm, stout, red, densely white-lanate; **Sep** broadly ovate, 7–8 × 5–6 mm, acute and apiculate, ecarinate, convex, reddish-orange, densely white-lanate, margins inconspicuously denticulate near the apex; **Pet** broadly spatulate, 11–12 × 9 mm, apex broadly acute, ecarinate, entire, orange, glabrous; **St** included; **Fil** 1 mm connate above the 3 mm high common tube, ±8 mm, pale orange towards the apex; **Anth** narrowly subtriangular, 3.5–4 mm, strongly recurved at anthesis; **Ov** narrowly suboblong, ±5 mm, pale yellow; **Sty** ±2.5 mm; **Sti** ±1.5 mm, orange, margins minutely crenulate.

Compared with *D. mezii* in the protologue (as *D. argentea*). — [F. Krapp]

**D. gracilis** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 516, 1896). **Type:** Bolivia, Santa Cruz (*d'Orbigny* 1006 [P, F [photo], G, GH [photo]]). — **Distr:** Brazil (Mato Grosso do Sul), Bolivia (Santa Cruz), Argentina (Chaco); seasonally deciduous lowland forests and savannas, dry rocky soil, 230–500 m. **I:** Smith & Downs (1974: 576); Vásquez & Ibsch (2012: 127).

[3b] **Ros** not described; **L** to 30 × 2–2.5 cm, suberect, **L** lamina narrowly triangular, quite green adaxially, closely appressedly pale cinereous-lepidote abaxially, margins serrate, **Sp** 4 mm; **Inf** 50 cm, simple; peduncle very slender, glabrous; peduncular **Bra** remote, very broadly ovate with a short acuminate apex, entire; fertile **Inf** part lax, few-flowered, minutely furfuraceous; floral **Bra** reflexed, suborbicular-ovate, apiculate,

±4 mm, much shorter than the sepals; **Fl** suberect, slender, subsessile; **Sep** very broadly elliptic, 7–9 mm, emarginate, nearly glabrous; **Pet** erect, obovate, 14–18 mm, rounded, scarcely if at all carinate, bright yellow; **St** equalling or slightly exceeding the petals; **Fil** connate above the common tube; **Anth** linear, acute, strongly recurved; **Sty** 2–3 × shorter than the ovary.

Lost for some 180 years before found again in Bolivia (Vásquez & Ibsch 2012). The recently described *D. barthlotii* is similar (see there for differences). Paggi & al. (2015) record the taxon also from the Brazilian state Mato Grosso do Sul.

**D. grandidentata** P. J. Braun & Esteves (Cact. Succ. J. (US) 80(6): 323, ill. (pp. 322–323), 2008). **Type:** Brazil, Mato Grosso do Sul (*Esteves Pereira & Braun* 659 [UFG, HAL]). — **Distr:** Brazil (Mato Grosso do Sul); on barren reddish-black rocks among shrubs, trees, orchids and cacti.

[2] **Ros** to 37 cm Ø but usually much smaller, stem ±6 × 5–6 cm, forming a small clump; **L** 23–29, to 23 × 3.1 cm, 5 mm thick, sheath to 4 cm wide, **L** lamina recurved, spreading, slightly coriaceous, succulent, glabrous, narrowly triangular to lanceolate, canaliculate, apex a hard brownish spine to 7 mm long, veined on both faces, margins with an inconspicuous pale yellow stripe, serrate, **Sp** pungent, uncinata, predominantly retrorse, 7–11 mm, narrowly triangular, shiny, light green to light yellow, with a brown-reddish tip, 14–23 mm apart towards the leaf tip, basally ± connected; **Inf** to 80 cm, usually simple or rarely with 1–3 branches; peduncle erect or slightly sinuous, ±40 cm, base reddish-green, red distally, shiny green to brownish-green elsewhere, glabrous or partly creamy-lepidote; peduncular **Bra** narrowly triangular to lanceolate, pungent, 58 mm (lowest) to 6 mm (uppermost), green to brownish, finely serrate; fertile **Inf** part erect, to 39 cm, rachis dark rose, distally rose to orange and red; floral **Bra** narrowly triangular to lanceolate, to 4.7 mm, rose, drying parchment-like; **Fl** ±17 × 8 mm, orange to yellowish, subsessile; **Sep** slightly triangular, 7.5 × 6.2 mm, succulent, abaxially carinate, reddish, margins pale; **Pet** 12 × 5–7 mm, orange; **St** exerted; **Fil**

apically free above the common tube, to 9 mm; **Anth** 5 mm, light yellow, strongly curved outwards, acuminate; **Ov** elongate-pyramidal,  $\pm 6 \times 2$  mm, light greenish-white; **Sty** 0.7–0.9 mm, orange; **Fr** ovoid, acute,  $\pm 13 \times 10$  mm, dark brownish, glossy; **Se** broad, drop-shaped, flattened, with a tiny acute tip towards the hilum, 3–4.5 mm  $\varnothing$  — [F. Krapp]

**D. granmogulensis** Rauh (Trop. subtrop. Pfl.-welt 65: 11–12, fig. 5, 1988). **Type:** Brazil, Minas Gerais (*Rauh* 56484 [HEID]). — **Distr:** Brazil (Minas Gerais); rocky fields, on rocks.

[3a] **Ros** acaulescent, in groups, spreading, many-leaved, 15 cm  $\varnothing$ , to 10 cm high; **L** to  $18 \times 1.5$  cm, sheath  $2.5 \times 2.5$  cm, with brownish base and green tip abaxially, glabrous, **L** lamina narrowly triangular, long-attenuate, slightly succulent, adaxially dark green and sparsely lepidote, abaxially veined and appressedly white-lepidote, **Sp** retrorse, hard, small, white; **Inf** to 60 cm, simple, erect; peduncle to 40 cm, green, glabrous, sparsely white-lanate-lepidote towards the apex; peduncular **Bra** subfoliaceous (lower) to narrowly triangular-acute (upper),  $\frac{1}{2}$  as long as the internodes, sparsely lepidote, slightly serrate; fertile **Inf** part lax, straight, to 20 cm, green, reddish towards the apex, densely lanate; floral **Bra** triangular, acuminate, small, shorter than or equalling the pedicels, inconspicuously serrate (lower); **Fl** spreading to ascending,  $8\text{--}10 \times 4\text{--}5$  mm, 3 mm at the throat, in the evening with fishy scent; **Ped** to 5 mm, stout, green to reddish, pubescent; **Sep** ovate,  $5 \times 3$  mm, obtuse, ecarinate, reddish, densely lanate; **Pet** broadly spatulate,  $6 \times 7$  mm, broadened towards the tip, obtuse, ecarinate, initially erect, later with reflexed tips, brilliant orange-red; **St** included; **Fil** free above the 2 mm high common tube, narrowing apically; **Anth** centripetally bent; **Sty** 2 mm, yellow.

Compared with *D. oligantha* (here treated as synonym of *D. saxatilis*) in the protologue. — [F. Krapp]

**D. hatschbachii** L. B. Smith (Phytologia 14: 480, t. 1, figs. 9–12, 1967). **Type:** Brazil, Paraná (*Hatschbach* 2725 [US]). — **Distr:** Brazil

(Paraná); low woods in Restinga vegetation. **I:** Smith & Downs (1974: 535).

[3a] Only known from fragments; **L** to  $85 \times 4.5$  cm, lamina linear-triangular, with pungent tip, initially or soon glabrous adaxially, appressedly white-lepidote abaxially, laxly serrate, **Sp** antrorsely uncinately, dark, 7 mm; **Inf** to 1.5 m, simple; peduncle slender, ferruginous-tomentose; peduncular **Bra** imbricate, linear-triangular from an ovate base, serrulate; fertile **Inf** part sublax, many-flowered, 40 cm, all parts incl. pedicels and sepals ferruginous-tomentulose; floral **Bra** narrowly triangular, slightly exceeding the pedicels (lower), serrulate; **Fl** spreading; **Ped** to 10 mm, straight, slender; **Sep** ovate, 8 mm, acute, carinate; **Pet** subrhombic, 14 mm, curved-spreading, colour not described; **St** included; **Fil** free above the common tube; **Sty** to 2 mm.

Insufficiently known.

**D. hebdingii** L. B. Smith (Phytologia 21: 90, t. 2, figs. 1–7, 1971). **Type:** Brazil, Rio Grande do Sul (*Croizat* 22495 [US]). — **Distr:** Brazil (Rio Grande do Sul); on rocks.

[1] **Ros** dense, spreading, many-leaved; **L**  $\pm 15 \times > 1.5$  cm, **L** lamina narrowly triangular, appressedly cinereous-lepidote on both faces, subdensely serrate, **Sp** slender, spreading; **Inf**  $> 1$  m, laxly  $3 \times$  branched; peduncle erect, slender,  $\pm 45$  cm; peduncular **Bra** very narrowly triangular, longer than the internodes, red, serrulate, divergent, wholly exposing the axis; fertile **Inf** part densely cinereous-lepidote, **Br** many-flowered, subdense to lax, to 30 cm; floral **Bra** broadly ovate, apiculate, 5 mm, much exceeded by the sepals; **Fl** suberect to spreading and sometimes slightly secund; **Ped** short; **Sep** ovate, 4.5 mm, broadly subacute; **Pet** spatulate, 7 mm, obtuse, yellow; **St** included; **Fil** free above the 1 mm high common tube; **Sty** slender, elongate; **Fr** 8 mm; **Se** with a narrow apically pointed wing.

Part of the “*Prionophyllum*” complex, and similar to *D. maritima*. — [F. Krapp]

**D. hohenbergioides** Leme & Esteves (J. Bromeliad Soc. 48(3): 124–126, ill., 1998). **Type:** Brazil, Bahia (*Esteves Pereira* E-385 [HB,

RB]). — **Distr:** Brazil (Bahia); ecology not described.

[1/2] **Ros** ±30-leaved; **L** ±60 × 4–5 cm, very rigid, succulent, sheath not described, **L** lamina uberect, very narrowly triangular, attenuate, acuminate, with pungent tip, greenish, finely veined, densely white-lepidote on both faces, laxly spinose, **Sp** triangular-uncinate, 5–9 mm, densely white-lepidote; **Inf** 1.8–2 m, laxly 2–3 × branched, erect; peduncle sulcate, 80–100 cm, green, white-sublanate, soon glabrous; peduncular **Bra** triangular, acuminate-caudate, ecarinate, erect, 50–100 × 20–30 mm, equalling to slightly exceeding (lowest) to shorter than the internodes (upper), greenish to ochre, white-lepidote to glabrescent, finely veined, laxly serrulate apically or entire; fertile **Inf** part dense, erect, ±70 cm, white-sublanate at anthesis, glabrescent; **Br** ±10, subsessile, densely strobilate-digitate, 7–10 cm, erect to suberect, axis white-lanate; primary **Bra** like the upper peduncular bracts but gradually reduced towards the apex, distinctly shorter than the branches; floral **Bra** suborbicular to triangular, acuminate, suberect, concave, ecarinate to slightly carinate near the apex, 10–14 × 13–15 mm, white-lanate at the base, glabrescent, chaffy towards the tip, minutely denticulate-crenulate to entire; **Fl** suberect at anthesis, ± ovoid-tubular, 16–17 mm, unscented; **Ped** ±2.5 mm, indistinct, stout; **Sep** suborbicular, 7–8 × 9 mm, subobtuse to slightly emarginate, very minutely mucronulate, ecarinate, orange-red, sparsely sublanate to glabrescent, entire; **Pet** subcordate, 13 × 11–12 mm, truncate-emarginate, ecarinate, erect at anthesis, orange-red, glabrous; **St** slightly exerted for  $\pm\frac{2}{3}$  of the anther length; **Fil** 10 mm, sometimes connate for ±1.5 mm above the 1.5 mm high common tube (according to the protologue, completely connate according to Fig. 3 in Pinangé & al. (2017)); **Anth** 3–4 mm, strongly recurved towards the apex, apiculate, base sagittate; **Ov** narrowly subpyramidal, ±6 mm; **Sty** indistinct, **Sti** orange, ±1.5 mm, margins irregularly scalloped.

Compared with *D. beateae* in the protologue. — [F. Krapp]

**D. horridula** Mez (Bot. Jahrb. Syst. 30 (Beiblatt 67): 5, 1901). **Type:** Brazil, Goiás

(*Glaziou* 22194 [B, F [photo], K]). — **Lit:** Leme & Miranda (2009: with ills.). **Distr:** Brazil (Goiás: Santo Antonio do Descoberto); rocky soils in Campo Rupestre vegetation, amongst herbs.

[3b] **Ros** compact, ±15 cm Ø, with a bulbous base formed by old leaf sheaths, probably solitary; **L** 35–40, dense, coriaceous, sheath 4.5–5 × 4–5 cm, **L** lamina sublinear, 10–12 × 0.8 cm, (sub-) erect, nearly flat near the base, canaliculate and obtusely carinate above and subulate towards the tip, green basally changing to reddish towards the tip, adaxially sparsely and abaxially densely white-lepidote but scales not obscuring the leaf colour, tip acuminate-caudate, pungent, margins subdensely spinose, **Sp** spreading to retrorse, 1–1.5 mm, reddish-brown, 2–3 mm apart; **Inf** 15–25 cm, simple, erect; peduncle 9–17 cm, subdensely white-furfuraceous to glabrous; peduncular **Bra** 10–20 × 5 mm, subfoliaceous (lowest) to ovate-subtriangular (upper), erect, stramineous, sparsely white-lepidote; fertile **Inf** part 3–4 cm, 5- to 7-flowered, subdensely to inconspicuously white-furfuraceous (incl. pedicel and sepals); floral **Bra** ovate, ±7 × 3 mm, acuminate, veined, stramineous, subspreading to reflexed; **Fl** 12–14 mm long and Ø, somewhat campanulate, strongly sweet-fragrant; **Ped** inconspicuous, ±2 × 3.5–4 mm Ø; **Sep** broadly ovate to suborbicular, ±5 × 4 mm, ecarinate, yellow with green tip to pale orange; **Pet** broadly obovate-spatulate from narrow base, ±10 × 6 mm, upper part spreading to spreading-ascending, yellow; **St** shorter than the petals but distinctly exposed at anthesis, connivent; **Fil** yellow, connate over the whole length and forming a tube ±8 mm long **Anth** narrowly subtriangular, ±2 mm, dark purplish-brown, basally connate; **Ov** ±2.5 × 1 mm, yellowish-white; **Sty** ±1 mm, yellowish; **Sti** conduplicate-spiral, yellow; **Fr** and **Se** unknown.

A rarely collected species, easily overlooked due to its small size. — [F. Krapp]

**D. ibicuiensis** Strehl (Bromélia 4(4): 14–16, ills., 1999). **Type:** Brazil, Rio Grande do Sul (*Strehl* 1098 [HAS 31720]). — **Distr:** Brazil (C Rio Grande do Sul); rocky outcrops, among grasses and herbs.

[2/3b] **Ros**  $\pm 20$ -leaved,  $\pm 60$  cm  $\varnothing$ ; **L**  $\pm 40 \times \pm 2$  cm, sheath not described, **L** lamina narrowly triangular, light green, flexible, slightly contorted, the inner ones erect, the outer spreading, glabrous adaxially, striate-lepidote abaxially, margins subentire with widely spaced minute **Sp** only; **Inf**  $\pm 2$  m, simple or sometimes branched, erect; peduncle  $\pm 70$  (30–140) cm, yellowish-green, glabrous; peduncular **Bra** long-lanceolate, acute,  $\pm 150 \times \pm 12$  mm and longer than the internodes (lowest), the others much smaller, lepidote at the base, margins membranous, sparsely irregularly spinose, soon drying; fertile **Inf** part densely to sparsely flowered, robust,  $\pm 55$  (40–80) cm, slightly lepidote to glabrous, yellowish-green; floral **Bra** narrow, slightly carinate basally, ending in a long acute pungent tip,  $\pm 40$  mm (lowest) or shorter (uppermost), lemon-yellow, finely serrate; **Fl** spreading, tubular with spreading limb, 20–24 mm; **Ped** 6–7 mm; **Sep** narrow, ovate, 10–15 mm, apex rounded, ending in a short spine, slightly carinate, yellow; **Pet** free, tongue-shaped, 15–20 mm, distally spreading, greenish-yellow; **St** included; **Fil**  $\frac{1}{3}$  of their length free above the common tube; **Fr** 13–15  $\times$  10 mm, dark brown at the apex, otherwise almost black, shiny; **Se** base acute, apex rounded, with a lateral wing,  $\pm 4$  mm wide, brown.

Similar to *D. dusenii*.

**D. ibiramensis** Reitz (Sellowia 14: 104, fig. 4, 1962). **Type:** Brazil, Santa Catarina (Reitz & Klein 2635 [HBR, US]). — **Lit:** Hmeljevski & al. (2011: genetics, conservation). **Distr:** Brazil (C-E Santa Catarina: Ibirama); ledges along streams, and rock islands, seasonally inundated; only known from the region of the type locality. **I:** Smith & Downs (1974: 552); Reitz (1983: t. 48).

[1/2] **Ros** solitary or forming small groups with age, acaulescent; **L** 30–40  $\times$  2.2 cm, rigid, sheath not described, **L** lamina narrowly triangular, glabrous above, cinereous-lepidote abaxially, sinuate-serrate, **Sp** 4 mm; **Inf** 1 m, paniculate; peduncle glabrous; peduncular **Bra** erect, foliaceous (lowest) to 15 mm (upper), serrate; fertile **Inf** part few- to 6-branched, subglabrous or sparsely lanate distally, **Br** ascending, laxly flowered; primary **Bra** like the upper peduncular

bracts, much shorter than the sterile branch bases; floral **Bra** triangular, recurved, pungent, shorter than the sepals, serrate; **Fl** suberect to reflexed; **Ped** 3 (–5) mm; **Sep** broadly elliptic, 7–9  $\times$  4 mm, rounded, entire, coriaceous, glabrous; **Pet** broadly ovate, 14  $\times$  8 mm, ecarinate with undulate margins, deep orange; **St** included; **Fil** free above the short common tube; **Sty** 2 mm.

Hmeljevski & al. (2011) studied the genetic diversity and mating system of this rare endemic, which is confined to a 4 km large rocky outcrop along the Rio Itajaí, and which is classified as critically endangered. The flowers are pollinated by the carpenter bee *Xylocopa brasiliatorum* as well as by the hummingbird *Thalurania glaucopsis*.

**D. incana** O. B. C. Ribeiro & Leme (J. Bromeliad Soc. 65(1): 23–26, ill. (incl. p. 18), 2015). **Type:** Brazil, Minas Gerais (*Ribeiro* 268 [BHCB, HB]). — **Distr:** Brazil (Minas Gerais: Nova Lima); iron-rich rock outcrops in Campo Rupestre vegetation, 1310 m; known only from the region of the type population.

[3a] **Ros**  $\pm 12$  cm  $\varnothing$ , sometimes asymmetrical, offsetting and forming dense colonies; **L** 8–10, dense and sometimes secund, subspreading to suberect, sheath 1.5–2  $\times$  3–4 cm, adaxially whitish, adaxially castaneous, glabrous towards the base, **L** lamina narrowly triangular, very succulent and rigid, 4.5–6  $\times$  1–1.4 cm, densely and coarsely cinereous-tomentose on both faces, tip a pungent spine, margins laxly spinose, **Sp** narrowly triangular, straight to slightly retrorse, 0.5–1 mm, 5–8 mm apart; **Inf** 25–55 cm, erect, simple; peduncle 25–35 cm, sparsely white-lepidote, pale orange to brownish-red; peduncular **Bra** 5–10  $\times$  5 mm, with suborbicular base and a long lanceolate-caudate lamina, erect, stramineous, veined and with raised midvein; fertile **Inf** part 6–10 cm, subdensely 11- to 16-flowered, rachis reddish, glabrous, distally slightly flexuose; floral **Bra** broadly ovate to triangular, acuminate to acute, 4.5–5  $\times$  4.5–5 mm, subspreading to suberect, finely veined, stramineous, slightly crenulate; **Fl** 12–13 mm, porrect-spreading,  $\pm$  secund, tubular, unscented; **Ped** 3.5–5 mm, stout, yellow-orange, glabrous, curved; **Sep** broadly ovate to

suborbicular, 4–5.5 × 3.5–4 mm, orange to reddish, convex, obtuse and apiculate, ecarinate, glabrous except the margins with recurved fimbriate trichomes; **Pet** broadly obcordate with narrowed base, 7.5 × 6.5–7 mm, orange-yellow, emarginate, ecarinate, (nearly) erect, basally connate for ±1.5 mm; **St** included and much shorter than the petals; **Fil** free above the common tube; **Anth** oblong-ovate, (almost) straight, base bilobed; **Ov** suboblong-ovoid, ±2.5 × 1.5 mm, yellow; **Sty** ±1 mm, distinct, yellow; **Sti** conduplicate-spiral, yellow; **Fr** and **Se** unknown.

Another member of the *D. saxatilis* complex, and compared with *D. brachyphylla*, *D. macedoi* and *D. oligantha* (here treated as synonym of *D. saxatilis*) in the protologue. — [U. Eggli]

**D. inflexifolia** Guarçoni & M. Sartori (Ann. Bot. Fenn. 49: 407–410, ills., 2012). **Type:** Brazil, Minas Gerais (*Guarçoni & Sartori* 1474 [VIC, R]). — **Lit:** Büneker & al. (2016: with ills.). **Distr:** Brazil (C Minas Gerais: Serro); Campo Rupestre vegetation on iron-rich igneous rocks (“pedra canga”) and rocky soil; only known from the small population at the type locality.

[2/3a] **Ros** solitary, dense, ±40-leaved, ±70 cm Ø, ±40 cm high; **L** 30–35 × 2.4–3 cm, outer reflexed, youngest inflexed, strongly succulent, sheath elliptic, ±3–3.3 × 5.9–6.3 cm, white, yellowish-cream at the apex adaxially, densely white-lepidote at the apex abaxially, dentate at the apex, **L** lamina narrowly triangular, indistinctly canaliculate, acute, with pungent tip, green, adaxially completely glabrous, abaxially densely white-lepidote (basally) to pubescent, margins rather densely spinose, **Sp** irregularly curved, 2.4–3.5 mm, amber with a brown apex, 7–17 mm apart; **Inf** 0.95–1.45 m, erect, simple or with up to 6 branches; peduncle erect, 25–67 cm, red, densely rusty-tomentose; peduncular **Br** linear-triangular to triangular with suborbicular base, erect and acuminate and pungent (upper), carinate, succulent (lowest), 36–65 × 3–6 mm (lowest) to 14–20 × 6–8 mm (upper), margins vinaceous adaxially (lowest), stramineous (upper), margins (lowest) or completely (upper) densely rusty-lepidote abaxially, fimbriate basally, entire apically; main axis of the fertile

**Inf** part to 45-flowered, 24–56 cm, branches 8- to 10-flowered, subdense, erect, rachis red, densely rusty-tomentose, basal-most branches with delayed development, suberect, curved or not, slightly flexuose, 4.5–21 cm; primary **Bra** similar to the upper peduncular bracts but slightly smaller, 13–15 × 5–6 mm; floral **Bra** carinate, triangular, convex, acuminate, pungent, 11–18 × 5–8 mm, stramineous, densely rusty-tomentose abaxially, entire to inconspicuously fimbriate; **Fl** 18–20 mm, ascending to spreading; **Ped** 5 mm, robust, red; **Sep** ovate to broadly triangular, 7.2–11 × 6.3–8.7 mm, obtuse, convex, strongly succulent, red to orange, densely rusty-tomentose abaxially, fimbriate; **Pet** rhomboid to elliptic, 11–14 × 8–11 mm, obtuse to retuse, strongly succulent, undulate after anthesis, orange, scarcely tomentose, margins in the upper ½ fimbriate; **St** included; **Fil** free above the 1.3–2.9 mm high common tube, 7.4–8.8 mm, yellowish-orange; **Anth** lanceolate to elliptic, yellow, 3–3.4 mm, base sagittate, apex obtusely apiculate; **Ov** pyramidal, 4.9–5.2 mm, yellow to greenish-yellow; **Sty** 0.7–0.8 mm, orange to brownish-orange towards the apex, **Sti** orange, 0.6–0.7 mm; **Fr** ovoid, acute, 14 × 10 mm, dark brown.

Part of the *D. sordida* complex together with *D. nobilis* and *D. ursina* (Büneker & al. 2016).

**D. insignis** Hassler (Annuaire Conserv. Jard. Bot. Genève 20: 316, 1919). **Type:** Paraguay, Concepción (*Fiebrig* 4615 [G, F [photo]]). — **Distr:** NE Paraguay (Concepción); dry open rocky ground. **I:** Smith & Downs (1974: 515).

≡ *Dyckia grandiflora* Mez (1919) (*nom. illeg.*, Art. 52.1); **incl.** *Dyckia insignis* [?] *flaviflora* Hassler (1919); **incl.** *Dyckia insignis* var. *macrantha* Hassler (1919); **incl.** *Dyckia insignis* var. *obtusiflora* Hassler (1919).

[3a] **Ros** shortly caulescent, stem 6–8 cm; **L** 20–35 × 1.5 cm, sheaths forming a bulb, broad, brown and lustrous abaxially, glabrous, **L** lamina linear-triangular, filiform-attenuate, appressedly white-lepidote, laxly serrate, **Sp** acicular, 3 mm; **Inf** 30–60 cm, simple; peduncle slender, 25–50 cm, striate, glabrous; peduncular **Bra** long-acuminate from a triangular-ovate base, the



lower 6–7 cm, exceeding the internodes, the upper 2 cm, shorter than the internodes, serrate like the leaves; fertile **Inf** part laxly 3- to 7-flowered, all parts including the flowers  $\pm$  lepidote; floral **Bra** like the upper peduncular bracts (lower) to triangular-ovate and filiform-attenuate and shorter (upper), entire; **Fl** erect to spreading; **Ped** 7–11 mm; **Sep** oblong-ovate, 10–12 mm, obtuse, finely fimbriate-serrulate; **Pet** erect, elliptic-oblong, 22–28 mm, subacute or obtuse, red to yellowish (brownish-red in the protologue of *D. grandiflora*); **St** exerted 10 mm; **Fil** free above the 1 mm high common tube; **Anth** linear, subsagittate at the base, strongly recurved; **Ov** conical, 10 mm; **Sty** 25 mm; **Fr** stoutly ovoid, long-beaked, 20  $\times$  14 mm; **Se** with a dorsal falciform hyaline wing, 4 mm.

**D. irmgardiae** L. B. Smith (Phytologia 15: 150, t. 7, figs. 8 and 9, 1966). **Type:** Brazil, Rio Grande do Sul (*Smith & al.* s.n. [US]). — **Distr:** Brazil (NE Rio Grande do Sul); ecology not recorded. **I:** Smith & Downs (1974: 535).

[3a] **Ros** spreading, very many-leaved, with a short and stout rhizome; **L** to 56  $\times$  1.8 cm, sub-rigid, sheath not described, **L** lamina very narrowly triangular, soon glabrous adaxially, closely appressedly pale-lepidote abaxially, laxly serrate, **Sp** antrorsely curved, black, 2 mm; **Inf** to 1 m, simple, erect; peduncle densely ferruginous-lanate; peduncular **Bra** densely imbricate, narrowly triangular from a broadly ovate base, ferruginous-lanate, serrulate; fertile **Inf** part densely many-flowered,  $\pm$ 30 cm, densely ferruginous-lanate; floral **Bra** like the upper peduncular bracts, mostly exceeding the flowers, serrulate; **Ped** 5 mm, stout, compressed; **Sep** ovate, 10 mm, acuminate, the posterior ones alate-carinate; **Pet** lamina subrhombic, 15 mm, colour not described; **St** included; **Fil** free above the common tube; **Sty**  $\pm$  none.

Similar to *D. reitzii*. — [F. Krapp]

**D. irwinii** L. B. Smith (Phytologia 14: 483, t. 1, figs. 16–19, 1967). **Type:** Brazil, Mato Grosso (*Irwin & al.* 16923 [US, NY]). — **Distr:** Brazil (E Mato Grosso); open Cerrado scrub and border of fields. **I:** Smith & Downs (1974: 552).

[1] **Ros** not described; **L** 60–70  $\times$  2–2.5 cm, sheaths suborbicular, 4 cm, castaneous with pale margins, **L** lamina linear-triangular, with pungent tip, appressedly whitish-lepidote on both faces, glabrescent adaxially, margins laxly serrate, **Sp** 2 mm, brown; **Inf** to 2.25 m, laxly few-branched; peduncle pale-lepidote, glabrescent; peduncular **Bra** subfoliaceous (lower) to narrowly triangular from a broadly ovate base (upper), much shorter than the internodes, serrulate; fertile **Inf** part 1 m, finely cinereous-lepidote, glabrescent; **Br** sub-erect, slightly flexuous, slender, elongate; primary **Bra** like the upper peduncular bracts, much shorter than the sterile bracteate branch bases; floral **Bra** broadly ovate, apiculate, mostly shorter than the pedicels; **Fl** laxly arranged, secund, curved-ascending; **Ped** to 5 mm, slender; **Sep** broadly ovate, 6–8 mm, obtuse; **Pet** suberect, broadly obovate, 9 mm or more, colour not described; **St** included; **Fil** connate above the common tube; **Sty**  $\pm$  none; **Fr** ovoid, acute, 15 mm; **Se** with a broad rounded subfalcate wing.

**D. joanae-marcoi** P. J. Braun & al. (Bromeliee 2008(1): 33–46, ills., 2008). **Type:** Brazil, Minas Gerais (*Esteves Pereira & Braun* 493 [UFG, HAL]). — **Distr:** Brazil (Minas Gerais: Mato Verde); rocky ground, between shrubs and grasses,  $\pm$ 900 m.

[3] **Ros** many-leaved, 20–30 cm  $\varnothing$ , 10–15 cm high, usually with some offsets; **L** 8–17  $\times$  1–2 cm, 5–15 mm thick, lamina succulent, very hard, stiff, breaking, adaxially flat to concave, apex pungent and brown, both faces grey- to sordidly white-lepidote, margins spinose-serrate, **Sp** brown, lower ones white-lepidote; **Inf** to 50 cm but usually shorter, simple, erect to ascending, stout; peduncle reddish, to 32 cm, sparsely white-lepidote; fertile **Inf** part 12–18 cm, 5- to 10-flowered, reddish, sparsely lepidote; floral **Bra** to 6 mm, very soon drying, later translucent; **Fl** erect in bud, then slightly nutant, 15–20  $\times$  10 mm; **Ped** 3–5 mm, thick; **Sep** broadly spatulate, to 13  $\times$  5–8 mm, basally connate, apical 7–10 mm free, succulent, convex, red to orange, white-lepidote, compressing the perianth, densely covered with thick nectar drops; **Pet** 16–17  $\times$  8–10 mm, reddish-orange to dark orange, upper

margins rolled back towards the end of anthesis; **St** included or shortly exerted; **Fil** 7–8 mm, free above the common tube (Pinangé & al. 2017: fig. 3); **Anth** yellow, 3 mm, strongly arching outwards; **Ov** incl. **Sty** 10 mm, light yellow; **Fr**  $\pm 13 \times 12$ –15 mm, blackish-brown; **Se** lentiform, slightly flattened in the hilum-micropylar region, 5–6 mm  $\varnothing$ , light brown.

Compared with *D. marnier-lapostollei* and *D. braunii*, and very similar. Fruit size has been taken from the table in the protologue, and appears incorrectly given in the description.

**D. jonesiana** Strehl (Bromeliaceae 42(5): 8–9, figs. 1–4, 2009). **Type:** Brazil, Rio Grande do Sul (*Silva & Strehl* 1172 [HAS]). — **Distr:** Brazil (S-C Rio Grande do Sul: Caçapava do Sul); on or between sandstone.

[3b] **Ros** with only  $\pm 7$  leaves, 15 cm  $\varnothing$ , with a bulbous base, rhizomatous and forming sparse groups; **L** 10–15  $\times$  1.2–1.5 cm, sheath ovate, 2 cm wide, white, **L** lamina succulent, triangular-acute, rather recurved, with hard and pungent tip, easily breaking, dark green to copper-coloured, densely white-lepidote esp. abaxially, very laxly serrate, **Sp** slender, 1–2 mm; **Inf** 60–80 cm, simple; peduncle erect, 40–60 cm; peduncular **Bra** triangular, amplexicaul, acute, membranous, longer (lower) or shorter (upper) than the internodes, white-lepidote; fertile **Inf** part lax, 20 cm, rachis slightly lepidote or glabrous, reddish; floral **Bra** membranous, ovate, 5–12  $\times$  11–13 mm, ecarinate or slightly carinate, orange to castaneous, white-lepidote esp. apically; **Ped** absent or short; **Sep** narrowly ovate, apex acute or roundish, ecarinate, covered by the bracts, 8–16 mm, orange-reddish, glabrous, margins membranous; **Pet** free, tongue-shaped, 20–24 mm, carinate, obtuse; **St** included; **Fil** connate above the  $\pm 7$  mm high common tube; **Anth** narrowly triangular, recurved; **Ov**  $\pm 15$  mm; **Fr** dehiscent to the base, 13–14  $\times$  10 mm, dark castaneous to nearly black, shining; **Se** acute at the base, apex rounded, with lateral wing,  $\pm 4$  mm, castaneous.

The rather small-sized plants are compared with *D. remotiflora* in the protologue. — [F. Krapp]

**D. julianae** Strehl (Vidalia 2(2): 2730, figs. 1–4, 2004). **Type:** Brazil, Rio Grande do Sul (*Strehl* 1427 [HAS]). — **Distr:** Brazil (E Rio Grande do Sul); on rock outcrops and stony ground, between grasses.

[3a] **Ros** squarrose,  $\pm 50$ - to 80-leaved, 20–30 cm  $\varnothing$ , subcaulescent, offsetting and forming dense clumps; **L** to 14–15  $\times$   $\pm 1.5$  cm, sheath 2.5  $\times$  3 cm, white with brown spots adaxially, both faces glabrous, **L** lamina narrowly acuminate, recurved, with acute pungent tip, somewhat succulent, pale green, white-lepidote on both faces, margins densely regularly spinose, **Sp** 2 mm, antrorse, 10–15 mm apart; **Inf** 80–100 cm, simple or sometimes branched; peduncle 20–30 cm; peduncular **Bra** almost verticillate near the peduncle base, leaf-like (lowest), 2–5  $\times$  1–1.5 cm, lamina long-triangular, apex long-acuminate, white-tomentose, margins serrate; fertile **Inf** part 20–40 cm, axis white-tomentose; floral **Bra** ovate-triangular, acute, 5–12  $\times$   $\pm 5$  mm, abaxially puberulous, somewhat carinate, (sub-) entire; **Ped** absent and **Fl** sessile, tubular to narrowly funnel-shaped, 16  $\times$  4 mm; **Sep** narrowly ovate, 6–8  $\times$  3–4 mm, ecarinate or slightly carinate towards the apex, basally green, distally brown, slightly white-puberulous abaxially; **Pet** ovate, 13–16  $\times$  5 mm, (sub-) erect, yellow; **St** included; **Fil** yellow, filiform, free above the common tube; **Anth** yellow, visible in the throat; **Ov**  $\pm 5 \times 3$  mm, yellow-green or brown; **Sty**  $\pm 6$  mm.

**D. kranziana** Leme (Phytotaxa 16: 12–14, ill., 2011). **Type:** Brazil, Mato Grosso (*Kranz* 122 [RB, HB]). — **Distr:** Brazil (Mato Grosso); Cerrado vegetation, on reddish soil or rocks.

[1/3b?] **Ros** dense,  $\pm 12$ -leaved, basally offsetting; **L** 29–32  $\times$  2–3.5 cm, stiff, slightly succulent, sheath inconspicuous, **L** lamina narrowly triangular, attenuate and strongly canaliculate towards the apex, suberect-arcuate, acuminate and with pungent tip, green, abaxially densely white-lepidote, adaxially subdensely white-lepidote, subdensely to laxly spinose, **Sp** narrowly triangular, straight to slightly retrorse, 2.5–5 mm, with castaneous tip, 6–15 mm apart; **Inf** to 85 cm, simple or sometimes with  $\pm 3$  late-developing branches; peduncle erect,  $\pm 65$  cm, green, sparsely

white-lanate to glabrous mainly towards the base; peduncular **Bra** acuminate, lowest sublinear and canaliculate-carinate and exceeding the internodes, upper ovate-caudate and shorter than the internodes, 18–25 × 10–12 mm, green, stramineous at anthesis (upper), inconspicuously white-lepidote to glabrous, veined, lowest laxly spinulose, upper densely finely denticulate-crenulate; fertile **Inf** part densely ±38-flowered, 10–30 cm, often deflexed-ascending, greenish to pale orange, densely white-lanate; **Br** when present spicate, 3–6 cm, densely 5- to 11-flowered, 10–12 cm; primary **Bra** narrowly lanceolate, acuminate-caudate, white-lepidote, veined; floral **Bra** ovate, acuminate, 7–15 × 6–8 mm, stramineous at anthesis, white-lepidote, veined, margins remotely denticulate-crenulate to entire; **Fl** suberect, 13–14 mm, narrowly ovate with narrow throat, unscented; **Ped** ±2 mm, pale orange, densely white-lanate; **Sep** broadly ovate, 6–7 × 6 mm, obtuse-emarginate, ecarinate, strongly convex, yellowish-orange, obscurely white-lanate, entire, sparsely fimbriate; **Pet** broadly obovate-spatulate, 10 × 8.5 mm, obtuse-emarginate, ecarinate, orange, glabrous; **St** equalling the petals to slightly exerted; **Fil** 1 mm connate above the 1 mm high common tube, 7.5–8 mm, pale orange; **Anth** narrowly subtriangular-sagittate, ±3 mm, recurved at anthesis, acuminate; **Ov** narrowly suboblong, ±4 mm; **Sty** ±1 mm, pale yellow, **Sti** ±1 mm, orange, margins scalloped; **Fr** subglobose, broadly acute and shortly beaked, 15 × 11 mm, olivaceous-castaneous, lustrous; **Se** nearly circular, obtuse, strongly flattened, 4–5 × 3.5–4.5 mm.

Similar to *D. velascana*.

**D. lagoensis** Mez (in Martius, Fl. Bras. 3(3): 483, 1894). **Type:** Brazil, Minas Gerais (*Warming* 2171 p.p. [C, F [photo]]). — **Distr:** Brazil (Minas Gerais); open Cerrado scrub and fields, on soil or on rocks. **I:** Smith & Downs (1974: 535).

[3b] **Ros** acaulescent; **L** to 40 × 1.2–1.6 cm, sheath not described, **L** lamina narrowly triangular, green, canescent or fuscous, sublepidote abaxially, laxly serrate, **Sp** slender, 1–2 mm; **Inf** to 1 m, simple; peduncle lepidote or finally glabrous; peduncular **Bra** broadly ovate with long

narrowly triangular lamina, equalling or exceeding the internodes, serrulate; fertile **Inf** part few-flowered, minutely and fugaciously lepidote; floral **Bra** suberect to spreading, suborbicular, lamina long narrowly triangular, exceeding the sepals and the lowest flowers, fimbriate-serrulate; **Fl** erect or suberect, to 12 mm; **Ped** 1–2 mm, stout; **Sep** ovate, broadly subacute or rounded, mucronulate or obtuse, 6–9 mm, slightly fimbriate; **Pet** erect, lamina broadly obovate, obtuse, slightly undulate, orange, subcarinate, slightly exceeding the sepals; **St** included; **Fil** 7 mm connate above the common tube; **Anth** narrowly triangular, recurved; **Sty** very short.

**D. leptostachya** Baker (Gard. Chron., ser. nov. 1884(2): 198, 1884). **Type:** Brazil, Paraná (*Anonymus* s.n. [K, GH [photo]]). — **Distr:** Brazil (Minas Gerais, Santa Catarina, Paraná, Mato Grosso, Rio Grande do Sul), Paraguay (Caaguazú, Itapúa), Bolivia (Chuquisaca, Santa Cruz), Argentina (Chaco, Corrientes, Entre Ríos); dry fields or open scrub (Cerrado vegetation). **I:** Smith & Downs (1974: 549); Reitz (1983: t. 51, as *D. remotiflora* var. *montevidentis*).

**Incl.** *Dyckia leptostachia* Baker (s.a.) (*nom. inval.*, Art. 61.1); **incl.** *Dyckia boliviensis* Mez (1896); **incl.** *Dyckia conspicua* Mez (1896); **incl.** *Dyckia hassleri* Mez (1903); **incl.** *Dyckia apensis* Mez (1919); **incl.** *Dyckia hassleri* fa. *gracilis* Hassler (1919); **incl.** *Dyckia hassleri* ssp. *basispina* Hassler (1919); **incl.** *Dyckia hassleri* var. *arenosa* Hassler (1919); **incl.** *Dyckia hassleri* var. *montana* Hassler (1919); **incl.** *Dyckia longifolia* Mez (1919); **incl.** *Dyckia rojasii* Mez (1919); **incl.** *Dyckia hassleri* var. *typica* Hassler (1919) (*nom. inval.*, Art. 26.1).

[2/3a] Plants very variable as to size; **Ros** ±15-leaved; **L** 40–100 × 1–3 cm, **L** lamina arching, narrowly triangular, long-attenuate, densely white-lepidote, soon glabrous adaxially, **Sp** slender, curved, 3–4.5 mm; **Inf** 50–150 cm, simple or few-branched; peduncle very slender, minutely lepidote or glabrous; peduncular **Bra** very broadly ovate, apiculate, much shorter than the internodes, entire; fertile **Inf** part 12–16 cm, rachis sparsely lepidote or glabrous; floral **Bra** spreading, very broadly ovate, abruptly contracted to an

acuminate point, 3–8 (–12) mm, much exceeded by the sepals; **Fl** suberect to spreading, 13–23 mm; **Ped** very short, stout; **Sep** broadly ovate, 6–12 mm, obtuse,  $\pm$  carinate, smooth, soon glabrous; **Pet** erect, broad, obtuse or emarginate, minutely crenulate, red-orange; **St** usually exerted; **Fil** free above the common tube; **Anth** acute, mucronate, recurved; **Sty** sometimes long or partially divided.

**D. limae** L. B. Smith (Phytologia 20: 179, t. 2, figs. 9–11, 1970). **Type:** Brazil, Pernambuco (*Lima* 61-3996 [IPA, US [photo]]). — **Distr:** Brazil (Pernambuco); in compact nearly barren sandy soil. **I:** Siqueiro Filho & Leme (2007: 315).

[1/2] **Ros** not described; **L**  $\pm 24 \times 1.5$  cm, curved, sheath 3.5 cm wide, stramineous to dark brown, densely serrulate at the apex, **L** lamina narrowly triangular, with pungent tip, appressedly pale-lepidote, laxly serrate, **Sp** slender, antroretrorely uncinata, 2 mm, brown; **Inf** 70–80 cm, depauperately compound with 1 or 2 small suberect branches, or simple; peduncle  $\pm$  straight, glabrous; peduncular **Bra** except the lowest triangular, remote, small, finely serrulate; fertile **Inf** part lax, rachis slender, flexuous, compressed, to 25 cm, all parts incl. pedicels and sepals appressedly pale-lepidote; floral **Bra** ovate, 6 mm, acuminate, slightly exceeding the pedicels (lowest), serrulate (lowest); **Fl** secund; **Ped** to 5 mm in fruit, rather stout; **Sep** ovate, 7 mm, broadly acute and apiculate, sulcate; **Pet** elliptic-rhomboid, 12 mm, obtuse, carinate, orange; **St** included; **Fil** 7 mm, connate for 2–4 mm with the petals but free above the common tube (or completely connate according to Fig. 3 of Pinangé & al. (2017)); **Sty**  $\pm 1$  mm; **Fr** subglobose, 15 mm.

Similar to *D. velascana* in general appearance.

**D. lindevaldae** Rauh (Trop. subtrop. Pfl.-welt 65: 12–17, figs. 6 and 7, 1988). **Type:** Brazil, Goiás (*Esteves Pereira* s.n. in *Rauh* 67425 [HEID]). — **Distr:** Brazil (N Goiás); terrestrial on weathered soil. **I:** Braun & al. (2008).

[3b] **Ros** many-leaved, 15–20 cm  $\varnothing$ , to 4 cm high, acaulescent or shortly caulescent, solitary or usually in groups, often dividing dichotomously;

**L** to 10  $\times$  3 cm, sheath to 1.5  $\times$  3.5 cm, greenish-white, castaneous at the base abaxially, glabrous, entire, **L** lamina narrowly triangular, acuminate, pungent, slightly succulent, strongly reflexed, both faces very densely tomentose (easily wiped away) giving a snow-white overall colour, serrate, **Sp** retrorse, to 4 mm, yellowish-brown, lanate,  $\pm 5$  mm apart; **Inf** to 30 cm, simple; peduncle slender, curved-ascending, to 15 cm, brownish-green, glabrous; peduncular **Bra** subfoliaceous (lower) or smaller (upper), oblong, triangular, acuminate, shorter than the internodes, glabrous at the broadened base, elsewhere sparsely lepidote, soon drying; fertile **Inf** part spirally  $\pm 12$ -flowered, rachis slender, flexuous, to 20 cm, reddish-brown, sparsely lepidote; floral **Bra** spoon-shaped, acute, carinate,  $\pm 7$  mm, equalling or slightly shorter than the sepals, brownish-green, initially sparsely lepidote, later glabrous, veined, slightly serrate; **Fl** erect-spreading, 10–12 mm, subsessile; **Sep** ecarinate, strongly convex, obtuse, 6–7  $\times$  4 mm, nearly glabrous, margins and tip ciliate; **Pet** broadly round to rhombic, 9–11 mm, erect, ecarinate, obtuse, pale orange-red, yellow towards the base, ciliate at the tip; **St** slightly exerted; **Fil** very shortly connate, white; **Ov** cylindrical, polygonally sulcate, 4 mm; **Sty** short, yellow, **Sti** shortly papillate; **Fr** and **Se** not described.

Similar to *D. marnier-lapostollei* var. *marnier-lapostollei*.

**D. linearifolia** Baker (Handb. Bromel., 131, 1889). **Type:** Brazil, Minas Gerais (*Saint Hilaire* 1010 [P, GH [photo]]). — **Distr:** Brazil (Minas Gerais, São Paulo); open scrub, savanna.

[3a] **Ros** not described; **L** 40–55  $\times$  1 cm, sheath suborbicular, 5 cm, dark castaneous, **L** lamina sublinear, strongly appressedly brown- or whitish-lepidote abaxially, laxly serrate towards the base, **Sp** slender, curved, 1.5 mm; **Inf** 40 cm and more, simple; peduncle very slender, glabrous; peduncular **Bra** ovate, acuminate, entire, remote; fertile **Inf** part subdense, many-flowered, completely glabrous; floral **Bra** spreading to reflexed, triangular-ovate, exceeding the pedicels but much shorter than the sepals; **Fl** spreading at anthesis, then erect; **Ped** to 7 mm, rather slender;

**Sep** broadly ovate, to 8 mm, obtuse; **Pet** lamina suberect, narrowly elliptic,  $\pm 15$  mm, obtuse, carinate, colour not described; **St** included; **Fil** free above the common tube; **Anth** linear, mucronulate, nearly straight; **Ov** not described; **Sty**  $\pm \frac{1}{3}$  as long as the ovary; **Fr** and **Se** not described. — [F. Krapp]

**D. lunaris** Leme (Selbyana 30(2): 131–133, fig. 2, 2010). **Type:** Brazil, Goiás (*Leme* 6359 [HB, RB]). — **Distr:** Brazil (Goiás); ecology not recorded.

[3b] **Ros** dense,  $\pm 30$ -leaved, with elongated basal shoots; **L** 29–40  $\times$  2.7–3.4 cm, strongly coriaceous, succulent, sheath wider than the lamina, **L** lamina narrowly triangular,  $\pm$  flat to slightly canaliculate, strongly recurved, apex long acuminate, subulate and pungent, green, sometimes yellowish-green basally and apically, adaxially glabrous, abaxially veined and inconspicuously white-lepidote, margins laxly spinose, **Sp** narrowly triangular,  $\pm$  straight to antrorsely uncinat, 6–9 mm, glabrous, greenish to reddish with yellowish tip, 10–40 mm apart; **Inf** 55–90 cm, simple, erect; peduncle 25–45 cm, green, subdensely white-lanate to glabrescent; peduncular **Bra** foliaceous to subfoliaceous, strongly recurved to suberect, upper ones long acuminate-caudate from a subtriangular-ovate base, distinctly exceeding the internodes, yellowish-green with red apex, upper ones stramineous at anthesis, densely veined, glabrous, margins laxly spinose; fertile **Inf** part 50- to 80-flowered, subdense to dense, 22–45 cm, rachis straight, (sub-) densely white-lanate; floral **Bra** long acuminate-caudate from an ovate base (lowest) to subtriangular-ovate and acuminate (upper), spreading to suberect-ascending, ecarinate, 30–55  $\times$  10–14 mm (lowest) to 12–30  $\times$  7–10 mm (upper), stramineous at anthesis, glabrous to inconspicuously white-lepidote, distinctly veined, subdensely and minutely spinulose; **Fl** spreading to suberect at anthesis, becoming erect afterwards, 19–23 mm, campanulate, unscented; **Ped** 3–7 mm, stout, orange, densely white-lanate; **Sep** ecarinate,  $\pm$  acute, adaxial ones asymmetrical-curved, subtriangular-ovate, abaxial one symmetrical, ovate, distinctly convex, 10–11  $\times$  5–6 mm, orange to

reddish, subobscurely white-lanate, entire, fimbriate; **Pet** broadly obovate, 11–13  $\times$  7 mm, apex rounded to cucullate, ecarinate, orange, abaxially subdensely white-lepidote; **St** included; **Fil** 4–5 mm connate above the 2 mm high common tube, 6–7 mm, apex pale orange; **Anth** ovate,  $\pm 3$  mm, strongly spirally recurved at anthesis, base sagittate, acute; **Ov** narrowly subpyramidal,  $\pm 5.5$  mm, yellowish; **Sty**  $\pm 2$  mm, **Sti** conduplicate-spiral,  $\pm 1.5$  mm, orange, minutely crenulate; **Fr** broadly ellipsoid-ovoid, shortly beaked, 14–15  $\times$  9–10 mm, dark castaneous, lustrous; **Se** flat, asymmetrical, subcuneate, base obtuse, 4–5  $\times$   $\pm 3$  mm.

Similar to *D. burle-marxii*. The only other species with asymmetrical sepals (and thus somewhat zygomorphic flowers) is *D. pontesii*.

**D. lutziana** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 107, t. 107, 1943). **Type:** Brazil, sine loco (*Foster* 1144-B [GH]). — **Distr:** Brazil (without recorded locality); never recollected. **I:** Smith & Downs (1974: 576).

[3b] **Ros** not described; **L** incompletely known, inner leaves to 10 cm, lamina linear, appressedly pale-lepidote on both faces, laxly serrulate; **Inf** to 80 cm, simple, very slender; peduncle glabrous; peduncular **Bra** remote, broadly ovate, acuminate, membranous, small, reddish; fertile **Inf** part lax, straight, to 9 cm, subglabrous; floral **Bra** like the peduncular bracts but apiculate, shorter than to barely exceeding the pedicels; **Fl** suberect to spreading; **Ped** 4–5 mm, slender; **Sep** elliptic, 8–9 mm, obtuse; **Pet** lamina broad, to 12 mm, orange-yellow when dry; **St** slightly exserted; **Fil** high-connate above the common tube; **Ov** not described; **Sty** slender, 2 mm.

**D. macedoi** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 2: 195, 1952). **Type:** Brazil, Minas Gerais (*Macedo* 2974 [US]). — **Distr:** Brazil (Minas Gerais); rocky fields.

[3a] **Ros** spreading, with a stout probably short stem; **L**  $\pm 6$ –8  $\times$  1.4 cm, suberect-recurved, sheath broad,  $> 3$  cm wide, **L** lamina narrowly triangular, with pungent tip, adaxially soon glabrous, abaxially appressedly cinereous-lepidote and inconspicuously veined, margins laxly



serrate, **Sp** nearly straight, 1.5 mm, dark; **Inf** 30 cm, simple; peduncle very slender, glabrous; peduncular **Bra** broadly ovate, acuminate, shorter than the internodes, 7 mm (uppermost), serrulate; fertile **Inf** part laxly 10-flowered, 4.5–5.5 cm, glabrous; floral **Bra** like the upper peduncular bracts,  $\pm$  equalling the pedicels; **Fl** spreading or reflexed; **Ped** 5 mm, slender; **Sep** oblong-elliptic, 5 mm, broadly obtuse, strongly convex; **Pet** shape not described, 7 mm, reddish drying to golden-yellow; **St** included; **Fil** free above the 0.5 mm high common tube; **Sty**  $\pm$  none.

*D. nana* is compared with this species in its protologue.

**D. machrisiana** L. B. Smith (Contr. Sci. Nat. Hist. Mus. Los Angeles County 17: 7, fig. 5, 1957). **Type:** Brazil, Goiás (*Dawson* 14153-A [R, US [photo]]). — **Distr:** Brazil (Goiás); fields and open Cerrado scrub.

[3a] **Ros** not described; **L** 25  $\times$  1.5 cm, sheath suborbicular, 3 cm wide, glabrous, **L** lamina linear-triangular, appressedly white-lepidote on both faces, margins laxly serrulate, **Sp** acicular, 1 mm; **Inf** 80 cm, simple; peduncle size not described, sparsely pale-lepidote; peduncular **Bra** broadly ovate, thin, abruptly contracted into a linear-triangular apex, all but the lowest much shorter than the internodes; fertile **Inf** part lax, slender, flexuose, sparsely pale-lepidote; floral **Bra** broadly ovate, acuminate, to 6 mm; **Fl** spreading or divergent; **Ped** 2–4 mm, stout; **Sep** ovate, 7 mm, obtuse, ecarinate, rather fleshy; **Pet** erect, elliptic, 10 mm, ecarinate, dark blackish, orange externally; **St** included; **Fil** free above the short common tube; **Ov** not described; **Sty**  $\pm$  none. — [F. Krapp]

**D. macropoda** L. B. Smith (Phytologia 14: 485, t. 1, figs. 25–28, 1967). **Type:** Brazil, Minas Gerais (*Pereira* 1622 p.p. [RB, US [photo]]). — **Distr:** Brazil (Minas Gerais: Diamantina region); rocky fields. **I:** Smith & Downs (1974: 568).

[3b] **Ros** not described; **L** 25  $\times$  1.5 cm, sheath suborbicular, 3 cm, stramineous, **L** lamina narrowly triangular, attenuate to a fine rigid point, smooth and glabrous adaxially, appressedly

whitish-lepidote abaxially (appearing ferruginous from soil deposits), laxly serrate, **Sp** retrorsely uncinata, 1.5 mm; **Inf**  $\pm$  50 cm, simple; peduncle very short, finely ferruginous-lepidote; peduncular **Bra** long-acuminate from an ovate base, much shorter than the internodes (uppermost), subentire; fertile **Inf** part laxly many-flowered, 25 cm, all parts incl. pedicels and sepals finely ferruginous-lepidote; floral **Bra** like the peduncular bracts, exceeding the sepals (lowest), entire; **Fl** spreading; **Ped** to 10 mm, slenderly cylindrical; **Sep** broadly ovate, 7 mm, rounded or apiculate, strongly convex, the posterior  $\pm$  carinate; **Pet** broadly rhomboid, 14 mm, carinate, orange; **St** included, **Fil** almost wholly connate; **Ov** not described; **Sty** very short. — [F. Krapp]

**D. maracasensis** Ule (Bot. Jahrb. Syst. 42: 197–198, 1909). **Type:** Brazil, Bahia (*Ule* 7019 [B, F [photo]]). — **Distr:** Brazil (Bahia: Maracás region); rocks. **I:** Smith & Downs (1974: 542).

[1] **Ros** dense; **L** to 20 cm, sheath suborbicular, short, **L** lamina narrowly triangular, attenuate, with pungent tip, densely lepidote abaxially, margins laxly serrate, **Sp** curved, 2 mm; **Inf** 1 m or more, racemose or paniculate, or simple; peduncle subangular, densely ferruginous-flocculose towards the apex; peduncular **Bra** erect, lanceolate-ovate with long, narrowly triangular, serrulate lamina, foliaceous and imbricate (lower) to shorter than the internodes (upper); fertile **Inf** part ferruginous-flocculose; primary **Bra** like the upper peduncular bracts, much shorter than the long compressed bases of the branches; floral **Bra** broadly ovate, apiculate, slightly exceeding the pedicels, finely serrate; **Fl** suberect or sometimes spreading and secund; **Ped** 5 mm, stout; **Sep** broadly ovate, 6 mm, obtuse; **Pet** broadly elliptic, 9 mm, obtuse, yellow; **Fil** 2 mm connate (or completely connate according to Fig. 3 of Pinangé & al. (2017)) above the common tube; **Ov** 4.5 mm; **Sty** 1.5 mm. — [F. Krapp]

**D. maritima** Baker (Handb. Bromel., 136, 1889). **Type:** Brazil, Rio Grande do Sul (*Tweedie* s.n. [K, GH [photo]]). — **Lit:** Waldemar & Irgang (2003: ecology). **Distr:** Brazil (S Santa Catarina, E Rio Grande do Sul), open rocky or turfy ground,

mostly near the coast. **I:** Smith & Downs (1974: 510); Reitz (1983: t. 47); Klein V. & Klein (2014: 76–77).

≡ *Prionophyllum maritimum* (Baker) Mez (1896); **incl.** *Dyckia tomentosa* Mez (1896).

[1] **Ros** spreading, many-leaved; **L** ±60 × to 4 cm, thick, rigid, sheath suborbicular, dark castaneous, glabrous, **L** lamina narrowly triangular, attenuate, with pungent tip, glabrous adaxially, minutely pale-lepidote abaxially, conspicuously veined, margins very laxly serrate, **Sp** broad, curved, 3–5 mm; **Inf** to 2 m and more, 3 × branched; peduncle straight, glabrous; peduncular **Bra** imbricate, foliaceous (lower) to narrowly triangular (upper), much reduced; fertile **Inf** part densely tomentose-lepidote; **Br** broadly spreading, many-flowered, subdense, to 25 cm; floral **Bra** spreading to reflexed, subulate-acuminate from a broad base, scarcely 3 mm; **Fl** perfect and unisexual, suberect to spreading; **Ped** very short; **Sep** broadly ovate, 5 mm, acute, greenish, densely brown-furfuraceous; **Pet** obtuse, 7–8 mm, yellow; **St** hardly exerted; **Fil** free above the very short common tube; **Ov** pyramidal, 3-sulcate; **Sty** longer than the ovary; **Fr** ±5 mm, ovoid, brown to almost black, dehiscing to below ½, shortly rostrate; **Se** oblong with a narrow lateral wing widened at the ends.

Belongs to the “*Prionophyllum*” complex. A naturally-occurring variegated plant was recently described as cultivar ‘Leopoldo Witeck’ (Lawn 2011). Waldemar & Irgang (2003) found a facultative association of the species with termites, and it grows esp. well on termite mounds.

**D. marnier-lapostollei** L. B. Smith (Bromeliad Soc. Bull. 16: 102, ills., 1966). **Type:** Brazil, Goiás? (*Anonymus ex cult. Marnier-Lapostolle* s.n. [US]). — **Lit:** Rauh (1985: 51–58); Braun & Esteves Pereira (2005). **Distr:** Brazil (SE Goiás).

[3a] **Ros** acaulescent, spreading, ±10-leaved, usually solitary or occasionally in small groups; **L** ±12 × ±4 cm, sheath suborbicular, 2 cm, glabrous, **L** lamina triangular, thick, strongly recurved, densely pale-lepidote on both faces and with silvery appearance, margins densely serrate, **Sp** coarse, retrorsely curved; **Inf** 50–100 cm, simple, erect; peduncle compressed, very slender,

glabrous; peduncular **Bra** broadly ovate, apiculate, small, entire, remote; fertile **Inf** part lax, few-flowered, slender, slightly flexuous, 19 cm, nearly glabrous; floral **Bra** broadly ovate, acuminate, shorter than the sepals, entire; **Fl** subsessile, spreading, 12 mm; **Sep** broadly ovate, 7 mm, rounded, cucullate, ecarinate; **Pet** subrhomboid, 12 mm, limb only slightly distinct from the claw, obtusely carinate, cucullate, orange; **St** equalling the petals; **Fil** free above the common tube; **Ov** not described; **Sty** ± none.

The description has been amended from data provided by Braun & Esteves Pereira (2005). These authors report hybrids with *D. machrisii*, with ± intermediate characters.

**D. marnier-lapostollei** var. **estevesii** Rauh (Trop. subtrop. Pfl.-welt 53: 55–56, figs. 26–28, 1985). **Type:** Brazil, Goiás (*Esteves Pereira* s.n. in *Horst* 5 [HEID]). — **Distr:** Brazil (E to SE Goiás); rocks, in Campo Rupestre vegetation. — Fig. 7.

[3a] **L** less densely lepidote, bluish-grey, partly glabrous, **Sp** to 6 mm; **Inf** to 80 cm, very slender; **Fl** scent less pronounced; **Anth** visible at anthesis.

**D. marnier-lapostollei** var. **marnier-lapostollei** — **Distr:** Brazil (E to SE Goiás); rocks, in Campo Rupestre vegetation, 1000 m and more. **I:** Rauh (1985: 51–58); Braun & Esteves Pereira (2005); Braun (2018: 72).

**Incl.** *Dyckia rauhii* hort. (s.a.) (*nom. inval.*, Art. 29.1).

[3a] **L** densely white-lepidote, silvery, **Sp** to 3 mm; **Inf** to 50 cm; **Fl** scent strong, fish-like; **Anth** included at anthesis.

**D. martinellii** B. R. Silva & Forzza (Novon 14: 168–170, ills., 2004). **Type:** Brazil, Rio de Janeiro (*Martinelli* 14413 [RB]). — **Distr:** Brazil (Rio de Janeiro: Paratimirim); granitic outcrops; narrowly endemic.

[3b] **Ros** ±60 cm Ø, with stout basal offshoots; **L** 23–38 × 2.2–2.6 cm, suberect-arcuate, sheath elliptic, 2.5–3 × 5–6 cm, castaneous abaxially, whitish adaxially, ± entire, **L** lamina lanceolate, apex attenuate, whitish abaxially, light green adaxially, spinose, **Sp** straight, patent-

**Fig. 7** *Dyckia marnier-lapostollei* var. *estesvesii*.  
(Copyright: U. Eggli)



antrorse, 3–4 mm, light green with a castaneous apex, 10–15 mm apart; **Inf** 70–100 cm, simple; peduncle erect, 55–70 cm (to 97 cm according to the protologue), green, sparsely white-lepidote; peduncular **Bra** subfoliaceous (lowest) to lanceolate-attenuate (upper), densely arranged, clasping the peduncle, erect, chartaceous, 11–12.5 × 0.9–1.2 mm (lowest), exceeding to rarely equalling the internodes (upper), stramineous, glabrous to sparsely lepidote, spinulose to inconspicuously serrulate; fertile **Inf** part 38- to 65-flowered, lax, straight, 30–43 cm, orange, sparsely white-lepidote; floral **Bra** elliptic to elliptic-attenuate, acuminate, exceeding to equalling the middle of the sepals, 4–12 × 3–6 mm, castaneous, white-lepidote, entire; **Fl** patent at anthesis, suberect afterwards; **Ped** 1–2 mm, to 4 mm in fruit, cylindrical, orange, sparsely lepidote; **Sep** ovate, 7–9 × 4–6 mm, apex rounded, orange, apex castaneous, white-lepidote; **Pet** obtrullate, 9–12 × 9 mm, apex emarginate, erect, orange, glabrous; **St** included; **Fil** ±1.5 mm connate (completely connate according to Fig. 3 of Pinangé & al. (2017)) above the 2.5 mm high common tube; **Anth** slightly sagittate at the base, attenuate and reflexed at the apex, ±3 mm; **Ov** ±7 mm; **Fr** ±15 mm; **Se** alate, ±3 mm.

Similar to *D. pseudococcinea*, and compared with *D. espiritosantensis* in the protologue of the latter.

**D. mauriziae** Esteves & Hofacker (Bromelie 2011(1): 39–42, ills., 2011). **Type:** Brazil, Goiás (*Carneiro* MBR-41 [UFG]). — **Distr:** Brazil (Goiás); steep slopes in yellow gravelly latosol.

[3b] **Ros** solitary or in small groups, with secund prostrate leaves, stem to 20 × 5 cm; **L** ±39 × 3.7 cm, inner ones straight, soon curved, coriaceous, rigid, succulent, margins narrow, sheath ±2.6 × 4.8 cm, white-yellowish, canescent-lepidote, **L** lamina flat, occasionally slightly concave, apex long-attenuate with a hard, pungent, light-brown, ±9 mm long tip, greenish-grey to pale green, both faces finely veined and with canescent scales, margins greenish-brown, serrate, **Sp** hard, pungent, antroretorse-uncinate, to ±4.8 mm, ±22 mm apart; **Inf** to 1.8 m, usually simple, in cultivation rarely paniculate, stout, erect; peduncle to 110 cm, pale greyish- or brownish-green, sparsely light-brown-lepidote; peduncular **Bra** linear to lanceolate, suberect or curved, foliaceous, long attenuate, acuminate, pungent, ±130 × 17 mm (lower) to 34 × 13 mm (uppermost), pale green to greenish-brown, canescent-lepidote, finely veined, laxly spinose, teeth

0.3–1.8 mm; fertile **Inf** part  $\pm 90$  cm, reddish-rose, densely  $\pm 20$ -flowered, conspicuously furrowed, with creamy papillae-like trichomes; floral **Bra** like the peduncular bracts but shorter, narrowly triangular,  $19 \times 8$  mm (lowest) to  $4.8 \times 3.8$  mm, pale orange, soon stramineous, with dense colourless papillae-like trichomes, finely veined, with ciliate margins; **Fl** pointing slightly side-wards, after pollination directed upwards, 21 mm, smaller towards the inflorescence tip, fragrant with slight sour scent; **Ped**  $\pm 3.7$  mm, red; **Sep** lanceolate to ovate,  $\pm 9.5 \times 6.5$  mm, succulent, carinate, bright orange-reddish, with papillae-like trichomes; **Pet** oblong,  $\pm 11.6 \times 7.2$  mm, obtuse, rigid, carinate apically, orange to orange-red, brilliant; **St** just visible in the throat; **Fil** 4–6 mm connate above the common tube, 9–11 mm, cream-coloured; **Anth** yellow,  $\pm 4.6 \times 1.3$  mm, recurved at anthesis; **Ov** narrowly subpyramidal,  $\pm 7 \times 3$  mm, whitish-yellow; **Sty**  $\pm 2.3$  mm, yellow; **Sti** fringe-like, yellow,  $\pm 1.6$  mm; **Fr** ellipsoid to ovoid, acuminate, 12–15  $\times$  9–11 mm, dark brownish, lustrous.

Similar to *D. estevesii* due to the fan-like and seemingly distichous leaf arrangement, and also compared with *D. mirandana* in the protologue.

**D. mello-barretoii** L. B. Smith (Phytologia 7: 109, t. 1, figs. 16–19, 1960). **Type:** Brazil, Minas Gerais (*Mello Barreto* 2122 [BHM, US [photo]]). — **Distr:** Brazil (Minas Gerais); sand and rocky fields. **I:** Smith & Downs (1974: 549).

[2/3a?] **Ros** not described; **L**  $> 30 \times 1.5$  cm, sheath not described, **L** lamina narrowly triangular, attenuate to an abruptly acute pungent tip, pale-lepidote between the veins, margins very laxly serrate, **Sp** slender, spreading, retrorsely curved, 4 mm; **Inf** probably  $> 1$  m, subsimple to compound; peduncle inconspicuously pale-lepidote at the nodes; peduncular **Bra** ovate, acuminate, the upper remote; fertile **Inf** part with a short 2-flowered **Br** at the base, lax, flexuous, appressedly stellately ferruginous-lepidote, rachis soon  $\pm$  glabrous; floral **Bra** reflexed, ovate and acuminate (lower) or suborbicular and apiculate (upper), 11 mm, nearly equalling (lower) to  $\frac{1}{2}$  as long (upper) as the sepals; **Fl** spreading; **Ped** 3 mm, stout; **Sep** broadly ovate,

8 mm, obtuse, erose; **Pet** lamina broadly obovate, to 13 mm, emarginate, ecarinate, colour not described; **St** included; **Fil** free above the common tube; **Anth** narrowly triangular, nearly straight, 3 mm; **Ov** not described; **Sty** simple, 2 mm.

Similar to *D. sordida*, and compared with *D. espiritosantensis* in the protologue of the latter. — [F. Krapp]

**D. mezii** Krapp (Ann. Bot. Fenn. 50(1): 73, 2013). **Type:** Brazil, Minas Gerais (*Glaziou* 17280-A [B, F [photo]]). — **Distr:** Brazil (Minas Gerais); ecology not recorded, not recently recollected.

$\equiv$  *Dyckia argentea* Mez (1894) (*nom. illeg.*, Art. 53.1).

[3a] **Ros** not described; **L** to  $30 \times 2$  cm, sheath suborbicular, large, **L** lamina narrowly triangular, abruptly acute, with pungent tip, coarsely lustrous-silvery-lepidote, laxly serrate, **Sp** coarse, uncinata, 3.5 mm; **Inf** 50–70 cm, simple; peduncle  $\pm$  furfuraceous towards the base, glabrous elsewhere; peduncular **Bra** ovate with acuminate tip, shorter than the internodes, serrulate; fertile **Inf** part subclax, many-flowered, glabrous; floral **Bra** lanceolate-triangular (lower) or ovate and acute (upper), exceeded by the sepals; **Fl** spreading at anthesis, later erect, 11 mm; **Ped** to 5 mm; **Sep** elliptic, 6 mm, obscurely apiculate; **Pet** erect, cuneiform-obovate, broadly rounded, scarcely or not at all carinate, orange; **St** included; **Fil** free above the common tube; **Anth** linear, acuminate, strongly recurved; **Sty** slightly shorter than the ovary.

See Braun & al. (2008) for a discussion of the name (as *D. argentea*) and the possible origin of the material on which it based.

**D. microcalyx** Baker (Handb. Bromel., 133, 1889). **Type:** Paraguay (*Balansa* 696 [P, GH [photo]]). — **Distr:** S Brazil, Paraguay, NE Argentina; dry rocky slopes and river banks, seasonally inundated.

[1/2] **Ros** not described; **L** 20–150  $\times$  1.5–3 cm, sheath scarcely wider than the lamina, **L** lamina narrowly triangular, pale-lepidote esp. abaxially, often glabrescent, typically subdensely



serrate but varying to entire, **Sp** 6 mm; **Inf** 40–200 cm, few-branched or rarely simple; peduncle erect, slender, glabrescent; peduncular **Bra** ovate with long acuminate pungent lamina, shorter than the internodes (at least the uppermost); fertile **Inf** part many-flowered, to 80 cm, soon glabrous, **Br** spreading, densely flowered, 6–26 cm; primary **Bra** like the peduncular bracts, small, usually shorter than the sterile branch bases; floral **Bra** broadly ovate or suborbicular, apiculate, 2 mm, much exceeded by the sepals; **Fl** 6–13 mm, subsessile; **Sep** suborbicular, 3–6 mm; **Pet** obovate, suberect, ecarinate, orange; **St** exerted or  $\pm$  equalling the petals; **Fil** free above the short common tube; **Sty**  $\pm$  equalling the ovary. — [F. Krapp]

**D. microcalyx** var. **microcalyx** — **Distr:** S Brazil (Mato Grosso, Paraná), Paraguay; dry rocky slopes. **I:** Rauh & Gross (1991: 9).

**Incl.** *Dyckia microcalyx* var. *inermis* Hassler (1919); **incl.** *Dyckia microcalyx* var. *micrantha* Hassler (1919); **incl.** *Dyckia minutiflora* Mez (1919).

[1/2] **L** to 150 cm, lamina relatively long and narrow; **Inf** mostly compound; **Sep** 3–4 mm. — [F. Krapp]

**D. microcalyx** var. **ostenii** L. B. Smith (Contr. Gray Herb. 104: 73, t. 3, fig. 16, 1934). **Type:** Argentina, Misiones (*Osten & Rojas* 8097 [MVM, GH [photo]]). — **Distr:** N Argentina (Misiones); rocky banks; only known from the type locality. **I:** Smith & Downs (1974: 549).

[2] **L** scarcely over 20 cm, lamina 3 cm wide, strongly spinose-serrate; **Inf** simple; **Sep** 6 mm. — [F. Krapp]

**D. milagrensis** Leme (Harvard Pap. Bot. 4(1): 164–166, fig. 21, 1999). **Type:** Brazil, Bahia (*Nahoum* s.n. in *Leme* 3391 [HB]). — **Distr:** Brazil (Bahia); Campo Rupestre vegetation, on rocks. — Fig. 8.

[2/3a] **Ros** propagating by basal shoots, dense, many-leaved; **L** 12–15  $\times$   $\pm$  1–1.5 cm, thickly succulent, sheath not described, **L** lamina very narrowly triangular, subulate-attenuate, spinescent-acuminate with pungent tip, suberect to spreading,

purplish-green, obscurely white-lepidote on both faces, partially glabrescent adaxially, veined, laxly spinose, **Sp** opposite, narrowly triangular,  $\pm$  straight, flat, 4–6 mm, densely white-lepidote; **Inf**  $\pm$  120 cm, simple or with 1 or 2 branches; peduncle erect,  $\pm$  70 cm, ferruginous, inconspicuously white-furfuraceous to glabrescent; peduncular **Bra** foliaceous (lowest) to narrowly triangular and acuminate, erect, 12–20  $\times$  4–6 mm (upper), white-lepidote, veined, laxly spinulose; fertile **Inf** part  $\pm$  45 cm,  $\pm$  46-flowered, subdense, suberect, subdensely white-furfuraceous; **Br** 10–15 cm, 4- to 7-flowered,  $\pm$  red; primary **Bra** like the upper peduncular bracts; floral **Bra** triangular, acuminate, 4–10  $\times$  3–4 mm, white-furfuraceous, veined, entire; **Fl** subspreading at anthesis, erect afterwards, the upper slightly secund, 15–16 mm, unscented; **Ped** 4–5 mm; **Sep** broadly ovate,  $\pm$  6  $\times$  6 mm, acute, ecarinate, reddish-orange, subdensely white-furfuraceous, entire with long-fimbriate apex; **Pet** broadly obovate-spatulate,  $\pm$  11  $\times$  4 mm, rounded, ecarinate, suberect, orange, glabrous; **St** just included; **Fil** free above the 2 mm high common tube (completely connate according to Fig. 3 in Pinangé & al. (2017)), complanate, 6 mm; **Anth**  $\pm$  2 mm,  $\pm$  straight, base shortly sagittate, apex obtuse; **Ov** narrowly subpyramidal,  $\pm$  6 mm; **Sty**  $\pm$  8 mm,  $\pm$  equalling the anthers, **Sti** orange.

Similar to *D. mezii* and *D. pectinata*. — [F. Krapp]

**D. minarum** Mez (in Martius, Fl. Bras. 3(3): 483, t. 91, 1894). **Type:** Brazil, Minas Gerais (*Regnell* II-283 [S, US]). — **Distr:** Brazil (Goiás, Minas Gerais, Santa Catarina, São Paulo); on rocks or open rocky ground, 900–1300 m. **I:** Reitz (1983, t. 49).

[3b] **Ros** acaulescent, dense, with bulbous base; **L** numerous, irregularly spreading, sheath suborbicular, large, pale brown, glabrous but apically lepidote, **L** lamina 20–35  $\times$  1 cm, linear-triangular, abruptly acute with thickened pungent tip, green to brownish-green, canaliculate, rigid, thick, densely pale-lepidote esp. abaxially, laxly serrate, **Sp** curved, 2 mm; **Inf** 25–75 cm, simple, erect; peduncle rather stout, tomentulose, glabrescent; peduncular **Bra** broadly ovate with



**Fig. 8** *Dyckia milagrensis*. (Copyright: F. Krapp)



long acuminate tip, equalling or exceeding the internodes, serrulate towards the apex; fertile **Inf** part usually lax at anthesis,  $\pm 30$ - to 40-flowered, 7–35 cm, white-furfuraceous; floral **Bra** spreading or reflexed, like the peduncular bracts, equaling or exceeding the flowers (lowest), usually serrulate; **Fl**  $\pm$  spreading; **Ped** to 4 mm; **Sep** broadly elliptic, 7–9 mm, acute, densely lanate-lepidote; **Pet** suborbicular, 11–14 mm, carinate, suberect, orange-yellow; **St** included; **Fil** 2 mm connate above the common tube; **Anth** narrowly triangular, acuminate, recurved; **Ov** massively pyramidal-triangular; **Sty** very short; **Fr** trigonous-ellipsoid, 14 mm, almost black, glossy; **Se** 4 mm, basally pointed, alate towards the tip.

**D. mirandana** Leme & Z. J. G. Miranda (J. Bromeliad Soc. 59(2): 75–78, ill., 2009). **Type:** Brazil, Goiás (*Miranda* s.n. in Leme 6380 [HB]). — **Distr:** Brazil (Goiás); sandy soil accumulating among quartzitic outcrops, Campo Rupestre vegetation.

[3a] **Ros**  $\pm$  distichously 10- to 15-leaved, solitary or scarcely offsetting; **L** 28–43  $\times$   $\pm 1$  cm, coriaceous, sheath suborbicular-ovate, 3.4  $\times$  4–5 cm, dark castaneous, lepidote, **L** lamina sublinear-attenuate, distinctly canaliculate, suberect-arcuate, apex long acuminate-caudate, pungent, green to reddish towards the apex,

abaxially inconspicuously white-lepidote, adaxially glabrescent towards the apex, distinctly veined on both faces, margins glabrous, sparsely spinose, **Sp** uncinata, antoretorse, 0.5–1 mm, castaneous, glabrous,  $\pm 15$  mm apart; **Inf** 20–25 cm, simple; peduncle erect with curved apex,  $\pm 8$  cm, dark purplish wine-red to blackish, glabrous; peduncular **Bra** erect, subcarinate, narrowly triangular, long acuminate-caudate, 12–18  $\times$  6–8 mm, exceeding to equalling the internodes, dark purplish wine-coloured, sparsely to densely white-lepidote towards the apex, veined; fertile **Inf** part  $\pm 9$ -flowered, deflected but rachis straight,  $\pm 6.5$  cm, dark purplish wine-red to blackish, glabrous; floral **Bra** subtriangular, acuminate, subcarinate, membranous, suberect, 7–10  $\times$  5–6 mm, dark purplish wine-red, sparsely white-lepidote, veined, inconspicuously denticulate to entire; **Fl** suberect,  $\pm 12$  mm, tubular, strongly sweet-fragrant; **Ped**  $\pm 1.5$  mm, stout; **Sep** acuminate, convex, subcarinate, 6–6.5  $\times$  3.5–4 mm, dark purplish wine-red, glabrous, entire; **Pet** broadly obovate-spatulate from a narrower base,  $\pm 10 \times 7.5$  mm, apex obtuse and apiculate to subacute, ecarinate, yellow; **St** exserted; **Fil** free above the 1.5–3 mm high common tube (according to the protologue, completely connate according to Fig. 3 of Pinangé & al. (2017)), yellow,  $\pm 8$  mm; **Anth** narrowly subtriangular,  $\pm 2$  mm, base

distinctly sagittate, acute, apically strongly recurved; **Ov** ovoid,  $\pm 4 \times 2$  mm, greenish; **Sty**  $\pm 1$  mm, yellowish, **Sti** subentire, yellow; **Fr** and **Se** not described. — [F. Krapp]

**D. mitis** A. Castellanos (Anales Mus. Nac. Hist. Nat. Buenos Aires, ser. 3, 36: 51, t. 2, 1929). **Type:** Argentina, Misiones (*Spegazzini* s.n. [BA]). — **Distr:** N Argentina (Misiones); ecology not recorded. **I:** Smith & Downs (1974: 570).

[3b] **Ros** not described; **L**  $\pm 18 \times 1$  cm, lamina attenuate, with pungent tip, laxly serrate, **Sp** curved, 3 mm, 4–6 mm apart; peduncle slender, 27 cm, glabrous; **Inf** 30 cm, simple; peduncular **Bra** amplexicaul at the base, shorter than the internodes; fertile **Inf** part 5–10 cm, rachis furfuraceous; floral **Bra** suborbicular, apiculate, shorter than the sepals, veined, lepidote; **Fl** sessile; **Sep** suborbicular,  $6 \times 8$ –10 mm, broadly rounded; **Pet** rhombic, 14 mm, rounded at the apex, erect, 14 mm, colour not described; **St** slightly exserted; **Fil** highly connate above the 3 mm high common tube; **Anth** slightly recurved, 3–3.5 mm; **Ov** pyramidal, 5 mm; **Sty** 6 mm.

Insufficiently known. — [F. Krapp]

**D. montezumensis** Leme (Phytotaxa 67: 23–25, ill., 2012). **Type:** Brazil, Minas Gerais (*Leme & Oliveira* 8315 [RB]). — **Distr:** Brazil (Minas Gerais); shrubby Cerrado vegetation.

[2/3b] **Ros** laxly  $\pm 10$ -leaved; **L** 40–53  $\times$  2.2–2.5 cm, thickly coriaceous, sheath suborbicular,  $\pm 2.5 \times 4.5$  cm, whitish towards the base, glabrous, **L** lamina narrowly triangular, distinctly canaliculate, arcuate, apex long acuminate-caudate, dark green to reddish wine-coloured, densely white-lepidote (esp. abaxially), distinctly veined, margins sparsely white-lepidote to glabrous, sparsely spinose, **Sp** narrowly triangular, antroretorse, 1.5–2.5 mm, dark castaneous, glabrous, 7–20 mm apart; **Inf** to 155 cm, simple or branched with 1 branch at the base; peduncle  $\pm 72$  cm, dark green to dark purplish wine-red, inconspicuously white-lepidote to glabrous, smooth; peduncular **Bra** broadly ovate to suborbicular at the base, narrowly sublinear-triangular, carinate, acuminate-caudate, erect,

10–40  $\times$  7–10 mm, much shorter than the internodes, stramineous, inconspicuously white-lepidote, strongly veined, remotely spinulose (lowest) to entire (upper); fertile **Inf** part  $\pm 25$ -flowered, lax to subdense, distichous to subpolystichous, rachis straight to flexuous towards the apex,  $\pm 35$  cm, dark purplish wine-red, subdensely white-lepidote; **Br** suberect,  $\pm 4$ -flowered,  $\pm$  polystichous,  $\pm 7.5$  cm, rachis flexuous, sterile base  $\pm 4$  cm; primary **Bra** like the basal floral bracts; floral **Bra** broadly ovate, acute to acuminate, ecarinate,  $3$ – $7 \times 2$ – $4.5$  mm, inconspicuously white-lepidote, veined, entire; **Fl** subspreading, 16–18 mm, campanulate; **Ped** 4 mm, dark purplish wine-red to nigrescent, subdensely white-lepidote; **Sep** ovate,  $\pm 6 \times 5$  mm, distinctly convex, apex obtuse to often emarginate, blackish wine-red, white-lepidote with glabrous apex; **Pet** broadly spatulate,  $13 \times 9$ –11 mm, obtuse-emarginate, ecarinate, orange, apex wine-colored; **St** deeply inserted; **Fil** completely connate above the 2 mm high common tube,  $\pm 9$  mm, orange; **Anth** sublinear,  $\pm 4$  mm, base bilobed, apiculate; **Ov** suboblong-ovoid,  $7$ – $8 \times \pm 2.5$  mm, greenish; **Sty**  $\pm 1$  mm, yellowish, **Sti** papillose, orange; **Fr** and **Se** unknown.

Closely related to *D. atratiflora*.

**D. monticola** L. B. Smith & Reitz (Sellowia 14: 104, fig. 3, 1962). **Type:** Brazil, Santa Catarina (*Reitz & Klein* 4789 [US, HBR]). — **Distr:** Brazil (Minas Gerais, Santa Catarina); open slopes, savanna, on rocks, 1250–1500 m. **I:** Smith & Downs (1974: 519).

[1/2?] **Ros** dense, many-leaved; **L** 23–27  $\times$  1–1.3 cm,  $\pm$  curved, sheath 3 cm wide, brown, lustrous and lepidote towards the apex adaxially, dull and glabrous elsewhere, **L** lamina linear, rigid, canaliculate, acute and mucronulate, appressedly cinereous-lepidote, soon glabrous adaxially, margins laxly serrate, **Sp** slender, antroretorse, 2.5 mm, brown; **Inf**  $\pm 70$  cm, with 6 basal branches (according to the protologue, simple according to Fig. 5 in Pinangé & al. (2017)); peduncle subterete, 40 cm, very dark when dry, flocculose, glabrescent; peduncular **Bra** broadly ovate, foliaceous-laminate or the uppermost acuminate,  $\pm$  equalling the upper

internodes, cinereous-lepidote, serrulate; fertile **Inf** part 28 cm, many-flowered, completely densely ferruginous-flocculose including pedicel and sepals; **Br** few-flowered with long sterile base; primary **Bra** like the upper peduncular bracts, to 17 mm; floral **Bra** acuminate from a broadly ovate base, spreading, slightly shorter than the sepals, serrulate; **Fl** spreading, to 15 mm; **Ped** 5 mm; **Sep** ovate-elliptic, to 10 mm, acute, incurved, rugose when dry, serrulate; **Pet** distinctly unguiculate, obovate, curved-spreading towards the apex, orange; **St** included; **Fil** 3 mm connate (completely connate according to Fig. 3 in Pinangé & al. (2017)) above the common tube; **Anth** narrowly triangular, 3.5 mm, recurved towards the apex; **Ov** slenderly ovoid; **Sty**  $\pm$  none, **Sti** 3-parted. — [F. Krapp]

**D. nana** Leme & al. (Rodriguésia 61(1): 36–37, figs. 4G–H and 5H–N, 2010). **Type:** Brazil, Minas Gerais (Leme & al. 7484 [RB, HB]). — **Distr:** Brazil (Minas Gerais: Diamantina); on white quartzite soil in grassy Campo Rupestre vegetation.

[3b] **Ros** dense, 8- to 10-leaved; **L** 6–8  $\times$  1.2–1.4 cm, coriaceous, sheath 2.5–3  $\times$  2.5–3.5 cm, castaneous abaxially, pale adaxially, glabrous towards the base, densely white-lepidote apically, **L** lamina narrowly triangular, distinctly canaliculate, suberect to  $\pm$  erect and slightly secund, acuminate with pungent tip, green, obscurely white-lepidote, distinctly veined, laxly spinulose, **Sp** subtriangular-acicular, spreading to slightly antrorse, 0.5–1 mm, 4–10 mm apart; **Inf** 19–29 cm, simple, erect; peduncle 15–20 cm, green, glabrous, smooth; peduncular **Bra** erect, subcarinate, long lanceolate-acuminate-caudate from a broadly subtriangular base, 5–11  $\times$  3–3.5 mm, stramineous, sparsely white-lepidote, veined, microscopically denticulate to  $\pm$  entire; fertile **Inf** part 4- to 6-flowered, subdense to lax, 2.5–5 cm, rachis  $\pm$  straight, smooth, greenish to orange-yellow, glabrous; floral **Bra** broadly ovate-subtriangular, acuminate-caudate, subcarinate, subspreading to suberect, 4–4.5  $\times$  3.5–4 mm, stramineous towards the apex, finely veined, fimbriate, remotely and irregularly denticulate to entire; **Fl** spreading and secund, 12–13 mm,

subtubular to slightly campanulate, unscented; **Ped** 3.5–5 mm, slender, terete, glabrous, yellow-orange, curved; **Sep** broadly ovate, 4–5.5  $\times$  3.5–4 mm, convex, apex obtuse and remotely and irregularly apiculate, ecarinate, orange, glabrous, retrorsely-curved fimbriate; **Pet**  $\pm$  broadly obcordate from a distinctly narrowed base,  $\pm$ 7.5  $\times$  6.5–7 mm, apex broadly emarginate, ecarinate, orange; **St** included; **Fil** 1.5 mm connate above the 1.5 mm high common tube, complanate, yellow; **Anth** oblong-ovoid,  $\pm$ 2.5 mm, base sagittate, acute, yellow,  $\pm$  straight; **Ov** suboblong-ovate,  $\pm$ 2.5  $\times$  1.5 mm, yellow; **Sty**  $\pm$ 1 mm, yellow, **Sti** shortly crenulate, lacerate, yellow.

Similar to *D. consimilis* and *D. macedoi*.

**D. nervata** Rauh (Trop. subtrop. Pfl.-welt 60: 21–24, figs. 13 and 14, 1987). **Type:** Brazil, Bahia (Rauh 56443 [HEID]). — **Distr:** Brazil (Bahia); quartzitic rocks, 1000 m.

[3a] **Ros**  $\pm$ 7-leaved, solitary or in groups, stem short, surrounded by old sheaths, slightly thickened at the base; **L** to 18  $\times$  to 1 cm, sheath broadly ovate, 2  $\times$  1.8 cm, white, densely lepidote abaxially, glabrous adaxially, strongly veined, **L** lamina erect (younger) to recurved (older), sturdy, strongly canaliculate, acute, with pungent tip, reddish-green, adaxially sparsely lepidote, abaxially densely white-lepidote, veined, **Sp** retrorse, 2 mm, brownish; **Inf** to 12 cm, simple; peduncle erect, 6 cm, olive-green, white-lanate-lepidote; peduncular **Bra** amplexicaul at the base, shorter than the internodes, appressed to the peduncle, soon drying; fertile **Inf** part lax, 5- to 7-flowered, erect, 5 cm, white-lanate; floral **Bra** with a broad sheath, lamina narrowly lanceolate, recurved, shorter than the sepals, olive-green, lanate, entire; **Fl** suberect; **Ped** short, stout; **Sep** free, broadly ovate, 5  $\times$  5 mm, obtuse, ecarinate, brilliant orange, abaxially sparsely lanate; **Pet** erect, spatulate, 10  $\times$  5 mm, obtuse, ecarinate, brilliant orange; **St** included; **Fil** free above the 5 mm high common tube, yellowish; **Ov** 5 mm, white; **Sty**  $\pm$ 2 mm, orange; **Sti** erect, shorter than the anthers.

Compared with *D. oligantha* (here treated as synonym of *D. saxatilis*) in the protologue. — [F. Krapp]

**D. niederleinii** Mez (in Martius, Fl. Bras. 3(3): 474, 1894). **Type:** Argentina, Misiones (*Niederlein* 229 p.p. [B, F [photo]]). — **Distr:** N Argentina (Misiones); open fields, terrestrial or on rocks. **I:** Smith & Downs (1974: 555).

**Incl.** *Dyckia missionum* Mez (1894); **incl.** *Dyckia missionum* var. *breviflora* Hassler (1919).

[1] **Ros** not described; **L** 25–50 × 1–3.5 cm, sheath not described, **L** lamina narrowly triangular, sparsely pale-appressed-lepidote abaxially, laxly serrate, **Sp** slender, curved, 4 mm; **Inf** 100–120 cm, few-branched, glabrous; peduncle slender; peduncular **Bra** broadly ovate with long-attenuate entire tips, shorter than the internodes; fertile **Inf** part with erect branches, elongate, very laxly flowered; primary **Bra** only a little larger than the floral bracts; floral **Bra** broadly ovate or suborbicular, apiculate, 5–8 mm, those of the branches much shorter than the sepals, those of the main inflorescence axis longer than the sepals, lustrous; **Fl** suberect, 13 mm; **Ped** 2–4 mm, very stout; **Sep** suborbicular, 5–7 mm, obtuse to shortly mucronate, carinate; **Pet** lamina spreading, elliptic, 13–15 mm, obtuse or emarginate, undulate, colour not described; **St** exserted; **Fil** highly connate for 6 mm above the common tube; **Anth** sublinear, 2 mm, acute, recurved; **Sty** ± equalling the ovary.

**D. nigrospinulata** Strehl (Bromeliaceae 42(5): 9–13, figs. 5–9, 2009). **Type:** Brazil, Rio Grande do Sul (*Strehl* 1602 [HAS]). — **Distr:** Brazil (Rio Grande do Sul); on rocks in a river. **I:** Klein V. & Klein (2014: 80).

[1] **Ros** open, ±60- to 200-leaved, ±1.5 m Ø; **L** 70–80 × 5–6 cm, sheath suborbicular, dark castaneous, glabrous, **L** lamina triangular, attenuate, stiff, with a strong pungent black tip, dark green, centre lighter, adaxially glabrous, abaxially lepidote, striate, **Sp** predominantly antrorsely curved, 5–7 mm, dark, 30–70 mm apart; **Inf** 2–2.5 m, compound, 3–4× branched; peduncle strong, green, glabrous; peduncular **Bra** broadly ovate with long-attenuate tip, 80–100 × 12–20 mm (lower) to 10–40 × 7–10 mm (upper), entire or lower ones with 3 mm long teeth towards the apex; fertile **Inf** part with easily removable white-woolly tomentum, 25–30 cm;

**Br** laxly many-spiked, at acute angles, somewhat pendent with ascending tip, 50–60 cm, ±2–5 cm apart; floral **Bra** triangular, acute, 1–2 mm, becoming shorter upwards, with brown tips, later stramineous, ± entire; **Fl** pointing upwards in bud but spreading at anthesis, later sometimes turned backwards, sessile, narrowly tubular; **Sep** free, rounded, 5–6 × 1–2 mm, green-yellow with a small spot at the apex; **Pet** free, erect, rounded, 7–10 × 1–2 mm, yellow; **St** exserted; **Fil** free, linear; **Ov** incl. style as long as the stamens; **Fr** 6–8 × 3–4 mm, black, glossy; **Se** elongate, ±3 × 1 mm, light castaneous.

Part of the “*Prionophyllum* complex”, and similar to *D. maritima*. The large size is exceptional for the genus *Dyckia*.

**D. nobilis** Büneker & al. (Phytotaxa 244(1): 60–63, ill., 2016). **Type:** Brazil, Minas Gerais (*Büneker & al.* 296 [HDCF, RB]). — **Distr:** Brazil (Minas Gerais: Serro); on sedimentary rocks; only known from the type locality.

[2/3b] **Ros** solitary, with short stem, 28–55 cm Ø; **L** 10–30, inner straight, outer suberect to recurved, sometimes secund, sheath ±5 × 4.5 cm, suborbicular, white with brown-greenish base, **L** lamina 25–80 × 2.1–6.2 cm, narrowly triangular, stiff and succulent, upper face flat or canaliculate, reddish-green, densely white-cinereously lepidote on both faces, tip extended into a 6 mm long spine, margins unarmed or serrate with laxly arranged **Sp** to 4 mm; **Inf** 60–170 cm tall, simple or paniculate, erect; peduncle 30–90 cm, reddish, basally white-tomentose, above brownish-ferruginous-tomentose; peduncular **Bra** ±50 mm, shorter than the internodes, basal ones leaf-like, upper ones erect, triangular, 10–25 × 13–26 mm; fertile **Inf** part 25–95 cm, with up to 8 (sub-) erect to upcurved branches at the base, laxly 27- to 110-flowered; primary **Bra** ovate-triangular; floral **Bra** ovate-triangular, 8–15 × 10–21 mm, brownish-ferruginous tomentose-lepidote, entire, basal ones sometimes longer than the flowers, upper ones shorter; **Fl** ±15 mm, porrect or slightly reflexed, tubular; **Ped** 2–3 mm, tomentose; **Sep** ovate-elliptic, convex, 5–7 × 7–9.5 mm, orange with reddish base, thick and succulent, basally



connate for 3 mm, sparsely ferruginous-tomentose; **Pet** suborbicular-rhomboidal, 10–13 × 18–20 (?) mm, orange, sparsely lepidote near the base; **St** included; **Fil** narrowly triangular, yellow-orange, to 9 mm, connate for ±1 mm above the 2 mm long common tube; **Ov** ±5 × 2.5 mm, subcylindrical, yellowish; **Sty** ±2 mm, orange; **Sti** conduplicate-spiral; **Fr** globose-ovoid, glossy brown or black; **Se** discoid, with hyaline wing.

Close to *D. sordida* and *D. inflexifolia*. The basally connate sepals are unusual in the genus. The measurements given in the protologue for the floral bracts and the petals, both described as potentially broader than long, are not supported by the drawings in fig. 2 of the protologue. — [U. Eggli]

**D. odorata** L. B. Smith (Phytologia 10: 485, t. 2, figs. 8 and 9, 1964). **Type:** Brazil, Goiás (*Dawson* 14578 [US, UC]). — **Distr:** Brazil (Goiás: Chapada de Veadeiros); ecology not recorded; known only from the type collection. **I:** Smith & Downs (1974: 515).

[3b] **Ros** not described; **L** 15 × 0.5 cm, sheath triangular-ovate, stramineous, smooth, sublustrous, sparsely lepidote towards the apex, **L** lamina narrowly triangular, appressedly white-lepidote, soon glabrous adaxially, laxly serrate, **Sp** slender, spreading, pale, 2 mm; **Inf** 10 cm, sessile without peduncle, simple, axis subdensely white-flocculose, with some flowers at the base, then with some aborted flowers in the middle, and well-developed flowers distally; floral **Bra** broadly ovate with long narrowly triangular serrate lamina (lower) to merely apiculate (upper), lower ones exceeding the flowers; **Fl** described as dimerous, spreading, strongly sweet-fragrant; **Ped** 3 mm, slender; **Sep** suborbicular, 5–6 mm, very broadly acute and minutely apiculate, pale-margined when dry; **Pet** lamina spreading, broadly rounded, 10 mm, orange; **St** much shorter than the petals; **Fil** almost completely connate; **Anth** sagittate, curved, 1.5 mm; **Ov** slenderly conical; **Sty** short but obvious and separate.

The sessile inflorescence without distinct peduncle and the dimerous flowers are notable and induce speculations that the taxon might be

based on an aberrant and/or depauperate specimen.

**D. orobanchoides** Mez (in Martius, Fl. Bras. 3 (3): 475, 1894). **Type:** Brazil, Minas Gerais (*Tamberlik* s.n. [W †, B [lecto]]). — **Distr:** Brazil (Minas Gerais: without exact locality); ecology not recorded; only known from the type collection.

[1?] Only known from the fragmentary lectotype; **L** unknown; peduncle glabrous; peduncular **Bra** ovate, acuminate, much shorter than the internodes, entire; **Inf** few-branched, sparsely short-tomentulose, **Br** ascending, subdensely flowered; floral **Bra** broadly ovate, acute, shorter than the pedicels, fimbriate at the apex; **Fl** spreading; **Ped** 3 mm; **Sep** broadly ovate-elliptic, 7 mm, apiculate, fimbriate, appressed-tomentulose; **Pet** suborbicular, ±11 mm, obtuse, carinate, erect, colour not described; **St** equalling or slightly exceeding the petals; **Fil** free above the common tube; **Anth** sublinear, acuminate, strongly recurved; **Sty** ± none.

Very insufficiently known and apparently never recollected.

**D. paraensis** L. B. Smith (Phytologia 13: 150, t. 7, figs. 10–12, 1966). **Type:** Brazil, Pará (*Fróes* 30030 [IAN, US [photo]]). — **Distr:** Brazil (Pará: Araguáia region); sandstone ledges, 600 m; only known from the type collection. **I:** Smith & Downs (1974: 576).

[3b] **Ros** subbulbous, many-leaved; **L** 50 × 2.5–3 cm, sheath broad, ±4 cm, **L** lamina recurved-spreading, very narrowly triangular, rigid, soon glabrous adaxially, closely appressedly cinereous-lepidote abaxially, very laxly serrate, **Sp** subspreading, 1.5 mm, black; **Inf** 70 cm, simple; peduncle erect, very slender, soon glabrous; peduncular **Bra** remote, acuminate from a broadly ovate base, very small, entire; fertile **Inf** part very lax, >20 cm, glabrous; floral **Bra** like the upper peduncular bracts but apiculate, to 5 mm; **Fl** spreading; **Ped** 3 mm, rather stout; **Sep** elliptic-oblong, 6 mm, broadly rounded, ecarinate, rather thin; **Pet** very broadly rounded, 10 mm, carinate, colour not described but presumably orange; **St** ± equalling the petals;



**Fil** shortly (to completely?, Pinangé & al. (2017: fig. 3)) connate above the common tube; **Sty**  $\pm$  none.

Compared with *D. duckei* in the protologue.

**D. pauciflora** L. B. Smith & Read (Phytologia 38: 138, t. 6, 1977). **Type:** Brazil, Goiás (*Hatschbach* 39429 [US, MBM]). — **Distr:** Brazil (Goiás); peak of a rock dome, 800 m.

[3b] **Ros** dense; **L**  $\pm 8 \times 1.7$  cm, sheath broad,  $\pm 1.5$  cm, **L** lamina recurved-spreading, narrowly triangular, both faces appressedly cinereous-lepidote, glabrescent adaxially, laxly serrate, **Sp** recurved, 3 mm, black; **Inf** 50 cm, stout, simple; peduncle green, glabrous; peduncular **Bra** acuminate or apiculate, very small, slightly longer (lower) to much shorter (upper) than the internodes, many, remote; fertile **Inf** part lax,  $\pm 6$ -flowered, rachis geniculate,  $\pm 5$  cm, glabrous; floral **Bra** suborbicular, apiculate, 3 mm,  $\pm$  equaling the pedicels; **Fl** subspreading; **Ped** slender; **Sep** broadly elliptic, 6 mm, obtuse; **Pet** very broadly rounded, 9 mm, ecarinate, orange; **St** included; **Fil** connate above the common tube; **Sty**  $\pm$  none.

Similar to *D. paraensis*. — [F. Krapp]

**D. paucispina** Leme & Esteves (Vidalia 1(1): 28–30, ill., 2003). **Type:** Brazil, Mato Grosso do Sul (*Esteves Pereira* 378 [HB, UFG]). — **Lit:** Braun & Esteves Pereira (2006a). **Distr:** Brazil (C Mato Grosso do Sul); on rocks in Cerrado vegetation.

[2/3a] **Ros** 10- to 16-leaved, forming small and dense clumps, stem subglobose,  $4 \times 3$  cm; **L**  $10\text{--}18 \times 1.8\text{--}2$  cm, very rigid, succulent, sheath wider than the lamina, broadly subreniform, greenish, inconspicuously lepidote at the apex, **L** lamina narrowly triangular, strongly recurved,  $\pm$  slightly canaliculate, subulate towards the very pungent tip, long-acuminate, dark green to reddish, adaxially subdensely white-lepidote, abaxially subobscurely white-lepidote abaxially, veined, margins glabrous to slightly white-floccose, entire or basally irregularly and very remotely spinose, **Sp** slightly uncinata, predominantly retrorse, 2–3 mm; **Inf** 70–105 cm, pseudosimple to laxly  $2 \times$  (rarely

$3 \times$ ) branched, erect; peduncle 45–58 cm, dark green, glabrescent towards the base, subdensely white-lanate towards the apex; peduncular **Bra** narrowly long-triangular to ovate-triangular from a suborbicular base, acuminate to acuminate-caudate, erect, distinctly shorter than the internodes, stramineous, white-floccose to glabrescent, veined, entire; fertile **Inf** part very slightly angled,  $\pm 15$  cm (simple) and  $\pm 23$ -flowered or to 30 cm (compound), straight, reddish, densely white-lanate at anthesis; primary **Br** 2–7, laxly arranged and late-developing, 7–10 cm, 11- to 15-flowered, subdense to dense mainly towards the apex, suberect, rachis flexuose to geniculate, pale orange, secondary **Br** incompletely known; primary **Bra** like the upper peduncular bracts; floral **Bra** suberect, ecarinate, lowest ovate-acuminate and  $6\text{--}7 \times 4\text{--}5$  mm, upper suborbicular-apiculate, to  $3\text{--}5 \times 4$  mm, stramineous towards the apex, white-lanate to glabrescent, veined, entire; **Fl** suberect and somewhat upwardly secund, 16–18 mm, tubular with slightly narrowed throat, unscented; **Ped** 2–3 mm, stout; **Sep** broadly ovate to ovate-elliptic,  $6\text{--}9 \times 5\text{--}6$  mm, apex obtuse and inconspicuously apiculate, ecarinate, pale orange, densely white-lepidote, fimbriate, entire or minutely crenulate; **Pet** broadly obovate-spatulate,  $11\text{--}13 \times 9\text{--}10$  mm, obtuse-emarginate, base very narrow, ecarinate, erect at anthesis, bright orange, abaxially white-floccose towards the base to glabrous; **St** slightly exceeding the petals; **Fil** free above the 2–3 mm high common tube, 10–12 mm, pale orange; **Anth** sublinear to subtriangular, 4–4.5 mm, strongly recurved, distinctly visible at anthesis, base sagittate, apiculate; **Ov** suboblong-ovoid to narrowly pyramidal, 5.5–6 mm, yellowish; **Sty**  $\pm 1$  mm, orange, **Sti**  $\pm 0.5$  mm, orange, irregularly recurved.

Similar to *D. burchellii* and *D. pulquinensis*. — [F. Krapp]

**D. pectinata** L. B. Smith & Reitz (Phytologia 14: 486, t. 1, figs. 29–32, 1967). **Type:** Brazil, Minas Gerais (*Pabst* 4129 [HB, US [photo]]). — **Distr:** Brazil (Minas Gerais: Conceição do Rio Verde to Cambuquira); dry sandstone outcrops. **I:** Smith & Downs (1974: 570).

[3b] **Ros** not described; **L** 14 × 0.8 cm, sheath broadly ovate, stramineous basally, **L** lamina very narrowly triangular, subulate-attenuate, appressedly cinereous-lepidote on both faces, ± glabrescent adaxially, subdensely pectinate-serrate, **Sp** flat, spreading, 6 mm; **Inf** 75 cm, simple; peduncle glabrous; peduncular **Bra** subfoliaceous (lower) to narrowly triangular (upper), thin, irregularly shorter than the internodes, serrulate; fertile **Inf** part laxly many-flowered, 21 cm, glabrous; floral **Bra** like the upper peduncular bracts, lowest ones exceeding the sepals, serrulate; **Fl** spreading to reflexed; **Ped** 3 mm, broadly obconical, constricted at the base; **Sep** broadly ovate, 7 mm, rounded, entire or apiculate, rugose when dry as if formerly fleshy, little if at all carinate; **Pet** obovate, 9 mm, carinate, red-orange; **St** included; **Fil** shortly (to completely?, Pinagé & al. (2017: fig. 3)) connate above the short common tube; **Sty** none.

Similar to *D. dawsonii*. — [F. Krapp]

**D. pernambucana** L. B. Smith (Phytologia 20: 179, t. 2, figs. 12–14, 1970). **Type:** Brazil, Pernambuco (*Lima* 65-4275 [IPA, US [photo]]). — **Lit:** Siqueiro Filho & Leme (2007: 316–318, with ill.). **Distr:** Brazil (Pernambuco); gneiss outcrops.

**Incl.** *Dyckia rupestris* W. Till & Morawetz (1990).

[2/3b] **Ros** ±30-leaved, dense, with a subglobose base to ±8 × 8 cm; **L** to 33 × 2.1 cm, very rigid and succulent, sheath broadly subreniform, ±2 × 4 cm, dark brown towards the base, subentire, **L** lamina narrowly triangular, nearly flat, arcuate, canaliculate towards the subulate pungent tip, dark greenish wine-red, distinctly veined, adaxially inconspicuously white-lepidote to glabrescent, abaxially densely cinereous-lepidote, margins irregularly densely to laxly serrate, **Sp** antrorse, uncinata, 0.5–1.5 mm, 2–25 mm apart; **Inf** to 80 cm, compound or simple; peduncle ± straight, 39–60 cm, sparsely to subdensely pale lanate; peduncular **Bra** erect, subfoliaceous (lower) or narrowly triangular (upper), shorter than the internodes, (sub-) densely pale-lepidote, serrulate; fertile **Inf** part lax, 25–45 cm, main axis 18- to 37-flowered, suberect, appressedly white-lepidote; primary **Bra** like the upper peduncular

bracts, much shorter than the long sterile branch bases; primary **Br** suberect, 14–21 cm, laxly 8- to 14-flowered, with a 2.5–7 cm long sterile base; floral **Bra** triangular-ovate, acuminate, (sub-) densely lanate, basal ones narrowly triangular, 10–12 × 5–6 mm, minutely denticulate, upper ± triangular, 5–8 × 4–6 mm, entire or microscopically denticulate; **Fl** 16–20 mm, suberect to slightly secund, campanulate, weakly fragrant; **Ped** 3–5 mm, stout; **Sep** broadly ovate, 6.5–9 × 6–7 mm, acute to narrowly obtuse and apiculate, ecarinate, orange, subdensely lanate; **Pet** broadly obovate-spatulate, 10–12 × 8–10 mm, obtuse, ecarinate, reddish-orange; **St** included; **Fil** 2–2.5 mm (to completely?, Pinagé & al. (2017: fig. 3)) connate above the common tube; **Anth** triangular, 2 mm, straight to slightly recurved; **Ov** suboblong, 5 mm, yellow; **Sty** 2 mm; **Sti** conduplicate-spiral, 1 mm, orange; **Fr** subglobose, 12–14 × 12 mm, dark brown, glossy, shortly rostrate; **Se** flat, asymmetrically subcuneate, ±4 × 2.5 mm.

Compared with *D. encholirioides* in the protologue, but the similarity is superficial (Siqueiro Filho & Leme 2007: 318). Rather, it is related to *D. limae* and similar to *D. secunda*. *D. rupestris* is synonymized on the base of Siqueiro Filho & Leme (2007: 316–318), and the description has been amended according to this source.

**D. piauiensis** Esteves & Gouda (Phytotaxa 164(4): 296–300, figs. 1 and 2A–F, 2014). **Type:** Brazil, Piauí (*Esteves Pereira* 375 [UFG]). — **Distr:** Brazil (Piauí: Canto do Burití); dry Cerrado vegetation, rocky soil or on rocks, in full sun or partial shade, 335 m; only known from the type locality.

[3b] **Ros** acaulescent, densely 19- to 25-leaved, 45–54 cm Ø, with bulbous base, with few basal offsets; **L** coriaceous, succulent, sheath broadly ovate, 2.5 × 3.8–4.6 cm, fairly succulent, both faces white and brilliant, distally somewhat brownish, margins minutely dark-spined, **L** lamina first erect, later curved and spreading, triangular-lanceolate, 21–26 × 2.8–3.4 cm, green, both faces finely veined, basal part densely appressedly furfuraceous-lepidote between the veins, adaxially glabrous distally, margins laxly

serrate, **Sp** mostly retrorsely uncinata, 0.5–4.3 mm, pale yellow and brown-tipped, 3–12 mm apart (distally to 27 mm); **Inf** 35–120 cm, simple, erect to  $\pm$  flexuous; peduncle 30–100 cm, sparsely lepidote; lower peduncular **Bra** leaf-like and to 7 cm, upper 0.8–4.2 cm, narrowly triangular to sublinear, with pungent tip, carinate, (pale) green, soon stramineous, sparsely serrulate; fertile **Inf** part 5.5–14 cm, rose-red, 7- to 16-flowered, sparsely white-lepidote; floral **Bra** broadly ovate,  $\pm 8 \times 2$  mm, acuminate, rose-red, carinate; **Fl**  $\pm 15 \times 8$  mm, spreading and slightly secund, broadly tubular; **Ped** stout, 3 mm (to 8 mm in fruit); **Sep** broadly ovate,  $7\text{--}9 \times 7$  mm, rounded or emarginate, strongly convex, incurved, ecarinate, red, smooth, sparsely white-lepidote to glabrous, margins minutely spinose; **Pet** shortly spatulate,  $10\text{--}13 \times 9$  mm, rounded or emarginate, slightly cucullate, orange; **St** included; **Fil** highly connate for 7–9 mm above the common tube; **Anth**  $\pm 3$  mm, yellow; **Ov** narrowly ovoid,  $6\text{--}7 \times \pm 3$  mm, pale yellow; **Sty**  $\pm 1$  mm; **Sti**  $\pm 2$  mm, crisped, orange with yellow margins; **Fr** ovoid,  $14\text{--}17 \times 11\text{--}13$  mm, dark brown, glossy.

Compared with the similar *D. pernambucana*, differing by larger retrorse leaf marginal spines, shorter inflorescences and characters of the flowers. — [F. Krapp]

**D. piracanjubensis** Esteves & Gouda (J. Bromeliad Soc. 66(3): 172–179, ill., 2017). **Type:** Brazil, Goiás (*Esteves Pereira* 355 [UFG 50537]). — **Distr:** Brazil (S Goiás: along the Rio Piracanjuba); isolated flat limestone rock outcrops, in full sun, 650 m.

[3b] **Ros**  $\pm 67$  cm  $\varnothing$ , solitary or forming dense clumps; stem to  $17 \times 6.5$  cm, hidden by the leaf sheaths; **L**  $\pm 40$ , spreading, the inner suberect to upward-secund, sheath  $2.5\text{--}3.2 \times 3.7$  cm, succulent, both faces glossy, base white, dark honey-coloured above, margins spinose, **L** lamina sublinear-triangular,  $35\text{--}53 \times 3$  cm, strongly canaliculate, pale green to brownish-green, finely veined, densely canescent-lepidote esp. abaxially, becoming glabrescent towards the tip, tip flat, dark brown, glossy, margins spinose, **Sp** uncinata, antorse except for the distal ones, to 3.5 mm, becoming smaller upwards, brown from green

base, 3–14 mm apart; **Inf** 1.8–2 m tall, simple; peduncle to 100 cm, straight to slightly sinuous, sparsely cinereous-tomentose; lower peduncular **Bra** leaf-like, to 9.5 cm, upwards becoming smaller, linear-lanceolate, carinate, pungent, serrate; flowering part  $\pm 72$  cm, cinereously whitish-lepidote; lower floral **Bra** triangular-lanceolate,  $\pm 15 \times 7$  mm, upper only 3 mm, all carinate, veined, serrulate, sparsely cinereous-tomentose, pungent; **Fl**  $16 \times 7$  mm  $\varnothing$ , subsessile to shortly pedicellate,  $\pm$  horizontally porrect, cup-shaped with slightly flaring limb; **Sep** triangular-lanceolate,  $\pm 7 \times 6$  mm, orange-yellowish, free, fleshy, densely white-tomentose, margins ciliate; **Pet**  $\pm 13 \times 9$  mm, orange-red, basally connate for 1–3 mm, entire, rounded or slightly emarginate, glabrous; **St** included; **Fil** whitish to pale yellow, to 7.6 mm, 2–3.5 mm connate above the common tube; **Anth**  $\pm 3 \times 1$  mm, dorsifixed near the base, strongly recurved at anthesis; **Ov**  $\frac{4}{5}$  superior, narrowly subprismatic,  $\pm 6 \times 2.5$  mm, gradually merging into the style; **Sty** yellow basally, orange distally, including stigma 3 mm; **Sti** lobes  $\pm 1.7$  mm, orange; **Fr** broadly ovoid,  $13\text{--}16 \times 9\text{--}13$  mm  $\varnothing$ , glossy dark brown, somewhat beaked; **Se** not described.

Compared with *D. goiana*, but also similar to *D. formosensis* (with fewer leaves, longer fertile inflorescence part, obtuse sepals and longer filaments) and *D. cangaphila* (smaller rosettes and shorter leaves, shorter and occasionally compound inflorescences, and pedicellate smaller flowers). — [U. Eggli]

**D. platyphylla** L. B. Smith (Phytologia 19: 283, t. 1, figs. 9–11, 1970). **Type:** Brazil, Bahia? (*Foster* 2489 [US]). — **Distr:** Brazil (Bahia?); not known from the wild with certainty. **I:** Smith & Downs (1974: 575).

[3b] **Ros** not described; **L** to  $23 \times 5$  cm, sheath suborbicular, 5 cm, yellowish, glabrous, **L** lamina narrowly triangular, thick, succulent, glabrous adaxially, appressedly whitish-lepidote abaxially, margins serrate, **Sp** slender, antroretrorsely curved, 3 mm, brown; **Inf** 80 cm, simple; peduncle slender, much compressed at the base, somewhat flexuous, glabrous; peduncular **Bra** broadly ovate and acuminate, small, much shorter than the

internodes, sparsely pale-lepidote, entire or sub-entire; fertile **Inf** part lax, many-flowered, 28 cm, glabrous; floral **Bra** broadly ovate, acuminate,  $\pm$  equalling the sepals (lower); **Fl** mostly suberect; **Ped** 1–2 mm, stout; **Sep** broadly ovate, 8 mm, rounded and cucullate, ecarinate; **Pet** elliptic, 11 mm, yellow; **St** included; **Fil** connate above the common tube; **Sty** none.

Similar to *D. aurea*. — [F. Krapp]

**D. polyclada** L. B. Smith (J. Bromeliad Soc. 39(5): 206–207, figs. 7 and 8, 1989). **Type:** Brazil, Rio Grande do Sul? (*Foster* 3096 [US, B, GH, NY]). — **Distr:** Brazil (Rio Grande do Sul?); ecology not recorded; only known from the type.

[1] **Ros** clustering, acaulescent; **L**  $>40 \times 2$  cm, erect to spreading, sheath pale, **L** lamina finely white-lepidote between the veins on both faces, margins laxly serrate, **Sp** curved, 5 mm, 20–25 mm apart; **Inf** to 2 m, seemingly terminal, laxly 2–3 $\times$  branched; peduncle erect, stout; peduncular **Bra** subfoliaceous, exceeding the internodes but exposing most of the axis; fertile **Inf** part densely white-flocculose; **Br** usually with 1 or 2 branches near the base, spreading to recurved, 50 cm, densely many-flowered; primary **Bra** very narrowly triangular, much shorter than the sterile branch bases; floral **Bra** ovate, acute, 4 mm; **Fl** spreading-ascending, narrowly elongately barrel-shaped; **Ped** very short; **Sep** suborbicular, 4 mm; **Pet** spatulate, not further described, yellow; **St** and **Sti** slightly exerted.

Described on the base of cultivated material without clear provenance. Apparently related to *D. selloa* of the “*Prionophyllum* complex”.

**D. pontesii** Büneker & al. (Rodriguésia 66(2): 500–503, ill., 2015). **Type:** Brazil, Rio Grande do Sul (*Büneker & Witeck* 212 [HDCF, RB, SMDB]). — **Distr:** S Brazil (S Rio Grande do Sul: Pinheiro Machado); conglomerate rock outcrops.

[1/3a?] **Ros** 18–60 cm  $\varnothing$ , offsetting and rhizomatous; **L**  $\pm 50$ , suberect to spreading, sheath suborbicular,  $\pm 3 \times 4.5$  cm, white, glossy, **L** lamina narrowly triangular, 15–35  $\times$  1.2–3.5 cm, stiff and succulent, straight to curved, adaxially

slightly canaliculate, green, sparsely lepidote only near the base, otherwise (sub-) glabrous, abaxially veined-striate, white-lepidote between the veins, tip a pungent spine to 6 mm, margins serrate-spinose, **Sp** slender and often inconspicuous, curved, 1–4 mm, laxly arranged, brown or yellowish; **Inf** 0.6–1.7 m tall, simple or branched; peduncle robust, 35–75 cm, green, subglabrous to densely white-flocculose-tomentose; basal peduncular **Bra** leaf-like, to 12 cm, as long as or longer than the internodes, erect, serrate, upper ones ovate to broadly elliptic, 2–6.5  $\times$  1.3–2.6 cm, entire or inconspicuously serrate; fertile **Inf** part 25–75 cm, laxly to subdensely 25- to 150-flowered, axis green or brownish-green, subglabrous to densely white-flocculose-tomentose; **Br** when present 1–7, erect or suberect-arcuate, near the base of the main axis; primary **Bra** like the upper peduncular bracts; floral **Bra** ovate-triangular, 10–21  $\times$  11–35 mm, the lower as long or longer than the flowers, the upper  $\pm \frac{1}{2}$  as long, bulging, basally green, above castaneous, subglabrous to white-tomentose; **Fl** sessile,  $\pm 20$  mm, suberect; **Ped** absent; **Sep** ovate-triangular, 6–9  $\times$  11–15 mm, brownish-yellow with greenish base, glabrous or sparsely tomentose-lepidote towards the tip, the adaxial ones carinate, the abaxial one ecarinate or slightly carinate; **Pet** obtrullate, 18–20  $\times$  10–13 mm, erect with slightly flaring tips, yellow, glabrous, tip rounded-cucullate; **St** included; **Fil** free above the common tube; **Anth** not described; **Ov**  $\pm 7 \times 4$  mm, whitish-yellow; **Sty**  $\pm 11$  mm; **Sti** not described; **Fr** ovoid, size not described, castaneous to black, very glossy.

The flowers are slightly asymmetrical (termed “zygomorphic” in the protologue) when observed from the bottom because the adaxial sepals are carinate and closer together than the ecarinate or slightly carinate abaxial sepal. The species is overall similar to *D. dusenii* and *D. elisabethae*. The only other species reported to have asymmetrical sepals (and thus zygomorphic flowers) is *D. lunaris*. — [U. Eggli]

**D. pottiorum** Leme (Phytotaxa 67: 26–28, ill., 2012). **Type:** Brazil, Mato Grosso do Sul (*Leme & al.* 8579 [RB, HB]). — **Distr:** Brazil

(Mato Grosso do Sul); shallow soil on flat or slightly inclined rock outcrops. **I:** Braun (2018: 71).

[3a] **Ros** distichously 12- to 18-leaved; **L** nearly prostrate, 23–41 × 1.5–2.5 cm, coriaceous, sheath reniform, ±2.5 × 4 cm, with castaneous base, greenish at the apex, base glabrous, towards the apex densely white-lepidote, **L** lamina sublinear-attenuate, strongly U-canaliculate, apical portion recurved, apex long acuminate-caudate, pungent-spinose, green or bronze to reddish, green specimens densely white-lepidote with glabrous apex, bronze and reddish specimens densely and coarsely white-lepidote abaxially and less dense adaxially, veined, margins glabrous, sparsely (apically) to densely spinose, **Sp** narrowly triangular to acicular, straight to prevailingly retrorse-uncinate, 1–3 mm, castaneous, 1–7 mm apart; **Inf** 23–52 cm, simple, erect; peduncle 10–34 cm, green to dark purplish wine-red, glabrous; peduncular **Bra** erect, subcarinate, long acuminate-caudate from a suborbicular base, 8–21 × 3–5 mm, densely white-lepidote to glabrous, veined, minutely spinulose; fertile **Inf** part densely 11- to 18-flowered, 6–11 cm, slightly flexuous, orange towards the apex, glabrous; floral **Bra** subtriangular-ovate, acuminate, ecarinate, suberect to subspreading, 4–8 × 3–4 mm, stramineous, thin-textured, glabrous, veined, inconspicuously denticulate to entire; **Fl** subspreading at anthesis and suberect-secund afterwards, 14–15 mm, subtubular, unscented; **Ped** 2–3 mm, stout; **Sep** ovate, ±6 × 5 mm, rounded and inconspicuously apiculate, ecarinate, orange to yellowish-orange, glabrous, entire; **Pet** broadly spatulate from a narrower base, ±11 × 9 mm, apex truncate and inconspicuously emarginate, ecarinate, orange to yellowish-orange; **St** ± equalling the petals; **Fil** free above the 1.5 mm high common tube, yellowish; **Anth** sublinear, ±4 mm, base distinctly bilobed, apiculate, slightly recurved near the apex; **Ov** ovoid, ±4.5 × 2 mm, yellowish; **Sty** ±1.5 mm, yellowish; **Sti** orange; **Fr** broadly fusiform, 12–15 × 8–10 mm, dark greenish-castaneous; **Se** suborbicular, flat, ±3.5 × 3 mm, castaneous.

Compared with *D. burchellii* and *D. coximensis* in the protologue. — [F. Krapp]

**D. princeps** Lemaire (Jard. Fleur. 3: tt. 224–225 + text, 1853). **Type:** Brazil, Minas Gerais (*Anonymus* s.n. [[icono] l.c. tt. 224–225]). — **Distr:** Brazil (Minas Gerais); ecology not recorded. **I:** Smith & Downs (1974: 515).

**Incl.** *Dyckia gigantea* K. Koch (1874) (*nom. illeg.*, Art. 52.1).

[2?] **Ros** dense, many-leaved, with a very short and stout rhizome covered with old sheaths; **L** 35–60 × 3 cm, arching-recurved, sheath suborbicular, large, **L** lamina narrowly triangular, flat, with pungent tip, glabrous adaxially, densely appressedly pale-lepidote abaxially, margins laxly serrate, **Sp** 3 mm; **Inf** 1 m or taller, amply compound; peduncle stout, short, ferruginous-tomentulose; peduncular **Bra** subfoliaceous, much exceeding the internodes, serrulate; fertile **Inf** part ferruginous-tomentulose; **Br** elongate, laxly flowered; primary **Bra** like the upper peduncular bracts, shorter than the sterile branch bases; floral **Bra** spreading, lanceolate-triangular, attenuate, exceeding the sepals; **Fl** spreading; **Ped** to 15 mm, stout; **Sep** broadly ovate, 9–10 mm, acute or apiculate, convex, ecarinate; **Pet** spreading, suborbicular, 25 mm, apiculate, red-orange; **St** included; **Fil** shortly connate above the common tube; **Anth** triangular, acuminate, strongly recurved; **Sty** very short. — [F. Krapp]

**D. pseudococcinea** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 108, t. 109, fig. 1, 1943). **Type:** Brazil, Rio de Janeiro (*Foster* 1144 [GH]). — **Lit:** Mendes & al. (2012: conservation). **Distr:** Brazil (Rio de Janeiro, São Paulo, Paraná); swampy meadows, on the ground or on rocks. **I:** Smith & Downs (1974, 542).

[3b] **Ros** dense, many-leaved; **L** 30 × 1–1.2 cm, sheath broadly elliptic, 3 cm, pale, glabrous, **L** lamina linear, attenuate, adaxially glabrous, appressedly whitish-lepidote abaxially, margins laxly serrate, **Sp** slender, spreading or retrorsely curved, 2 mm; **Inf** 60–100 cm, simple; peduncle slender, ± glabrous at anthesis; peduncular **Bra** narrowly triangular from an ovate base, the uppermost slightly shorter than the internodes, minutely serrulate; fertile **Inf** part lax, 17–25 cm, ± glabrous; floral **Bra** ovate, acuminate, ± equalling the sepals (lowest), minutely serrulate; **Fl**



spreading at anthesis, then suberect; **Ped** 3–4 mm; **Sep** ovate, 7–9 mm, acute, cucullate; **Pet** broadly elliptic, 12 mm, obtuse, ecarinate, suberect, orange; **St** much shorter than the petals; **Fil** 2 mm connate above the common tube; **Sty** very short.

Available information on the geographical range of this species is conflicting. Material identified as this species has been extensively reported from the Brazilian states as detailed above, but according to Mendes & al. (2012), as well as the Brazilian Red List for plants, *D. pseudococcinea* is endemic to the restingas of Maricá, Rio de Janeiro, and is classified as critically endangered.

**D. pulquinensis** Wittmack (Meded. Rijks-Herb. [Leiden] 29: 88, 1916). **Type:** Bolivia, Santa Cruz (*Herzog* 1849 [L, B, F [photo]]). — **Distr:** Bolivia (Santa Cruz); dry rocky slopes, 1900 m. **I:** Smith & Downs (1974: 552).

[2] **Ros** not described; **L** 14–25 × 0.6–1 cm, sheath suborbicular, 3 cm, dark castaneous, **L** lamina linear-triangular, pungent, appressedly cinereous-lepidote, glabrescent adaxially, margins very laxly serrate, **Sp** stout, retrorsely curved, 5 mm; **Inf** 80 cm, few-branched; peduncle very slender, very sparsely white-lepidote; peduncular **Bra** triangular-ovate, acute, much shorter than the internodes, upper ones 8 mm; **Inf** branches flexuous, very slender, laxly and secundly flowered; primary **Bra** like the upper peduncular bracts, much shorter than the sterile bracteate branch bases; floral **Bra** broadly ovate, apiculate, 3 mm; **Fl** 15 mm, glabrous, subsessile; **Sep** broadly ovate-elliptic, 8 mm, apiculate, fuscous when dry; **Pet** broadly obovate, 14 × 6 mm, rounded, golden-yellow; **St** slightly exerted; **Fil** free above the 1.5 mm high common tube; **Anth** narrowly triangular, 4.5 mm, distinctly recurved towards the apex; **Ov** slenderly ellipsoid, 9 mm; **Sty** none.

*D. crassifolia* is sometimes treated as synonym of this species. — [F. Krapp]

**D. pumila** L. B. Smith (Phytologia 13: 151, t. 7, fig. 13, 1966). **Type:** Brazil, Goiás (*Irwin & Soderstrom* 7365 [US, NY]). — **Distr:** Brazil (Goiás); steep rocky scree. **I:** Smith & Downs (1974, 565).

[3a] **Ros** nearly acaulescent, densely many-leaved; **L** 13 × 0.7 cm, sheath suborbicular, 2.5 cm wide, brown, glabrous, laxly and minutely serrate apically, **L** lamina linear-triangular, pungent, thick, white-lepidote, glabrous adaxially with age, margins laxly serrate, **Sp** slender, spreading, 2 mm, brown; **Inf** 18 cm, simple; peduncle erect, slender, very finely white-lepidote, soon glabrous; peduncular **Bra** ovate, attenuate, small, much shorter than the internodes, obscurely serrulate; fertile **Inf** part lax, few-flowered, 2–5 cm, very sparsely white-stellate-lepidote; floral **Bra** like the peduncular bracts but entire, to 6 mm; **Ped** 2 mm, broadly obconical; **Sep** broadly elliptic, 6 mm, rounded and apiculate, the posterior ones carinate; **Pet** very broadly subacute, 10 mm, orange; **St** barely exerted; **Fil** free above the short common tube; **Sty** ± none; **Fr** subglobose, apiculate, 13 mm, dark castaneous.

Similar to *D. duckei*. — [F. Krapp]

**D. racemosa** Baker (Handb. Bromel., 132, 1889). **Type:** Brazil, Goiás (*Gardner* 4015 [K, K [photo]]). — **Distr:** Brazil (Goiás); dry hills.

[3b] **Ros** not described; **L** >40 × >2 cm, sheath not described, **L** lamina narrowly triangular, covered with a membrane of fused scales abaxially, margins laxly serrate, **Sp** 1.5 mm; **Inf** >85 cm, simple; peduncle very slender, glabrous; peduncular **Bra** remote, broadly ovate, acuminate, entire; fertile **Inf** part lax, >15 cm, minutely furfuraceous; floral **Bra** broadly elliptic, obtuse or sometimes minutely mucronate, to 3 mm; **Fl** ascending, 10 mm, glabrous; **Ped** to 6 mm; **Sep** elliptic-ovate, 6 mm, obtuse; **Pet** erect or suberect, subrhombic, obtuse, slightly carinate, red; **St** included; **Fil** high-connate above the common tube; **Anth** narrowly triangular, acuminate, slightly recurved; **Sty** ½ as long as the ovary.

**D. racinae** L. B. Smith (J. Bromeliad Soc. 38 (6): 248–249, figs. 5 and 6, 1988). **Type:** Brazil, Rio Grande do Sul? (*Foster* 3095 [US, B, GH, NY]). — **Lit:** Dorneles & al. (2014: with ill.). **Distr:** Brazil (Rio Grande do Sul: near São Pedro do Sul); open Pampa vegetation on shallow stony soil.

[1] **Ros** spreading, acaulescent; **L** >55 × 4 cm, sheath pale, **L** lamina obscurely lepidote abaxially between the veins, glabrous adaxially, margins laxly serrate, **Sp** curved, 5 mm; **Inf** to >2 m, seemingly terminal, laxly amply 2× branched; peduncle erect; peduncular **Bra** subfoliaceous, exceeding the internodes but exposing most of the peduncle; **Inf** branches glabrous, lax, somewhat secundly flowered, 50 cm; primary **Bra** very narrowly triangular, much shorter than the sterile branch bases; floral **Bra** attenuate from a broadly ovate base, ± equalling the sepals, enlarging in fruit to 25 mm; **Ped** very short at anthesis, to 6 mm in fruit, stout; **Sep** broadly ovate-lanceolate, 6–7 × 3–4 mm, rounded and apiculate, glabrous to sparsely pilose; **Pet** obovate to spatulate, 12–13 × 5–6 mm, obtuse, glabrous, golden-yellow with paler margins; **St** just included; **Fil** free above the common tube; **Anth** triangular with curved apex and cordate base; **Fr** ovoid, beaked, black; **Se** with asymmetric lateral wings.

Part of the “*Prionophyllum* complex”, and similar to *D. selloa*. Dorneles & al. (2014) provide an amplified description based on recently collected material. They argue that the species is close to *D. cabreræ*, which differs by larger flowers on longer pedicels.

**D. ragonesei** A. Castellanos (Lilloa 10: 454, fig. 2, 1944). **Type:** Argentina, Santa Fé (Castellanos s.n. [BA 19465, US [photo]]). — **Distr:** N Argentina (Entre Ríos, Santa Fé, Santiago del Estero), Bolivia (Santa Cruz), Paraguay (Boquerón, Amambay, Canindeyú); rocky slopes. **I:** Smith & Downs (1974, 555).

[2/3b?] **Ros** not described; **L** 40 × 1.2 cm, sheath broadly triangular, curved, semi-amplexicaul, 3 × 6 cm, **L** lamina linear-triangular, serrate, **Sp** curved, 4 mm, brown; **Inf** 60–80 cm, paniculate or simple; peduncle elongate, furfuraceous; peduncular **Bra** deltoid, shorter than the internodes; fertile **Inf** part yellow-furfuraceous; **Br** subdensely flowered; floral **Bra** broadly triangular, to 7 mm, tomentose-lepidote; **Fl** ±16 mm, sessile; **Sep** ovate, 8 mm, obtuse, margins hyaline; **Pet** 14–15 mm, broadly and irregularly rounded, undulate, golden-yellow; **St** distinctly exserted; **Fil** 3–5 mm connate above the

2 mm high common tube; **Anth** oblong, apiculate, straight, 5 mm; **Sty** 1 mm; **Fr** pyramidal, 17 × 12 mm; **Se** with a falcate wing, 4–5 × 5 mm.

Usually cited as endemic for Argentina, but also reported from Bolivia and Paraguay as shown above (E. Gouda, pers. comm., Dec. 2016).

**D. rariflora** Schultes *fil.* (in Roemer & Schultes, Syst. Veg. 7(2): 1195, 1830). **Type:** Brazil, Minas Gerais (*Martius* s.n. [M, F [photo]]). — **Distr:** Brazil (Minas Gerais); rocky fields, savanna, terrestrial or on rocks; ±1000 m. **I:** Smith & Downs (1974: 552).

[3b] **Ros** not described; **L** to 14 × ±1 cm, sheath broadly ovate, large, **L** lamina narrowly triangular, attenuate, with pungent tip, sparsely pale-appressed-lepidote abaxially, margins laxly serrate, **Sp** stout, curved, 3 mm; **Inf** to 50 cm, simple or branched; peduncle somewhat lepidote; peduncular **Bra** broadly ovate, acuminate, shorter than the internodes, entire or serrulate; fertile **Inf** part with a few short branches at the base, lax or subdense towards the apex, few-flowered, soon glabrous; floral **Bra** reflexed, broadly ovate, apiculate, 7–10 mm, equalling or shorter than the sepals; **Fl** spreading; **Ped** very short but distinct; **Sep** broadly ovate, 6 mm, broadly subacute; **Pet** suberect, broad, 9 mm, obtuse, carinate, orange; **St** included; **Fil** high-connate above the common tube; **Anth** elliptic, apiculate, straight or slightly recurved; **Sty** 1/5 as long as the ovary.

Some early illustrations purporting to represent this species in fact show *D. remotiflora* (Smith & Downs 1974: 526).

**D. reitzii** L. B. Smith (Anais Bot. Herb. “Barbosa Rodrigues” 2: 14, tt. 1–3, 1950). **Type:** Brazil, Santa Catarina (*Reitz* 2690 [US, HBR]). — **Distr:** Brazil (Minas Gerais, Paraná, Santa Catarina, Rio Grande do Sul); sandstone ledges and rocky soil, 1500–2500 m. **I:** Reitz (1983: t. 50); Klein V. & Klein (2014: 77, 79).

[3b] **Ros** dense, ±100-leaved; **L** to 38 × 1–2 cm, sheath suborbicular, 3.5 cm wide, brown, soon glabrous, laxly serrulate, **L** lamina triangular-linear, attenuate, with pungent tip, smooth and glabrous adaxially, cinereous and strongly veined abaxially, margins laxly serrate, **Sp** curved,

1.5–3 mm, antrorse, 10 mm apart; **Inf** 50 cm, simple; peduncle slender, ferrugineous-flocculose; peduncular **Bra** densely imbricate, lanceolate, acuminate, cinereous-flocculose, serrulate; fertile **Inf** part densely  $\pm$ 30-flowered, 9–12 cm, ferrugineous-flocculose to subglabrous; floral **Bra** like the peduncular bracts, exceeding the flowers; **Fl** subspreading, some with additional petals; **Ped** 5 mm, stout; **Sep** ovate, 8–9 mm, acute and cucullate, densely ferrugineous-tomentose; **Pet** rhomboid, 16 mm, somewhat spreading, yellow or reddish-yellow; **St** included; **Fil** high-connate above the common tube; **Ov** pyramidal; **Sty** short; **Sti** slightly contorted.

**D. remotiflora** Otto & A. Dietrich (Allg. Gartenzeitung 1: 129, 1833). **Type:** Brazil (*Sellow* s.n. [B, K]). — **Distr:** Brazil (Minas Gerais, Paraná, São Paulo, Santa Catarina, Rio Grande do Sul), Uruguay, N Argentina (Entre Ríos).

$\equiv$  *Dyckia rariflora* var. *remotiflora* (Otto & A. Dietrich) Baker (1889).

[3a] **Ros** offsetting, rhizome short and stout; **L** 10–25  $\times$  0.8–1.2 cm, arching, flat, sheath broadly ovate or suborbicular, large, **L** lamina narrowly triangular, with pungent tip, evenly dark green, appressedly pale-lepidote esp. abaxially, laxly serrate, **Sp** slender, curved, 1–3 mm; **Inf** to 1 m, simple; peduncle stout, sparsely tomentulose at the nodes; peduncular **Bra** suborbicular, the lowest laminate, all but the lowest much shorter than the internodes; fertile **Inf** part lax, 12–20 cm, sparsely tomentulose when young; floral **Bra** broadly ovate, shorter than the sepals; **Fl** divergent to spreading; **Ped** very short, stout; **Sep** ovate, apiculate,  $\pm$  carinate; **Pet** lamina spreading, trapeziform, obtuse, carinate, dark orange; **St** included; **Fil** free above the common tube; **Anth** narrowly triangular, recurved; **Sty** as long as or longer than the ovary.

Some early illustrations labelled *D. rariflora* in fact show *D. remotiflora* (Smith & Downs 1974: 526).

**D. remotiflora** var. *angustior* L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 108, 1943). **Type:** Brazil, Rio Grande do Sul (*Bornmueller* 351 [GH]). — **Distr:** Brazil (Rio Grande do Sul); ecology not recorded.

[3a] Upper peduncular **Bra** and floral **Bra** acuminate. — [F. Krapp]

**D. remotiflora** var. *montevidensis* (K. Koch) L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 108, 1943). **Type:** Uruguay, Montevideo (*Sellow* s.n. [B]). — **Distr:** Brazil (Rio Grande do Sul), Uruguay, N Argentina (Entre Ríos); dry open rocky ground, to 50 m.

$\equiv$  *Dyckia montevidensis* K. Koch (1874)  $\equiv$  *Dyckia rariflora* var. *montevidensis* (K. Koch) Baker (1889).

[3a] Upper peduncular **Bra** and floral **Bra** with broad apiculate tip; **Sep** nearly or quite straight, 6–8 mm; **Pet** 11–17 mm.

Formerly also cited to occur in Santa Catarina, but the references relate to *D. leptostachya* (Reitz 1983: 516–517). — [F. Krapp]

**D. remotiflora** var. *remotiflora* — **Distr:** Brazil (Minas Gerais, Paraná, São Paulo, Rio Grande do Sul), Uruguay; rocky fields, savanna, on rocks or terrestrial. — Fig. 9.



**Fig. 9** *Dyckia remotiflora* var. *remotiflora* (Birolini s.n.: Uruguay; Maldonado, Punta Ballena). (Copyright: U. Eggli)

**Incl.** *Dyckia rariflora* var. *cunninghamii* Baker (1889); **incl.** *Dyckia vaginosa* Mez (1894).

[3a] Upper peduncular **Bra** and floral **Bra** with broad apiculate tip; **Sep** cucullate, 8–10 mm; **Pet** 17–23 mm. — [F. Krapp]

**D. remotiflora** var. **tandilensis** (Spegazzini) Cabrera (Fl. Prov. Buenos Aires 4(1): 449, 1968). **Type:** Argentina, Buenos Aires (*Spegazzini* 219 [LP]). — **Distr:** Argentina (Buenos Aires); ecology not recorded; only known from the type collection and apparently extinct.

≡ *Dyckia montevidensis* var. *tandilensis* Spegazzini (1901).

[3a] Upper peduncular **Bra** and floral **Bra** with broad acuminate tip; **Sep** cucullate; **Pet** <10 mm. — [F. Krapp]

**D. retardata** S. Winkler (Doc. Nat. 3: 42–43, fig. 4, 1982). **Type:** Brazil, Rio Grande do Sul (*Winkler* 7424 [ICN]). — **Distr:** Brazil (Rio Grande do Sul); dry granitic rocks.

[1] **Ros** to 60 cm Ø, acaulescent or with very short stem, many-leaved; **L** to 35 × 3 cm, sheath not described, **L** lamina glabrous, marginal **Sp** to 4 mm; **Inf** to 1.5 m, 2× branched; peduncle glabrous; peduncular **Bra** foliaceous, acuminate, exceeding the internodes (lower) or shorter (upper), glabrous, entire; **Inf** branches of 2. order often originating pairwise, younger parts of the axes white-furfuraceous; floral **Bra** triangular, small, to 2 mm; **Fl** sessile; **Sep** acuminate, to 8 mm, yellowish, white-lanate; **Pet** with rounded tip, to 10 mm, yellow, abaxially white-lepidote; **St** included and just equalling the petals; **Fil** free above the common tube; **Sty** terminally capitate, exerted for 2 mm.

The protologue has only a short and incomplete description. The species is said to be notable because older inflorescences can simultaneously have flowers and ripe fruits.

**D. retroflexa** S. Winkler (Doc. Nat. 3: 44, fig. 5, 1982). **Type:** Brazil, Rio Grande do Sul (*Winkler* 7410 [HPA]). — **Distr:** Brazil (Rio Grande do Sul); shady rocks.

[1] **Ros** to 40 cm Ø, acaulescent or with very short stem; **L** to 25 × 3 cm, sheath not described,

**L** lamina dark green, both faces glabrous, margins with **Sp** to 5 mm; **Inf** to 1.2 m, 2× branched; peduncular **Bra** long-acuminate, exceeding the internodes, tip brown, white-lepidote, finely spinose; floral **Bra** triangular, very small, to 1 mm; **Fl** directed backwards at anthesis, sessile; **Sep** oblong-ovate, to 5 mm, appressedly white-lepidote; **Pet** to 9 mm, with broadly rounded tip, yellow, abaxially villous; **St** slightly exerted, visible at anthesis; **Fil** free above the common tube; **Sty** appearing capitate but 3-fid, distinctly exceeding the petals.

Part of the “*Prionophyllum* complex”, and morphologically similar to *D. rigida*.

**D. richardii** P. J. Braun & Esteves (Cact. Succ. J. (US) 80(6): 321, ill. (pp. 319–320), 2008). **Type:** Brazil, Goiás (*Esteves Pereira* 366 [UFG]). — **Lit:** Braun & Esteves Pereira (2009b). **Distr:** Brazil (Goiás); outcrops of reddish strongly fragmented sedimentary rocks, in full sun. **I:** Braun (2018: 68).

[3a] **Ros** 19–29 cm Ø, solitary or sometimes forming groups with age, with bulbous base and 17–30 (–57) living leaves, with a stem 1.4–4.3 × 2.4–3.2 cm; **L** 10–18 × 2.3–2.7 cm, fleshy, green to light green, sheath concave, ±2.7 × 4.5 cm, brilliant white, sometimes brownish abaxially, **L** lamina succulent, erect (younger) or recurved (older), narrowly triangular, canaliculate and V-shaped in cross-section, with pungent orange-green to reddish tip, adaxially bright green, sparsely white-lepidote abaxially, strongly veined, margins laxly and irregularly serrate, **Sp** flattened, retrorse, sometimes straight, 3.5–5 mm, brown to dark or reddish-brown, hard, pungent; **Inf** to 30 cm, simple; peduncle slightly thickened at the nodes; peduncular **Bra** leaf-like and slightly secund (lowest) to somewhat leaf-like and lanceolate and acute (upper), lowest to 23 mm, entire, glabrous, lower ones serrate, upper ones soon withering; fertile **Inf** part 7- to 13-flowered, dense apically, 7.5–23 cm, rachis light green at the base, reddish-green in the flowering region, glabrous; floral **Bra** obtuse, mucronate, ±4 × 3.5 mm, reddish-orange, glabrous; **Fl** ±17 mm, sessile; **Sep** to 8 × 5 mm, ecarinate, succulent, reddish to orange-yellow; **Pet** to 12 mm, obtuse,

erect, yellow to orange-yellow; **St** exerted; **Fil** free above the short common tube, white,  $\pm 11$  mm; **Anth** light yellow, arching outwards; **Ov** subpyramidal at the base, greenish-white; **Sty**  $\pm 1.5$  mm; **Fr** ellipsoid-ovoid, to  $14 \times 12$  mm, shiny dark brown. — [F. Krapp]

**D. rigida** Strehl (*Vidalia* 2(2): 32–34, figs. 9–12, 2004). **Type:** Brazil, Rio Grande do Sul (*Strehl* 1502 [HAS]). — **Distr:** Brazil (Rio Grande do Sul); hillsides, slopes and cliffs, 500 m.

[1] **Ros** 50- to 60-leaved, 100 cm  $\varnothing$ , caulescent with a stem to  $40 \times 10$  cm; **L** sheath ovate,  $10\text{--}12 \times 8\text{--}10$  cm, glossy, brown, **L** lamina  $55\text{--}60 \times 6\text{--}10$  cm, lanceolate-triangular, acuminate, acute with pungent tip, adaxially dark green, abaxially white-veined, margins spinose, **Sp** antrorse, uncinata, 5 mm, black; **Inf** to 1.8 m,  $2\text{--}3 \times$  branched; peduncle stout,  $\pm 50$  cm, brownish-green; lowest peduncular **Bra** long-triangular, acute,  $10\text{--}20 \times 4$  mm, sparsely serrate, shorter than the internodes, laxly arranged, slightly serrate; fertile **Inf** part lax, 50–80 cm, axis brownish-green, finely white-lepidote; **Br** 27–35 cm; floral **Bra** triangular, acute,  $1\text{--}2 \times 1$  mm, abaxially puberulous, subtentire; **Fl** irregularly arranged, sometimes  $\pm$  verticillate, narrowly tubular with slightly flaring throat; **Ped** 1–2 mm; **Sep** ovate,  $3\text{--}4 \times 2$  mm, apiculate to rounded and sometimes apiculate, pale green or pale brown, white-lepidote abaxially; **Pet** spatulate with narrowed base,  $\pm 6 \times 3\text{--}4$  mm, rounded, yellow, glabrous; **St**  $\pm$  as long as the petals; **Fil** yellow, free; **Anth** just exerted,  $\pm 3$  mm, yellow to pale brown; **Ov**  $3\text{--}4 \times 2$  mm, green; **Sty**  $\pm 8$  mm, white; **Fr** and **Se** not described.

Part of the “*Prionophyllum* complex”, and morphologically similar to *D. retroflexa*. Commonly confused with *D. maritima*.

**D. rondonopolitana** Leme (*Phytotaxa* 67: 28–30, ill., 2012). **Type:** Brazil, Mato Grosso (*Kranz* 123 [RB]). — **Distr:** Brazil (Mato Grosso); reddish sandstone outcrops, Cerrado vegetation.

[3a] **Ros** densely 20- to 30-leaved, slowly off-setting, acaulescent; **L**  $20\text{--}22 \times 1\text{--}1.5$  cm,

$3\text{--}5$  mm thick, coriaceous, sheaths wider than the lamina, **L** lamina narrowly triangular, apically slightly canaliculate, arcuate, apex long acuminate-caudate and recurved, pungent, green to reddish, adaxially (sub-) densely white-lepidote with glabrescent apex, abaxially densely white-lepidote and finely veined, margins subdensely spinose, **Sp** acicular, spreading to retrorse,  $3\text{--}6$  mm, densely white-lepidote,  $6\text{--}12$  mm apart; **Inf**  $\pm 38$  cm, simple; peduncle  $\pm 20$  cm, reddish, glabrous; peduncular **Bra** subtriangular-ovate, acuminate-caudate, membranous, erect,  $6\text{--}15 \times 5\text{--}8$  mm, greenish-yellow to reddish and soon stramineous towards the apex, white-lepidote to glabrous, veined, lowest ones remotely spinulose; fertile **Inf** part densely  $\pm 40$ -flowered, suberect, straight,  $\pm 14$  cm, yellowish-orange, glabrous; basal floral **Bra** like the upper peduncular bracts, broadly subtriangular-ovate, acuminate to acute, ecarinate, convex, membranous,  $6\text{--}10 \times 5\text{--}9$  mm, distinctly shorter than the sepals, greenish-yellow, glabrous, remotely crenulate to entire; **Fl** subspreading,  $17\text{--}18$  mm,  $\pm$  barrel-shaped with narrow throat; **Ped**  $\pm 3$  mm, stout; **Sep** ovate,  $\pm 8 \times 6.5$  mm, convex, apex obtuse or erose, membranous, yellow, glabrous; **Pet** spatulate,  $\pm 13 \times 10$  mm, subacute, ecarinate, yellow; **St** slightly exerted; **Fil** free above the 2 mm high common tube,  $10\text{--}11$  mm, whitish; **Anth** narrowly subtriangular, recurved at anthesis,  $\pm 4$  mm, base bilobed, acuminate; **Ov** suboblong-ovoid,  $\pm 3.5 \times 1.5$  mm, yellowish; **Sty**  $\pm 0.5$  mm, yellowish; **Sti** distinctly scalloped-lacerate, yellow,  $\pm 1$  mm.

Compared with *D. dawsonii* in the protologue, but with broader leaves and different marginal spines, and with shorter inflorescences with more numerous and densely arranged larger flowers.

**D. saxatilis** Mez (in A. & C. de Candolle, *Monogr. Phan.* 9: 518, 1896). **Type:** Brazil, Minas Gerais (*Schwacke* 8948 [B, F [photo]]). — **Distr:** Brazil (Minas Gerais, Bahia, Goiás, Mato Grosso); rocky fields, savanna, terrestrial or on rocks. **I:** Smith & Downs (1974: 558, 565, 568); Rauh & Gross (1988: 18, as *D. oligantha* var. *crystallina*).



**Incl.** *Dyckia hilaireana* Mez (1896); **incl.** *Dyckia oligantha* L. B. Smith (1958); **incl.** *Dyckia oligantha* var. *crystallina* Rauh (1988).

[3b] **Ros** symmetrical, 13–46 cm Ø, with a bulbous base densely covered with old leaf sheaths; **L** 15 × 1.1 cm, spreading-arcuate, sheath suborbicular, 4 cm wide, **L** lamina narrowly triangular, flat to slightly canaliculate, pale green abaxially, slightly ribbed, closely appressedly finely-lepidote, margins at least in the apical 1/3 laxly serrate, **Sp** slender, antrorse, 1.5–2.3 mm, 19–30 mm apart; **Inf** 40 cm, simple; peduncle very slender, ± compressed, soon glabrous; peduncular **Bra** ovate to elliptic to oblong, acuminate, shorter than the internodes, entire or upper ones minutely fimbriate; **Inf** simple, lax, to 14 cm, lepidote; floral **Bra** reflexed, broadly ovate, acuminate, equalling or exceeding the sepals, without prominent midrib, minutely fimbriate; **Fl** erect to spreading, 11 mm, orange; **Ped** very short but distinct; **Sep** broadly ovate-elliptic, ±8 mm, obtuse, minutely fimbriate, subglabrous; **Pet** erect, lamina very broadly obovate, emarginate; **St** included; **Fil** 2 mm connate above the common tube; **Anth** triangular-elliptic, subacute, slightly recurved; **Sty** 1–2 mm.

*D. saxatilis* forms a complex that includes, inter alia, *D. consimilis* and *D. rariflora* as well as the recently described *D. concepcionensis*, *D. ferrisicola* and *D. sulcata*.

**D. schwackeana** Mez (in Martius, Fl. Bras. 3 (3): 478, 1894). **Type:** Brazil, Minas Gerais (*Schwacke* 5857 [B]). — **Distr:** Brazil (S-C Minas Gerais); rocky fields.

[3b] **Ros** acaulescent, 40- to 50-leaved, slowly offsetting, with a bulbous base and a short thick rhizome; **L** inner erect, outer recurved, sheath depressedly semiorbicular, brown, **L** lamina 6 × 1.2 cm, narrowly triangular, attenuate with strongly pungent tip, appressedly cinereous-lepidote abaxially, margins very laxly serrulate, **Sp** acicular, straight or curved, to 3 mm; **Inf** to 30 cm, erect, simple; peduncle slender, to 20 cm, furfuraceous towards the apex; peduncular **Bra** ovate with linear lamina, exceeding the internodes, obscurely serrulate; fertile **Inf** part ±5 cm, few-flowered, furfuraceous; floral **Bra**

broadly ovate with narrowly triangular lamina, equalling the sepals of the lower flowers; **Fl** lowest erect, upper spreading, 11–12 mm; **Ped** 0.5–1 mm; **Sep** narrowly elliptic, to 7 mm, obtuse or apiculate, abaxially furfuraceous, with narrow pellucid margin; **Pet** to 11 mm, obovate, broadly rounded, erect with slightly flaring limb, obovate, broadly obtuse, obscurely carinate, orange; **St** deeply included; **Fil** 2 mm connate above the common tube; **Anth** short, stout, obtuse, scarcely recurved; **Ov** ellipsoid-trigonal, deeply three-sulcate; **Sty** stout, 1/5 – 1/4 as long as the ovary; **Sti** minute; **Fr** and **Se** not described.

**D. secunda** L. B. Smith (Phytologia 14: 487, t. 1, figs. 37–41, 1967). **Type:** Brazil, Bahia (*Irwin & al.* 14723 [NY]). — **Distr:** Brazil (Bahia); ecology not described, ±850 m.

[3b] **Ros** not described; **L** >25 × to 2.4 cm, sheath not described, **L** lamina very narrowly triangular, appressedly cinereous-lepidote on both faces but becoming ± glabrous adaxially, margins laxly serrate, **Sp** retrorsely curved, 2 mm, brown; **Inf** 90 cm, simple; peduncle very slender, glabrous; peduncular **Bra** remote, triangular, acuminate, lower ones subfoliaceous, upper ones small, subentire; fertile **Inf** part very laxly secund-flowered, to 23 cm, sparsely and fugaciously pale-lepidote; floral **Bra** acute, distinctly exceeding the pedicels (lowest), entire; **Fl** spreading; **Ped** 3 mm, cylindrical; **Sep** ovate, 7 mm, rounded, thin, brownish; **Pet** apparently rather fleshy, lamina broadly rhomboid, 12 mm, ecarinate, brown; **St** included; **Fil** short-connate above the common tube; **Sty** ±1 mm.

The laxly secund inflorescence and the brown flowers are notable.

**D. secundifolia** Leme (Phytotaxa 67: 31–33, iils., 2012). **Type:** Brazil, Mato Grosso (*Kranz* 129 [RB, HB]). — **Distr:** Brazil (Mato Grosso); shallow soils in depressions and crevices of sandstone rock outcrops.

[3b] **Ros** dense, 25- to 30-leaved; **L** 8–11 × 1–1.4 cm, coriaceous, sheath suborbicular, **L** lamina narrowly triangular, ± flat, suberect to ± erect and unilaterally curved, acuminate, with pungent tip, light green, adaxially

subdensely to laxly white-lepidote, abaxially subdensely white-lepidote, veined, margins glabrous, laxly to subdensely spinose, **Sp** narrowly triangular, straight or sometimes slightly antrorse, 0.5–1 mm, glabrous, pale castaneous, 4–10 mm apart; **Inf** 55–62 cm, simple, erect; peduncle  $\pm 30$  cm, reddish towards the apex, sparsely and inconspicuously white-lepidote to glabrous; peduncular **Bra** erect, obtusely if at all carinate, broadly triangular from a slightly gibbose base, long laminate to acuminate,  $10\text{--}21 \times 4\text{--}7$  mm, reddish to stramineous, subdensely white-lepidote to glabrescent, veined, remotely denticulate to entire; fertile **Inf** part 14- to 22-flowered, lax, straight, 23–25 cm, rachis orange-red, subdensely but inconspicuously white-lepidote to glabrescent; floral **Bra** ovate, acuminate-caudate (lowest) to narrowly acute and apiculate (upper), suberect to  $\pm$  spreading at anthesis, ecarinate,  $5\text{--}9 \times 3.5\text{--}5$  mm, orange-red, apex stramineous, subdensely and inconspicuously white-lepidote, finely veined, subentire to entire; **Fl** suberect to  $\pm$  spreading at anthesis, erect afterwards, 16–17 mm, tubular, unscented; **Ped** 2.5–3 mm, orange, sparsely white-lepidote to glabrous; **Sep** broadly ovate,  $7\text{--}8 \times 6\text{--}7$  mm, emarginate, ecarinate, strongly convex, orange-red, subdensely white-lepidote to glabrous, entire, densely fimbriate; **Pet** subrhomboid-orbicular,  $11\text{--}13 \times 11$  mm, obtuse-emarginate, ecarinate, orange to reddish-orange, glabrous, inconspicuously crenulate; **St** equalling the petals or slightly shorter; **Fil** 8–10 mm, 1.5–2 mm connate above the 2 mm high common tube, pale orange towards the apex; **Anth** narrowly subtriangular, 3–3.5 mm, strongly recurved at anthesis, base bilobed, apiculate; **Ov** narrowly suboblong,  $\pm 6$  mm, pale yellow; **Sty**  $\pm 1$  mm; **Sti**  $\pm 1.5$  mm, orange, minutely crenulate-lacerate.

Compared with *D. coximensis* in the protologue.

**D. selloa** (K. Koch) Baker (Handb. Bromel., 136, 1889). **Type:** Uruguay? (*Sellow* 3339 [B, GH, NY, US]). — **Distr:** Brazil (Rio Grande do Sul), Uruguay?; sandstone cliffs. **I:** Smith & Downs (1974: 512).

$\equiv$  *Prionophyllum selloum* K. Koch (1874); **incl.** *Dyckia grandifolia* Baker (1889); **incl.** *Dyckia macracantha* Baker (1889); **incl.** *Dyckia myriostachya* Baker (1889).

[1] **Ros** acaulescent; **L** rigid, arching, sheath conspicuous, reniform (outer) to ovate (inner), castaneous abaxially, glossy, glabrous except abaxially near the apex, margins minutely spinose, **L** lamina to  $30 \times 3.3$  cm, thinly to densely cinereous-lepidote esp. abaxially, with pungent tip, margins laxly serrate, **Sp** stout, deltoid-cuspidate, straight to retrorse, 6 mm; **Inf**  $> 70$  cm, compound and  $2\text{--}3 \times$  branched; peduncle 45–60 cm, stout, glabrous; peduncular **Bra** leaf-like, much exceeding the internodes, appressedly lepidote, margins strongly spinose; fertile **Inf** part 30 cm, glabrous, **Br** numerous, spicate, the lowest to 20 cm, those with perfect flowers lax or sometimes flowers subverticillate, those with pistillate flowers dense in the apical  $\frac{1}{2}$ ; primary **Bra** narrowly lanceolate, attenuate, much shorter than the branches, usually entire, quickly deciduous; floral **Bra** broadly ovate, apiculate, 2–3 mm; **Fl** divergent to spreading, sessile, perfect **Fl** to 13 mm, pistillate **Fl** 6 mm; **Sep** suborbicular or broadly ovate, 5 mm (perfect flowers) or 2 mm (pistillate flowers), apiculate, together forming an urceolate structure that embraces the petals; **Pet** obovate to lanceolate, somewhat spreading, 11–12 mm (perfect flowers) or 5–5.5 mm (pistillate flowers), acute or obtuse, yellow; **St**  $\pm$  equalling the petals or slightly shorter; **Fil** free above the short common tube; **Anth** 2.5 mm or  $< 1$  mm and sterile in pistillate flowers; **Ov** narrowly pyramidally trigonous in perfect flowers or almost globose in pistillate flowers; **Sty** slender, elongate,  $2 \times$  as long as the ovary, **Sti** contorted and forming a club-shaped structure; **Fr** and **Se** not described.

*D. selloa* is the type species of *Prionophyllum*. The above description is largely based on Mez (1891–1892: 500–501). The dimorphic flowers (perfect, female) are notable and are described in detail by Mez, while Baker (1889) does not mention them. The only other species where similarly dimorphic flowers have been recorded is *D. maritima* Smith & Downs (1974), and it remains unknown whether other species assigned

to the “*Prionophyllum* complex” also show this characteristic.

**D. sellowiana** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 520, 1896). **Type:** Brazil (*Sellow* Brom. Paris 52 [P, GH [photo]]). — **Distr:** Brazil (Distrito Federal, Minas Gerais); bushy fields, Campo Rupestre vegetation.

[3b] **Ros** not described; **L**  $\pm 25 \times 1$  cm, sheath not described, **L** lamina narrowly triangular, with pungent tip, appressedly pale-lepidote abaxially, laxly serrate, **Sp** curved, 2 mm; **Inf**  $>70$  cm, simple; peduncle slender, glabrous; peduncular **Bra** remote, triangular, pungent, serrulate; fertile **Inf** part lax,  $\pm 20$  cm, sparsely furfuraceous or glabrous; floral **Bra** spreading to reflexed, ovate with long triangular lamina, 8–10 mm, exceeded by the sepals, minutely puberulent; **Fl** spreading or reflexed at anthesis, 12 mm; **Ped** short but distinct, stout; **Sep** elliptic, 6.5 mm, subobtuse, glabrous; **Pet** lamina erect, obovate, broadly rounded, scarcely if at all carinate, colour not described; **St** included; **Fil** high-connate above the common tube; **Anth** subtriangular, acute, strongly recurved.

Insufficiently known, and described on the base of material without known provenance.

**D. sickii** L. B. Smith (Arq. Jard. Bot. Rio de Janeiro 15: 330, fig. m–q, 1958). **Type:** Brazil, Pará (*Sick* B-613 [RB, US]). — **Distr:** Brazil (Pará); on rocks. **I:** Smith & Downs (1974: 565).

[3a] **Ros** not described; **L** to  $20 \times 0.7$  cm, sheath suborbicular,  $\pm 2$  cm wide, brown abaxially, soon glabrous, subdensely serrulate, **L** lamina very narrowly triangular, with pungent tip, glabrous adaxially, sulcate when dry, finely appressedly whitish-lepidote abaxially or the veins glabrous, margins laxly serrate, **Sp** slender, curved, 1.5 mm; **Inf** 45 cm, simple; peduncle erect, very slender, glabrous; peduncular **Bra** broadly ovate with a very narrow triangular lamina, very small, entire, remote; fertile **Inf** part very lax, slender, slightly flexuous, 20–22 cm, glabrous; floral **Bra** short-acuminate from a broadly ovate base, 7 mm, entire; **Fl** divergent or more often spreading; **Ped** 4 mm, cylindrical; **Sep**

broadly ovate, 5 mm, sometimes erose at the apex, ecarinate, very obscurely lepidote; **Pet** broadly obovate, 10 mm, obtusely carinate, orange-yellow; **St** very slightly exerted; **Fil** free above the common tube; **Anth** oblong, strongly curved; **Ov** slenderly pyramidal; **Sty** very short. — [F. Krapp]

**D. silvae** L. B. Smith (Phytologia 13: 151, t. 7, figs. 14 and 15, 1966). **Type:** Brazil, Pará (*Silva* 784 [IAN]). — **Distr:** Brazil (Pará); on rocks in “Campo” vegetation. **I:** Smith & Downs (1974: 542).

[3a] **Ros** spreading, many-leaved, acaulescent; **L**  $25 \times 2$  cm, rigid, thick, sheath suborbicular, 3 cm wide, brown, nearly glabrous, **L** lamina linear-triangular, filiform-attenuate, appressedly white-lepidote, glabrous adaxially with age, margins laxly serrate, **Sp** slender, spreading, 3 mm, brown; **Inf** 66 cm, simple; peduncle erect, slender, very sparsely white-lepidote, soon glabrous; lower peduncular **Bra** leaf-like, upper broadly ovate-attenuate, small but nearly all exceeding the internodes except the uppermost; fertile **Inf** part subdensely many-flowered, 18 cm, very sparsely white-lepidote; floral **Bra** like the uppermost peduncular bracts, lowest  $\pm$  equalling the sepals, serrulate; **Ped** 3 mm, subcylindrical, thick, strongly constricted at the base and appearing articulate; **Sep** 6–7 mm, ovate, obtuse with a wide thin margin; **Pet** to  $17 \times 6$  mm, broadly rounded, strongly carinate, curved-spreading, yellow; **St** completely included; **Fil** free above the short common tube; **Sty** none. — [F. Krapp]

**D. simulans** L. B. Smith (Arq. Bot. Estado São Paulo ser. 2, 1: 108, t. 110, 1943). **Type:** Brazil, Minas Gerais (*Foster* 570 [GH]). — **Distr:** Brazil (Minas Gerais); rocky fields, 1300 m. **I:** Smith & Downs (1974: 530).

[3a] **Ros** not described; **L**  $7\text{--}8 \times 0.8\text{--}1$  cm, rigid, sheath suborbicular, large, **L** lamina narrowly triangular, with pungent tip, appressedly cinereous-lepidote, margins laxly serrate, **Sp** spreading, 2 mm; **Inf** to 30 cm, simple; peduncle slender, furfuraceous, soon glabrous; peduncular **Bra** ovate, long-acuminate, exceeding the

internodes, serrulate; fertile **Inf** part insufficiently known, probably becoming lax, 4 cm when young, densely furfuraceous; floral **Bra** broadly ovate, acute,  $\pm$  equalling the flowers (lowest), minutely serrulate; **Fl** spreading; **Ped**  $\pm$  3 mm, stout; **Sep** broadly ovate, 9–10 mm, obtuse, cucullate; **Pet** suborbicular, slightly exceeding the sepals, reddish, glabrous; **St** included; **Fil** free above the 2 mm high common tube; **Sty** very short. — [F. Krapp]

**D. sordida** Baker (Handb. Bromel., 132, 1889). **Type:** Brazil, Minas Gerais (*Saint Hilaire* 402 [P, GH [photo]]). — **Lit:** Guarçoni & al. (2012). **Distr:** Brazil (Minas Gerais); rocky slopes, 1300–1400 m.

**Incl.** *Dyckia duarteana* L. B. Smith (1967).

[3a] **Ros** usually caespitose, 32- to 50-leaved; **L** 50 cm or longer, sheaths suborbicular, 4 cm, dark castaneous, **L** lamina very narrowly triangular, green with reddish margins, adaxially sparsely lepidote, abaxially densely or sparsely and inconspicuously lepidote, margins almost entire, **Sp** only few, 1 mm, almost obsolete; **Inf** to 1 m, simple; peduncle stout, sparsely floccose; peduncular **Bra** subfoliaceous, shorter than the internodes (upper), entire; fertile **Inf** part many-flowered, very lax,  $\pm$  40 cm, densely ferruginous-tomentose; floral **Bra** reflexed, broadly ovate, acute, slightly shorter than the sepals; **Fl** spreading or reflexed, to 18 mm; **Ped** 3–5 (–15) mm; **Sep** broadly elliptic, 8–11 mm, obtuse, free or inconspicuously connate at the base, densely brown-ferruginously lepidote; **Pet** erect, conspicuous, limb suborbicular and slightly flaring, neither undulate nor carinate, colour not described but presumably orange; **St** included; **Fil** free above the common tube; **Anth** short, subtriangular, apiculate, scarcely recurved; **Sty** very short; ovules with narrow asymmetric wings.

The description above was completed from data presented by Büneker & al. (2016), but some doubts persist as to the pedicel length, said to be 3–5 (–15) mm long in the key on p. 58, but the illustrations on p. 64 show almost sessile flowers.

*D. sordida* forms a complex with *D. inflexifolia* and *D. ursina* (Guarçoni & al. 2012), as well as with *D. nobilis* (Büneker & al. 2016). These last

authors argue that other species such as *D. mello-barretoii* and *D. elata* are also similar. All species are endemic to the Serra do Espinhaço of Minas Gerais. The complex is characterized by peduncles, inflorescence axes and sepals covered with brown-ferruginous trichomes, orange petals, (sub-)triangular antepetalous filaments, and filaments free above the common tube.

**D. spinulosa** L. B. Smith & Reitz (Phytologia 14: 486–487, t. 1, figs. 33–36, 1967). **Type:** Brazil, Minas Gerais (*Duarte* 7409 [HB, US [photo]]). — **Distr:** Brazil (Minas Gerais); savanna, on rocks; only known from the type collection. **I:** Smith & Downs (1974: 570).

[3b] **Ros** not described; **L** 35  $\times$  1.6 cm, sheath suborbicular, 3 cm, pale brown, **L** lamina linear-triangular, appressedly cinereous-lepidote on both faces, becoming  $\pm$  glabrous adaxially, margins laxly serrate, **Sp** mostly retrorsely uncinata, 1 mm; **Inf** 85 cm, simple; peduncle sparsely and finely pale-lepidote; peduncular **Bra** ovate, the lower ones dense and with long linear lamina, the upper acuminate, shorter than the internodes, serrulate; fertile **Inf** part laxly many-flowered, to 27 cm, finely white-lepidote at first; floral **Bra** like the upper peduncular bracts, equalling the middle of the sepals (lowest), serrulate; **Fl** curved-ascending; **Ped** 5 mm, slender, angled, not constricted; **Sep** ovate, 7 mm, rounded and apiculate, strongly convex; **Pet** rhomboid, 10 mm, colour not described but presumably orange; **St** included; **Fil** short-connate above the common tube; **Sty**  $\pm$  none. — [F. Krapp]

**D. stenophylla** L. B. Smith (Phytologia 14: 487, t. 1, figs. 42–45, 1967). **Type:** Brazil, Goiás (*Irwin & al.* 9728 [US, NY]). — **Distr:** Brazil (Goiás); soil-filled rock crevices, 1175 m. **I:** Smith & Downs (1974: 575).

[3b] **Ros** dense, globose, many-leaved; **L** to 16  $\times$  0.5 cm, sheath suborbicular, 2 cm, brown, **L** lamina linear, finely subulate-attenuate, appressedly whitish-lepidote on both faces, soon glabrous, margins laxly serrate, **Sp** slender, recurved, 2 mm; **Inf** to 30 cm, simple; peduncle glabrous; peduncular **Bra** broadly ovate, linear-laminate (lowest) or acuminate, remote, small,

microscopically serrulate; fertile **Inf** part laxly few-flowered, to 10 cm, fugaciously white-lepidote; floral **Bra** like the upper peduncular bracts, equalling the sepals (lowest) or shorter, microscopically serrulate; **Ped**  $\pm 1$  mm, stout but distinct; **Sep** broadly ovate, 6 mm, rounded; **Pet** lamina broadly elliptic, 8–10 mm, orange; **St** included; **Fil** connate above the common tube; **Sty** none. — [F. Krapp]

**D. stolonifera** P. J. Braun & Esteves (Cact. Succ. J. (US) 81(6): 301, ill. (p. 303), 2009). **Type:** Brazil, Mato Grosso do Sul (*Esteves Pereira* 627 [UFG]). — **Distr:** Brazil (Mato Grosso); borders of rock outcrops,  $\pm 150$  m.

[3a] **Ros** with  $\pm 19$  living leaves, stem  $\pm 8 \times 2.9$  cm, semi-underground, with 1–6 stolons emerging above the ground and to 16 cm long, becoming submerged, forming new rosettes 5–16 cm apart from the mother plant; **L**  $\pm 38 \times \pm 2.6$  cm, rigid, coriaceous, first slightly erect, later recurved-spreading, sheath  $\pm 1.8 \times 4.7$  cm, cream-coloured to brownish adaxially, brilliant dark brownish and apically lepidote abaxially, **L** lamina triangular-lanceolate, olive-green to dark purple-greenish, concave, with blunt yellowish tip, densely veined, adaxially slightly glossy and sparsely lepidote, abaxially greyish-lepidote, **Sp** predominantly retrorse,  $\pm 2.7$  mm,  $\pm$  cream at the base, dark brown at the tip, 4.3–16 mm apart; **Inf** to 95 cm, simple, erect; peduncle  $\pm 55$  cm, pale greyish-green with a brownish hue; peduncular **Bra** hard, carinate, amplexicaul (upper ones semi-amplexicaul), lower ones to  $21 \times 8$  mm, adaxially scattered-lepidote, veined, margins cream, membranous; fertile **Inf** part slightly contorted,  $\pm 24$  cm, rachis rose to reddish,  $\pm$  glabrous; floral **Bra**  $\pm 4 \times 2.3$  mm, rose, brilliant; **Fl** spreading to erect,  $\pm 20$  mm, subsessile; **Sep** elongate-oval, 8–12  $\times$  7.2 mm, succulent, carinate, reddish-orange, margins pale; **Pet**  $\pm 17 \times 11$  mm, abaxially orange, basally more reddish, margins delicately yellow; **St** exserted; **Fil** free above the 5 mm high common tube, erect, to 15 mm, white-yellowish; **Anth** yellow, slightly triangular, 4–5  $\times$  1.4 mm, acute, recurved; **Ov** slightly triangular-elongate,  $\pm 7 \times 2$  mm, white with a very pale yellowish hue; **Sty**

$\pm 1$  mm, **Sti** complex,  $\pm 2.9$  mm, apex fringed, yellow; **Fr** glossy dark brownish.

**D. strehliana** H. Büneker & R. Pontes (Revista Brasil. Bioci. 11(3): 284–289, figs. 1–2, 2013). **Type:** Brazil, Rio Grande do Sul (*Büneker & al.* 101 [HDCF, SMDB, SP]). — **Distr:** Brazil (Rio Grande do Sul); basaltic river banks, periodically flooded.

[2/3a] **Ros** 16- to 54-leaved, 8–19 cm  $\varnothing$ , rhizomatous; **L** 6–15  $\times$  1.1–2.6 cm, rigid, succulent, sheath elliptic to orbicular, 2–3.5  $\times$  2.5–4.4 cm, white, both faces glossy, **L** lamina triangular, straight or inflexed, with reddish pungent tip, veined abaxially, usually entire, rarely spinose with 1–10 spines per margin; **Inf** 35–120 cm, simple or rarely with 1–4 suberect branches; peduncle erect, slender, 19–60 cm, tomentose; peduncular **Bra** leaf-like, ovate to elliptic, longer (lower) to shorter than the internodes (upper); fertile **Inf** part 13- to 34-flowered (40–60 when branched), 18–40 cm, rachis white-tomentose; floral **Bra** ovate-triangular, slightly carinate, apex attenuate, 11–16  $\times$  6–11 mm, stramineous; **Fl** suberect at anthesis,  $\pm 20$  mm; **Ped** absent or short; **Sep** ovate to elliptic, 8–10  $\times$  4–8 mm, ecarinate to slightly carinate, yellow or green, tomentose; **Pet** erect, obovate to obtrullate, 14–18  $\times$  6–11 mm, yellow; **St** included or equaling the petals; **Fil** shortly connate above the common tube; **Ov**  $\pm 5 \times 3$  mm, whitish-yellow; **Fr** 15–20 mm.

Similar to *D. brevifolia* and *D. distachya*. Plants are periodically flooded in their native habitat.

**D. subinermis** Mez (in Martius, Fl. Bras. 3(3): 487, 1894). **Type:** Argentina, Misiones (*Niederlein* 1205 [B, F [photo]]). — **Distr:** N Argentina (Misiones); ecology not described.

[3a] **Ros** acaulescent, densely leaved; **L** to 20  $\times$  7 cm (inner ones) or wider, sheath broad, dark brown, glabrous, **L** lamina linear, attenuate, subdensely closely appressedly pale-lepidote abaxially, entire or very laxly serrate, **Sp** few, 0.5 mm; **Inf** 50 cm, simple; peduncle rather stout, puberulous towards the apex; peduncular **Bra** long-acuminate from a broadly ovate base,



to 2 cm, shorter than the internodes, entire; fertile **Inf** part lax, puberulous-lepidote; floral **Bra** reflexed, ovate, acuminate, 7 mm, much shorter than the sepals, entire; **Fl** erect, 18 mm, glabrous; **Ped** 4 mm, stout, angled, articulate; **Sep** ovate, 9.5 mm, rounded and mucronate; **Pet** suberect, suborbicular, 17 mm, rounded at the apex, undulate, carinate, yellow when dry; **St** included; **Fil** free above the common tube; **Anth** narrowly triangular, strongly recurved; **Sty** none and **Sti** sessile, strongly spirally contorted; **Fr** subellipsoid-trigonal,  $\pm 15 \times 6$  mm, glossy brown, acute; **Se**  $2 \times 3$  mm, basally somewhat acute, apically broadly rounded, with hyaline wing.

**D. sulcata** Guarçoni (Phytotaxa 188(3): 170–172, ill., 2014). **Type:** Brazil, Minas Gerais (*Guarçoni & Paixão* 1663 [VIC]). — **Distr:** Brazil (Minas Gerais: Serro); in sand on quartzitic rock outcrops, 1000 m; only known from the type locality.

[3a] **Ros** 20–43 cm  $\emptyset$ ; **L** 10–27, asymmetrically spreading-arcuate to erect, sheath suborbicular,  $1.5\text{--}4.3 \times 2.3\text{--}6.7$  cm, white to cream, upper  $\frac{1}{3}$  of the abaxial face white-lepidote and inconspicuously aculeate, **L** lamina very narrowly triangular,  $9.9\text{--}17.8 \times 0.9\text{--}1.4$  cm, flat to shallowly canaliculate, very succulent and rigid, green, or basally rarely wine-red on the upper face, upper face sparsely white-lepidote in the lower  $\frac{1}{2}$ , lower face strongly ribbed and densely white-lepidote at the base esp. between the ribs, apex acute and pungent, margins spinose except the apical  $\frac{1}{3}$ , **Sp** patent to slightly retrorse, dark brown, 0.7–1.4 mm, 10–20 (–26) mm apart; **Inf** (24–) 38–62 (–71) cm, simple, erect; peduncle 16–48 cm, green to brown, white-lepidote; peduncular **Bra** shorter than the internodes, lower  $8\text{--}60 \times 1\text{--}9$  mm, upper  $6\text{--}14 \times 4\text{--}8.6$  mm, ovate, long-acuminate, spine-tipped, carinate, abaxially white-tomentose; fertile **Inf** part laxly 5- to 18-flowered, rachis orange, white- to cinereously tomentose becoming glabrous; floral **Bra** reaching to the middle of the sepals, ovate-triangular and long-acuminate, spine-tipped,  $3.8\text{--}7.8 \times 2.8\text{--}5.9$  mm, orange to stramineous with green base, white-tomentose, fimbriate; **Fl** 14–19 mm, slightly reflexed or rarely patent,  $\pm$  tubular with flaring mouth; **Ped** 2.4–6.4 mm,

stout, orange, white-tomentose; **Sep** triangular to ovate,  $5.9\text{--}8.9 \times 4.4\text{--}6.9$  mm, orange, fleshy, obtuse to acute, white-lepidote, fimbriate; **Pet** obovate to somewhat obtrullate,  $9.7\text{--}13.1 \times 6.7\text{--}10.6$  mm, orange, obtuse to slightly emarginate, crenulate; **St** included; **Fil** yellow, to 9.5 mm, free above the 1.6–3.3 mm long common tube; **Anth** elliptic; **Ov** oblong, orange, 5.3–10.3 mm; **Sty** orange, 0.9–2.1 mm; **Sti** conduplicate-spiral, 0.6–0.7 mm, yellow; **Fr** ovoid, dark brown,  $11.4\text{--}13.7 \times 9.2\text{--}10.3$  mm; **Se** not described.

Part of the *D. saxatilis* complex, and compared with *D. saxatilis* and *D. brachyphylla* (both with symmetrical rosettes and leaves without spines in the apical  $\frac{1}{3}$ ). — [U. Eggli]

**D. tenebrosa** Leme & H. Luther (Selbyana 19 (2): 183–184, fig. 1, 1998). **Type:** Brazil, Minas Gerais (*Leme & al.* 2895 [HB, SEL]). — **Distr:** Brazil (Minas Gerais); rocky fields, terrestrial, 1000–1300 m.

[3a] **Ros** not described; **L**  $\pm 14 \times \pm 1.5$  cm, rigid, thick, sheath not described, **L** lamina spreading-recurved, very narrowly triangular, attenuate towards the involute-subulate apex, acuminate-caudate, green to reddish, adaxially glabrous, abaxially densely white-lepidote and veined, margins laxly spinose, **Sp** retrorse, uncinate, 1.5–2 mm; **Inf** 30–40 cm, simple, erect; peduncle 20–30 cm, yellowish-green, subdensely white-floccose; peduncular **Bra** linear-triangular from a broadly ovate base, long-acuminate, erect, distinctly carinate,  $10\text{--}20 \times 7$  mm, green at the base, reddish at the apex, veined, white-floccose to glabrescent, remotely denticulate-crenulate, apical ones like the floral bracts; fertile **Inf** part 4- to 9-flowered, lax,  $\pm 9$  cm, slender, flexuous, completely white-sublanate at anthesis except the petals; floral **Bra** broadly ovate-triangular, subcarinate, acuminate-caudate (lowest) to shortly acuminate (upper),  $6\text{--}10 \times 5\text{--}8$  mm, veined, entire but upper ones remotely denticulate near the apex; **Fl** suberect to spreading at anthesis,  $\pm 16$  mm; **Ped** 2–3 mm, stout; **Sep** ovate,  $7\text{--}8 \times 5$  mm, apex narrowly obtuse, ecarinate, fimbriate, reddish-green, entire; **Pet** broadly spatulate,  $\pm 12 \times 9$  mm, narrowly obtuse, base very narrow, ecarinate, subspreading at anthesis,

reddish-brown to wine-red with orange base, glabrous; **St** included; **Fil** free above the 2 mm high common tube,  $\pm 6$  mm, pale orange; **Anth** very narrowly triangular,  $\pm 2.5$  mm, strongly recurved, base sagittate, acuminate; **Ov** narrowly subpyramidal,  $\pm 5$  mm, green; **Sty** 2–4 mm, yellow; **Sti** elliptic,  $\pm 1$  mm, wine-red; **Fr** and **Se** not described.

Similar to *D. machrisiana* and compared with *D. oligantha* as well as *D. hilaireana* (here both treated as synonyms of *D. saxatilis*).

**D. tenuis** Mez (in Martius, Fl. Bras. 3(3): 484, 1894). **Type:** Brazil, Goiás (*Gardner* 3479 [BM, K]). — **Distr:** Brazil (Goiás, Mato Grosso); ecology not recorded.

**Incl.** *Dyckia morreniana* Mez (1894); **incl.** *Dyckia kuntzeana* Mez (1896).

[2/3a] **Ros** not described; **L** 20–40  $\times$  1.5–1.7 cm, sheath small, **L** lamina narrowly triangular, attenuate, with pungent tip, appressedly pale-lepidote abaxially, margins laxly serrate, **Sp** slender, spreading to spreading-reflexed, 1.5–2 mm; **Inf** 40–50 cm, simple or racemose; peduncle slender, minutely furfureaceous or soon glabrous; lower peduncular **Bra** subfoliaceous, upper ones  $\pm$  as long as the internodes and entire or sparsely serrulate; fertile **Inf** part few-flowered, lax, minutely furfureaceous; floral **Bra** divergent to spreading, (broadly) ovate with narrowly triangular tips, usually  $\pm$  equalling the flowers (lower), entire; **Fl** erect or suberect, 10–12 mm; **Ped** to 3 mm, stout; **Sep** ovate-elliptic, 6–7 mm, acute or obtuse, glabrous or subglabrous; **Pet** lamina suberect, broadly acute or obtuse, reddish; **St** exserted; **Fil** free above the common tube; **Anth** recurved; **Sty** very short or none.

Described on the base of incomplete material, and insufficiently known.

**D. tobatiensis** Hassler (Annuaire Conserv. Jard. Bot. Genève 20: 309, 1919). **Type:** Paraguay, Cordillera (*Hassler* 2099 [G, F [photo]]). — **Distr:** C Paraguay (Cordillera); denuded hill slopes.

[1] **Ros** not described; **L** 40–50  $\times$  3 cm, thickly fleshy-coriaceous, sheath not described, **L** lamina narrowly triangular, both faces shortly brownish-

furfureaceous-lepidote, margins strongly serrate, **Sp** antrorsely curved, strong, 6–8 mm, wholly lepidote; **Inf** to 95 cm, paniculately branched; peduncle 50–80 cm, glabrous; peduncular **Bra** much shorter than the internodes; fertile **Inf** part glabrous, **Br** 4–5, laxly flowered, divergent, 15 cm; primary **Bra** ovate, mucronulate, 10 mm; floral **Bra** subreflexed, triangular-ovate, apiculate, to 5 mm,  $\pm$  equalling or shorter than the pedicels; **Fl**  $\pm 17$  mm; **Ped** 4–5 mm; **Sep** ovate, 6.5 mm, evenly rounded at the apex; **Pet** subrhomboid-ovate, 17  $\times$  8 mm, obscurely carinate, golden-yellow; **St** equalling or slightly exceeding the petals; **Fil** free above the common tube; **Anth** narrowly elliptic, 3.5  $\times$  1.5 mm, acute, barely recurved; **Ov** pyramidal, 10 mm; **Sty** exserted; **Sti** globose, contorted.

**D. tomentella** Mez (Repert. Spec. Nov. Regni Veg. 16: 69, 1919). **Type:** Paraguay (*Fiebrig* 4046 [B, GH]). — **Distr:** N Paraguay (Presidente Hayes?, Amambay?); ecology not recorded.

[3a] **Ros** and **L** not described; **Inf**  $> 80$  cm, simple; peduncle erect, very slender, 60 cm; peduncular **Bra** acuminate from a very broadly ovate base, much shorter than the internodes, prominently striate, entire; fertile **Inf** part rather few-flowered, sublax, straight, 20 cm, appressedly cinereous-lepidote; floral **Bra** subspreading, very broadly ovate, 7 mm, apiculate, not much shorter than the sepals, entire; **Fl** suberect to erect, subsessile; **Sep** very broadly elliptic, 6 mm, rounded and emarginate at the apex; **Pet** erect, claws very short, lamina very broadly trapeziform-orbicular, to 10 mm, very broadly rounded and slightly emarginate, ecarinate, golden-yellow, with minutely undulate margins; **St** 2 mm longer than the petals; **Fil** broad, free above the common tube; **Sty** very short.


The original description is based on very incomplete material. Tropicos (accessed Dec. 2016) lists two recent collections from Paraguay, whose collection notes report caespitose rosettes and yellow flowers.

**D. trichostachya** Baker (Handb. Bromel., 133, 1889). **Type:** Brazil, Minas Gerais (*Sellow* Brom. Paris 59 [P, GH [photo]]). — **Distr:** Brazil

(Minas Gerais); rocky fields, terrestrial or on rocks. **I:** Smith & Downs (1974, 523).

**Incl.** *Dyckia micracantha* Baker (1889).

[2] **Ros** not described; **L** 50 × >2 cm, sheath not described, **L** lamina narrowly triangular, densely lepidote esp. abaxially, margins laxly serrate, **Sp** 1.5 mm; **Inf** to 1.3 m, few-branched at the base or pseudo-simple with branch buds in the axils of the lower bracts; peduncle stout, 100 cm, soon glabrous; peduncular **Bra** broadly ovate with narrowly triangular acuminate lamina, exceeding the internodes, serrulate; fertile **Inf** part 30 cm, sparsely ferruginous-tomentose; primary **Bra** much shorter than the branches; floral **Bra** broadly ovate, acute, lower ones equalling or exceeding the flowers and serrulate; **Fl** suberect to spreading, 12–13 mm; **Ped** short, stout; **Sep** broadly elliptic, 7–12 mm, obtuse, ± glabrous; **Pet** erect, suborbicular, ecarinate, colour not described; **St** included; **Fil** free above the common tube; **Anth** linear, slightly recurved; **Sty** very short. — [F. Krapp]

**D. tuberosa** (Vellozo) Beer (Fam. Bromel., 157, 1857). **Type:** Brazil (*Vellozo* s.n. [[]: Vellozo, Fl. Flumin. Icon. 3: t. 136, 1835]). — **Lit:** Vosgueritchian & Buzato (2006: ecology, with ill.). **Distr:** Brazil (Minas Gerais, Paraná, São Paulo, Santa Catarina); dry fields and open scrub, Cerrado vegetation, 800–1300 m. **I:** Smith & Downs (1974: 565); Reitz (1983: t. 52).

≡ *Tillandsia tuberosa* Vellozo (1829); **incl.** *Dyckia coccinea* Mez (1894).

[3a] **Ros** many-leaved, with bulbous base, acaulescent, slowly caespitose; **L** 15–50 × ±1 cm, erect to spreading, sheath broadly ovate or suborbicular, large, persistent and forming a bulb, **L** lamina straight to ± curved, narrowly triangular, abruptly acute and pungent, usually involute, glabrous adaxially, appressedly pale-lepidote abaxially, laxly and evenly serrate, **Sp** curved, dark; **Inf** 35–100 cm, simple; peduncle slender, lepidote or glabrescent; peduncular **Bra** erect, broadly ovate with narrowly triangular thick lamina, much shorter than the internodes (upper), serrulate; fertile **Inf** part lax, few- to many-flowered, ± glabrous; floral **Bra** spreading or reflexed, lancolate-triangular, acuminate, usually

shorter than the sepals, serrulate; **Fl** spreading to slightly downwards-pointing at anthesis, broadly tubular, erect in fruit; **Ped** 2–3 mm; **Sep** ovate, 5–7 mm, acute or obtuse, strongly convex; **Pet** claw broad, lamina suberect, broadly obovate, 9–14 mm, carinate-complicate, reddish or orange; **St** included; **Fil** free above the common tube; **Anth** narrow, recurved; **Ov** ±5 mm, narrowly pyramidal; **Sty** ±1 mm; **Sti** contorted.

Vosgueritchian & Buzato (2006) found 3 species of hummingbirds as pollinators of the flowers. The inflorescences are also visited by several species of ants. Only ±55% of the plants of the study population in São Paulo State flowered, and asexual reproduction appears to be important.

**D. tubifilamentosa** Wanderley & G. Sousa (Hoehnea 41(2): 315–319, figs. 1–2, 2014). **Type:** Brazil, Piauí (*Wanderley & al.* 2630 [SP, TEPB]). — **Distr:** Brazil (Piauí); rocky soil or rock outcrops in Caatinga and transitions to Cerrado vegetation.

[3b] **Ros** in small clumps or solitary; **L** distichous or secund, 13–17 cm, sheath broad, oval, 2–2.5 × 3–4 cm, fleshy, whitish to greenish, entire, **L** lamina straight to curved, narrowly triangular with mucronate tip, green or brownish to vinaceous, cinereous-lepidote, strongly spinose, **Sp** 1–2 mm, brown and brittle, erect to retrorse; **Inf** 22–58 cm, simple; peduncle 10–50 cm, green to vinaceous, glabrous; lowest peduncular **Bra** subfoliaceous, creamy-green, entire, the remaining peduncular **Bra** 20 × 8–20 mm, shorter than the internodes, ovate to filiform, apex attenuate, reddish-brown, entire; fertile **Inf** part lax, 2- to 10-flowered, secund or rarely distichous, slender, slightly geniculate; floral **Bra** ovate, apex caudate, 3–5 mm, green to reddish-brown, entire; **Fl** sessile to subsessile, 28–32 mm; **Sep** ovate, 8–11 mm, apiculate, green with translucent dots and dark reddish wrinkles at the base, entire; **Pet** oblong-lanceolate, 17–20 mm, acute, slightly cucullate, green or with dark reddish wrinkles at the apex, entire; **St** exerted, 20–28 mm; **Fil** entirely connate above the common tube, white becoming vinaceous to purplish; **Anth** sagittiform, connivent, divergent after anthesis, 5–6 mm,

creamy-yellow; **Ov**  $\pm 10$  mm; **Sty**  $\pm 11$  mm; **Sti** spirally-conduplicate; **Fr**  $14 \times 9$  mm, brown; **Se** (round-) ovoid to falciform,  $4.2 \times 2.5$  mm, light to dark brown, with corky wings.

Unique in the genus by having small green petals, and a long-exserted white staminal tube that becomes wine-red to purplish after anthesis. The spirally-conduplicate stigma lobes, as well as petal colour, are reminiscent of species of *Encholirium*.

**D. tweediei** Mez (in Martius, Fl. Bras. 3(3): 485, 1894). **Type:** Argentina, Santiago del Estero (*Tweedie* s.n. [K]). — **Distr:** N Argentina (Santiago del Estero, Salta); terrestrial or on rocks.

[3a] **Ros** acaulescent; **L**  $50 \times \pm 1.5$  cm or longer, sheath broad, thick, dark brown, **L** lamina narrowly triangular, rigid, canaliculate, densely pale-lepidote abaxially, margins subdensely serrate, **Sp** slender, 2 mm; **Inf** 1 m or more, simple; peduncle slender, subglabrous; peduncular **Bra** very broadly ovate, abruptly acute, much shorter than the internodes, entire; fertile **Inf** part rather lax, subsecund, tomentellous-lepidote; floral **Bra** subspreading, broadly ovate, to 6 mm, abruptly acute or subrounded, shorter than the sepals; **Fl** ascending or the uppermost erect, 19 mm, subsessile; **Sep** elliptic-ovate, to 8 mm, incised-emarginate, lepidote-tomentellous; **Pet** erect, broadly obovate, 15–16 mm, rounded, ecarinate,  $\pm$  undulate, yellow; **St** exserted; **Fil** free above the common tube; **Anth** triangular, acute, slightly recurved; **Ov** narrowly bottle-shaped, with six longitudinal furrows; **Sty** thick,  $\frac{1}{2}$  as long as the ovary; **Sti** with 3 free spreading lobes; **Fr** not described.

**D. uleana** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 517, 1896). **Type:** Brazil, Goiás (*Ule* 3134 [Herb. Taubert  $\dagger$ ?, B]). — **Distr:** Brazil (Goiás); ecology not recorded.

[3b] **Ros** not described; **L**  $\pm 50 \times 3.5$  cm, lamina narrowly triangular, with pungent tip, densely pale-lepidote abaxially, margins densely finely serrate, **Sp** to 2 mm; **Inf**  $\pm 1$  m, simple; peduncle stout, furfuraceous-lepidote; peduncular **Bra** broadly ovate, acuminate, with pungent tip, much shorter than the internodes, entire; fertile

**Inf** part subdense but interrupted at the base, densely ferruginous-lepidote; floral **Bra** spreading or reflexed, ovate, acuminate to acute, to 10 mm, equalling or shorter than the sepals; **Fl** somewhat erect to divergent, to 13 mm, subsessile; **Sep** broadly ovate-elliptic, 7 mm, obtuse, abaxially densely tomentose; **Pet** suberect, rhomboid, subobtuse, carinate, colour not described; **St** included; **Fil** high-connate above the common tube; **Anth** linear, subacute, recurved; **Sty** very short; **Fr** not described.

Compared with *D. edwardii* in the protologue of the latter, and description completed from the tabular comparison.

**D. ursina** L. B. Smith (Arq. Bot. Estado São Paulo 2(1): 109, t. 111, 1943). **Type:** Brazil, Minas Gerais (*Foster* 636 [GH]). — **Lit:** Büneker & al. (2016: with ill.). **Distr:** Brazil (Minas Gerais: Serra do Cipó); dry open rocky ground, 1100–1400 m; only known from a single population. **I:** Smith & Downs (1974: 517).

[2/3a] **Ros** usually solitary; **L** usually arching and secund, to  $60 \times 3\text{--}3.5$  cm, sheath suborbicular, glabrous towards the base, laxly serrulate, **L** lamina very narrowly triangular, margins very laxly serrate, **Sp** slender, curved, 3 mm, lepidote basally, glabrous elsewhere; **Inf**  $> 1$  m, simple or few-branched; peduncle stout, brown-lanate; peduncular **Bra** erect, subfoliaceous (lower) to narrowly triangular (upper), longer or shorter than the internodes; fertile **Inf** part sub-laxly flowered, very densely dark brown-lanate throughout; floral **Bra** broadly ovate, 8–20 mm, short-acuminate, the lower  $\pm$  equalling the sepals, entire; **Fl** spreading, (sub-) sessile; **Sep** elliptic, to 15 mm, acute, margins wholly obscured by the brown-lanate indumentum; **Pet** narrowly elliptic and without a distinct claw, only slightly exceeding the sepals, orange, lanate abaxially; **St** included; **Fil** free above the short common tube; **Sty** simple, very short.

The inflorescences are conspicuously densely brown-lanate and typical for the *D. sordida* complex (Büneker & al. 2016).

**D. velascana** Mez (in Martius, Fl. Bras. 3(3): 476, 1894). **Type:** Argentina, La Rioja (*Hieronymus*

& *Niederlein* 66 [B, CORD]). — **Distr:** N to N-C Argentina (Catamarca, Córdoba, La Rioja, San Luis, San Juan, Tucumán, Jujuy, Salta); rocky slopes, 750–3000 m. **I:** Smith & Downs (1974: 544); Subils (2009: 348).

[1] **Ros** offsetting, forming dense colonies; **L** 23–50 × 4 cm, spreading, sheath suborbicular, 5 cm, pale, **L** lamina narrowly triangular, appressedly pale-lepidote abaxially, margins spinose, **Sp** antrorsely uncinata, 4 mm; **Inf** to 1 m, paniculate, lax; peduncle 60–70 cm, erect, lepidote; peduncular **Bra** erect, broadly ovate, lowest narrowly triangular and serrulate, apical ones apiculate, much shorter than the internodes; **Inf** branches very densely flowered, short; primary **Bra** cinereous-lepidote-pubescent, shorter than the sterile branch base; floral **Bra** reflexed, acuminate from a broadly ovate base, to 5 mm, puberulous; **Fl** subsessile, spreading, to 14 mm; **Sep** ovate, to 8 mm, rounded and mucronulate, glabrous and lustrous with a ferruginous-puberulous base; **Pet** erect, subreniform, 10–12 mm, broadly rounded and minutely emarginate, not undulate, ecarinate, sulphur-yellow; **St** exserted; **Fil** free above the common tube; **Anth** sublinear, acute; **Ov** ±6 mm, oblong and narrowly pyramidal; **Sty** 0.5 mm; **Se** ±2.5 mm, with a circular wing.

No other species of the genus reaches similarly high altitudes.

**D. velloziifolia** Mez (Repert. Spec. Nov. Regni Veg. 16: 70, 1919). **Type:** Paraguay, Caaguazú (*Hassler* 9576 [B]). — **Distr:** SE Paraguay (Caaguazú); campos.

[3a] Only known from fragmentary material; **Ros** dense; **L** to 12 × 0.4 cm, lamina first erect, then irregularly curved-spreading, subulate to acicular, glabrous, entire or older ones with a few minute **Sp** basally; **Inf** to 50 cm, simple (?); peduncle stout, length not described but much exceeding the leaves, glabrous; peduncular **Bra** very broadly ovate, acuminate, all short-laminate, much shorter than the internodes; fertile **Inf** part very lax at least at the base, stout, glabrous; floral **Bra** like the peduncular bracts but with shorter lamina, suberect to erect, to 12 mm, exceeding the flowers, violet-tinged when dry; **Fl** erect, to

11 mm; **Ped** short; **Sep** very broadly elliptic, 6 mm, rounded and with a few teeth at the apex, submembranous; **Pet** erect, broadly rounded and slightly emarginate, ecarinate, lemon-yellow; **St** much shorter than the petals; **Fil** free above the very short common tube, very broad and almost foliaceous; **Sty** very stout.

**D. vestita** Hassler (Annuaire Conserv. Jard. Bot. Genève 20: 315, 1919). **Type:** Paraguay, Concepción (*Fiebrig* 5311 [G, F [photo]]). — **Distr:** Paraguay (Concepción); campos.

[1/2?] Only known from fragments; **Ros** and **L** unknown; **Inf** with 7 branches, >60 cm, **Bra** erect or suberect, subaxly flowered, to 30 cm, fulvous-tomentose; primary **Bra** ovate, acuminate, fulvous-tomentose; floral **Bra** ovate, acuminate, to 11 mm, equalling the sepals, fulvous-tomentose; **Fl** erect to spreading, to 20 mm, subsessile; **Sep** oblong-ovate, 11 mm, rounded at the apex, tomentose; **Pet** ovate, 18 mm, subacute, erect, ± carinate, pale yellow; **St** equalling the petals; **Fil** 3.5 mm (to completely?, Pinangé & al. (2017: fig. 3)) connate above the common tube; **Anth** linear, acute, sagittate at the base, strongly recurved; **Ov** pyramidal, 13 mm; **Sty** none. — [F. Krapp]

**D. vicentensis** Strehl (Bromeliaceae 42(5): 13–15, figs. 10–13, 2009). **Type:** Brazil, Rio Grande do Sul (*Strehl* 1375 [HAS]). — **Distr:** Brazil (C-W Rio Grande do Sul: São Vicente do Sul); on rocks.

[2/3] **Ros** acaulescent, 30- to 40-leaved, 20–25 cm Ø; **L** 8–12 × 1–1.3 cm, recurved to spreading, tough, sheath broad, 1 × 4 cm, white, bright, glabrous, **L** lamina green, sometimes reddish basally, with pungent tip, glabrous and shiny adaxially, cinereous-lepidote abaxially, sometimes densely white-lepidote basally, marginal **Sp** slightly hooked, predominantly retrorse, 2 mm, with brown tip and green base, ±5 mm apart; **Inf** 70–100 cm, simple or rarely branched; peduncle erect, green to reddish, white-lepidote and lanate; peduncular **Bra** long-triangular, asymmetrical, few, concentrated at the base of the stem; primary **Bra** narrowly linear to subtriangular from an ovate base, lower ones longer than the



internodes, veined, slightly serrate, upper ones shorter and  $\pm$  inflated and scale-like; floral **Bra** spreading, ovate, acute, never pungent, curved, carinate, longer than the sepals, 10–15 mm, slightly reddish, chaffy-lepidote, entire; **Fl** spreading at anthesis, later erect, 18–20 mm, tubular; **Ped** 3–5 mm; **Sep** oval, 8–10 mm, narrowly marginate, base inflated, ecarinate, appressed to the petals, acute, obtuse to apiculate, orange-reddish; **Pet** free, lamina broad, 18–20 mm, ecarinate, apex roundish, yellow to reddish; **St** included; **Fil** erect, 13 mm, orange-yellow, “joined at the base” according to the protologue but degree of connation with the common tube not described; **Anth** 4 mm, linear, yellow; **Ov**  $\pm 5$  mm; **Sty**  $\pm 5$  mm; **Sti** 7 mm.

**D. virgata** Mez (Repert. Spec. Nov. Regni Veg. 16: 68, 1919). **Type:** Paraguay, Presidente Hayes (*Rojas* 46 [B]). — **Distr:** C Paraguay (Presidente Hayes); ecology not recorded. **I:** Smith & Downs (1974: 542).

[3b] Only known from fragments; **Ros** unknown; **L** 120  $\times$  2.5 cm, coriaceous, lamina attenuate to a slenderly subulate apex, subglabrous, margins densely serrate basally, laxly serrate elsewhere, **Sp** acicular, 1.5 mm; **Inf** >30 cm, simple (?), slenderly virgate, very laxly many-flowered, slender, all parts including bracts, pedicels and sepals brownish-tomentellous, glabrescent; floral **Bra** reflexed, ovate, broadly acute, strongly convex, 4 mm, much shorter than the sepals, entire; **Fl** suberect to subspreading, slender, orange when dry, subsessile; **Sep** broadly elliptic,  $\pm 5$  mm, rounded and emarginate; **Pet** erect, 13 mm, broadly subacute, ecarinate; **St** exserted; **Fil** high-connate above the common tube; **Sty** short. — [F. Krapp]

**D. waechteri** Strehl (Bromeliaceae 42(5): 15–17, figs. 14–19, 2009). **Type:** Brazil, Rio Grande do Sul (*Strehl* 1086 [HAS]). — **Distr:** Brazil (C-W Rio Grande do Sul: São Francisco de Assis); on rocks.

[1?] **Ros** with  $\pm 40$  living leaves, to 40 cm  $\varnothing$ , caulescent; **L** 33–38  $\times$  2–2.3 cm, flexuous, long and acute, sheath 3–3.2  $\times$  2.5–2.7 cm, white, white-lepidote, serrate, **L** lamina arching, with

slightly pungent tip, light green, glabrous adaxially, white-lepidote abaxially, **Sp** antrorse, 3–4 mm, light green with castaneous tip, 10–15 mm apart; **Inf** 1.6–1.7 m, compound or rarely simple; peduncle elliptical in cross section, furfuraceous to glabrous, brittle, 1.5–1.6 m, green, covered with white powder; peduncular **Bra** amplexicaul, narrowing abruptly, long-acuminate from a wide base, membranous, green at the base, serrate, drying from the tip; fertile **Inf** part lax, reddish-white; **Br** 3–6, at acute angles, 30–70 cm; floral **Bra** triangular, acute, mucronate, 8–10  $\times$  5–8 mm, base green, apical  $\frac{1}{2}$  becoming brown, drying quickly, slightly lepidote; **Fl** erect to subspreading, 20 mm, sessile; **Sep** obovate and roundish, 8–11  $\times$  8–11 mm, mucronate, sometimes crenate at the apex, carinate, free in the upper  $\frac{1}{2}$ , green, turning yellow basally and orange or rose towards the apex, thick-textured; **Pet** obovate-rounded, 16–18  $\times$  5–8 mm, erect and quite recurved, thick-textured, orange-rose; **St** becoming visible in the throat; **Fil** free above the common tube, yellowish; **Anth** orange; **Ov** 6–7 mm; **Sty** 6 mm, orange; **Fr** 18–20  $\times$  12–15 mm, dark brown, shiny; **Se** discoid, 3  $\times$  5 mm, 1 mm thick, with a lateral wing. — [F. Krapp]

**D. walteriana** Leme (Phytotaxa 67: 33–35, ill., 2012). **Type:** Brazil, Paraná (*Kranz* 13 [RB, HB]). — **Distr:** Brazil (Paraná); on almost horizontal granitic rock outcrops; known from a single population only.

[1] **Ros** dense,  $\pm 50$ -leaved, propagating by basal shoots; **L** 75–90  $\times$  3–3.4 cm,  $\pm 5$  mm thick, stiffly succulent, sheath inconspicuous, **L** lamina narrowly triangular, attenuate and slightly canaliculate towards the pungent apex, suberect-arcuate, acuminate, green, abaxially finely veined, densely white-lepidote, margins laxly spinose, **Sp** narrowly triangular, predominantly antrorse-uncinate, 3–10 mm, densely white-lepidote, with castaneous tip, 15–25 mm apart; **Inf**  $\pm 2.1$  m, broadly 2 $\times$  branched; peduncle erect,  $\pm 80$  cm, greenish-purple, subdensely to sparsely pale castaneous-lanate and densely covered with white wax; peduncular **Bra** narrowly triangular, acuminate and spinescent, stramineous,

canaliculate towards the apex, 60–110 × 20–25 mm, subdensely white-lepidote, veined, densely spinulose; fertile **Inf** part dense, ±120 cm, rachis straight to slightly flexuous, greenish-purple, subdensely pale castaneous-lanate to glabrous and densely covered with white wax; **Br** ±12, laxly arranged, densely 100- to 140-flowered, 40–60 cm, with a 4–8 cm long sterile base, straight, greenish to greenish-purple, densely castaneous-lanate, soon glabrous and densely covered with white wax, terminal part of the main axis not distinct from the branches; primary **Bra** like the upper peduncular bracts, subspreading, 30–50 × 10–20 mm; floral **Bra** triangular-ovate to broadly triangular, acute, shorter than the sepals, 3–5 × 3–4 mm, stramineous, densely castaneous-lanate, veined; **Fl** subverticillate, ± spreading, 16–17 mm, broadly campanulate, unscented; **Ped** ±1 mm, green, densely castaneous-lanate; **Sep** orbicular, 3.5–5 × 4–5 mm, obtuse-emarginate, ecarinate, strongly convex, greenish, obscurely castaneous-lanate, entire; **Pet** elliptic to oblong-elliptic, 12 × 6–7 mm, obtuse-emarginate, ecarinate, yellow, glabrous; **St** exerted at anthesis; **Fil** free above the 1–2 mm high common tube, 11–12 mm, yellow; **Anth** suboblong, ±3 mm, slightly recurved at anthesis, base bilobed, acute; **Ov** narrowly ovoid, ±6–7 × 3 mm, yellow; **Sty** 5–7 mm, yellow, **Sti** ±1 mm, yellow, margins crenulate; **Fr** subglobose, acute, 14 × 10 mm, dark castaneous, glossy; **Se** subtriangular, strongly complanate, ±3 × 2 mm.

Compared with *D. agudensis* and *D. selloa* in the protologue.

**D. warmingii** Mez (in Martius, Fl. Bras. 3(3): 481, 1894). **Type:** Brazil, Minas Gerais (*Warming* s.n. [C, F [photo]]). — **Distr:** Brazil (C Minas Gerais: Lagoa Santa); savanna, terrestrial.

[3b] Only known from fragments; **Ros** and **L** unknown; **Inf** probably >50 cm, simple; peduncular **Bra** remote, broadly ovate, acuminate, entire; fertile **Inf** part lax, finely and fugaciously whitish-furfuraceous; floral **Bra** spreading or reflexed, like the peduncular bracts, nearly equalling the sepals (lower); **Fl** spreading or reflexed at anthesis, to 15 mm; **Ped** 2–3 mm,

stout, articulate; **Sep** broadly ovate, 6–8 mm, acute, ± straight; **Pet** suberect, broadly obovate, obtuse, undulate, ± orange; **St** included; **Fil** high-connate above the common tube; **Anth** triangular, acute, recurved towards the apex; **Sty** short. — [F. Krapp]

**D. weddelliana** Baker (Handb. Bromel., 132, 1889). **Type:** Brazil, sine loco (*Weddell* 2584 [P, GH [photo]]). — **Distr:** C Brazil (Minas Gerais?, Goiás?); savanna, terrestrial. **I:** Smith & Downs (1974: 542).

[2] **Ros** not described; **L** 30–40 × 2–3 cm, sheath suborbicular, 4 cm, brown, glabrous, **L** lamina narrowly triangular, attenuate, minutely lepidote abaxially, margins laxly serrate, **Sp** straight, slender, 2 mm; **Inf** 1.2–1.5 m, simple or few-branched; peduncle stout, soon glabrous; peduncular **Bra** erect, the upper remote, broadly ovate, acute, entire; fertile **Inf** part elongate, subdensely many-flowered, ferruginous-furfuraceous; floral **Bra** ovate with triangular apices, reflexed, ±9 mm; **Fl** suberect to spreading, 11 mm; **Ped** 3 mm, stout; **Sep** elliptic, 6 mm, obtuse; **Pet** erect or suberect, obovate, broadly rounded, ± carinate, colour not described; **St** included; **Fil** high-connate above the common tube; **Anth** linear, acute, strongly recurved; **Sty** ½ as long as the ovary.

Described on the base of material without origin other than “Central Brazil”, and insufficiently known. — [F. Krapp]

## References

- Baker, J. G. (1889) Handbook of the *Bromeliaceae*. London (GB): G. Bell & Sons. <https://doi.org/10.5962/bhl.title.51681>.
- Bernardello, L. M. [ & al. 1991], Galetto, L. & Juliani, H. R. (1991) Floral nectar, nectary structure and pollinators in some Argentinean *Bromeliaceae*. *Ann. Bot. (Oxford)*, n.s. 67(4): 401–411. <https://doi.org/10.1093/oxfordjournals.aob.a088174>
- Braun, P. J. [ & al. 2008], Esteves Pereira, E. & Scharf, U. (2008) *Dyckia joanae-marcoi*. Eine neue, sukkulente Bromelie aus dem nördlichen Minas Gerais, Brasilien. *Bromelie* 2008(1): 33–46, ill., map.
- Braun, P. J. (2018) Xeromorfe Bromelien aus Brasilien (1)/Xeromorphic Bromeliads from Brazil (1): *Dyckia*. *Bromelie* 2018(2): 68–77, ill.

- Braun, P. J. & Esteves Pereira, E. (1991) *Dyckia braunii* Rauh. Eine neue, weissbereifte Blattsukkulente aus Zentralbrasilien. *Kakt. and. Sukk.* 42(3): 58–60, ills.
- Braun, P. J. & Esteves Pereira, E. (2005) Succulent and xeromorphic Bromeliads of Brazil. Part 1. *Dyckia marnier-lapostollei* L. B. Smith. *Cact. Succ. J. (US)* 77(6): 284–292, ills. [https://doi.org/10.2985/0007-9367\(2005\)77\[284:SAXBOB\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[284:SAXBOB]2.0.CO;2).
- Braun, P. J. & Esteves Pereira, E. (2006a) Succulent and xeromorphic Bromeliads of Brazil. Part 2. *Orthophytum horridum*, *Dyckia paucispina* and *Bromelia estevesii*. *Cact. Succ. J. (US)* 78(1): 31–35, ills. [https://doi.org/10.2985/0007-9367\(2006\)78\[31:SAXBOB\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[31:SAXBOB]2.0.CO;2).
- Braun, P. J. & Esteves Pereira, E. (2006b) Succulent and xeromorphic Bromeliads of Brazil. Part 3. *Encholirium maximum*, *Orthophytum burle-marxii* and *Dyckia goehringii*. *Cact. Succ. J. (US)* 78(4): 160–164, ills. [https://doi.org/10.2985/0007-9367\(2006\)78\[160:SAXBOB\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[160:SAXBOB]2.0.CO;2).
- Braun, P. J. & Esteves Pereira, E. (2009a) *Dyckia edwardii* P. J. Braun & al. *Kakt. and. Sukk.* 60(7): xxv–xxvi (index card 2009/13), ills.
- Braun, P. J. & Esteves Pereira, E. (2009b) *Dyckia richardii* P. J. Braun & Esteves. *Kakt. and. Sukk.* 60(7): xxvii–xxviii (index card 2009/14), ills.
- Büneker, H. M. [& al. 2016], Pureza Soares, K. & Coelho de Assis, L. (2016) The *Dyckia sordida* complex (*Bromeliaceae*, *Pitcairnioideae*) and a new species from Minas Gerais, Brazil. *Phytotaxa* 244(1): 57–68, key, ills. <https://doi.org/10.11646/phytotaxa.244.1.4>.
- Butcher, D. (2010) *Dyckia estevesii* revisited. *J. Bromeliad Soc.* 60(2): 82–84, ills.
- Dorneles, M. P. [& al. 2014], Oliveira, J. M. S. de & Cantorow, T. S. do (2014) *Dyckia racinae* L. B. Sm. (*Bromeliaceae*): Morphological description emphasizing the reproductive structures. *Iheringia, Bot.* 69(2): 397–303, ills.
- Esteves Pereira, E. & Gouda, E. J. (2017) A new *Dyckia* (*Bromeliaceae*) from the south region of Goiás, Brazil: *Dyckia piracanjubensis*. *J. Bromeliad Soc.* 66(3): 172–181, ills.
- Fagundes, N. F. & Mariath, J. E. D. (2010) Morphoanatomy and ontogeny of fruit in *Bromeliaceae* species. *Acta Bot. Brasil.* 24(3): 765–779, ills. <https://doi.org/10.1590/S0102-33062010000300020>.
- Guarçoni, E. A. E. [& al. 2012], Sartori, M. A. & Paula, C. C. de (2012) *Dyckia inflexifolia* (*Bromeliaceae*), a new species from Brazil. *Ann. Bot. Fenn.* 49: 407–411, ills.
- Guarçoni, E. A. E. [& al. 2014], Alves Azevedo, A. & Ferreira da Costa, A. (2014) *Dyckia sulcata* (*Bromeliaceae*), a new species from Minas Gerais, Brazil, with notes on leaf anatomy. *Phytotaxa* 188(3): 169–175, ills. <https://doi.org/10.11646/phytotaxa.188.3.6>.
- Hmeljevski, K. V. [& al. 2011], Reis, A., Montagna, T. & Sedrez dos Reis, M. (2011) Genetic diversity, genetic drift and mixed mating system in small subpopulations of *Dyckia ibiramensis*, a rare endemic bromeliad from southern Brazil. *Conservation Genet.* 12: 761–769. <https://doi.org/10.1007/s10592-011-0183-3>.
- Klein V., L. F. & Klein, J. (2014) Die Bromelien in den atlantischen Wäldern der Nord-Ost-Küste von Rio Grande do Sul/Brasilien — Teil 4/Schluss. *The Bromeliads in the Atlantic forest of the northeast coast of Rio Grande do Sul/Brazil — part 4/final part.* *Bromelie* 2014(2): 74–85, ills.
- Krapp, F. (2013) Phylogenie und Evolution der Gattung *Dyckia* (*Bromeliaceae*). Kassel (DE): Universität Kassel; unpublished Ph.D. thesis.
- Krapp, F. [& al. 2014], Pinangé, D. S. de B., Benko-Iseppon, A. M., Leme, E. M. C. & Weising, K. (2014) Phylogeny and evolution of *Dyckia* (*Bromeliaceae*) inferred from chloroplast and nuclear sequences. *Pl. Syst. Evol.* 300(7): 1591–1614, ills., maps. <https://doi.org/10.1007/s00606-014-0985-0>.
- Kriek, C. (2008) Ecologia reprodutiva de *Dyckia encholirioides* var. *encholirioides* (Gaud.) Mez. (*Bromeliaceae*) em costões oceânicos em Florianópolis, Santa Catarina. Florianópolis (BR): Universidad Federal de Santa Catarina, Departamento de Fitotecnia; unpublished M.Sc. thesis.
- Lawn, G. (2011) *Dyckia* ‘Leopoldo Witeck’. *J. Bromeliad Soc.* 61(3): 136–137, ills.
- Leme, E. M. C. & Miranda, Z. de J. G. (2009) Studies on *Dyckia* from Central Brazil — part II. Two sweetly fragrant species from Goiás. *J. Bromeliad Soc.* 59(2): 71–79, ills.
- Machado, T. M. [& al. 2016], Forzza, R. C. & Stehmann, J. R. (2016) *Bromeliaceae* from Caparaó National Park, Minas Gerais/Espírito Santo states, Brazil, with notes on distribution and conservation. *Oecol. Australis* 20(2): 133–146, ills. <https://doi.org/10.4257/oeco.2016.2002.10>.
- Mendes, S. P. [& al. 2012], Costa, C. G. & Toni, K. L. G. de (2012) Androecium development in the bromeliad *Dyckia pseudococcinea* L. B. Sm. (*Pitcairnioideae* — *Bromeliaceae*), an endangered species endemic to Brazil: Implications for conservation. *Flora (Jena)* 207(8): 622–627, ills. <https://doi.org/10.1016/j.flora.2012.06.016>.
- Mez, C. (1891–1892) *Bromeliaceae*. In: Martius, C. F. P. von & al. (eds.): *Flora Brasiliensis*, 3(3): 173–286, tt. 51–62 (= fasc. 110, 1891); pp. 281 [sic]–430, tt. 63–80 (= fasc. 112, 1892). Leipzig (DE): F. Fleischer. <http://biodiversitylibrary.org/page/136410>.
- Monteiro, R. F. & Forzza, R. C. (2016) Flora das cangas da Serra dos Carajás, Pará, Brasil: *Bromeliaceae*. *Rodriguésia* 67(5): 1253–1265, ills., keys. <https://doi.org/10.1590/2175-7860201667523>.
- Paggi, G. M. [& al. 2015], Louzada, R. B., Ishii, I. H., Takahasi, A., Arruda, R. C. O. & Lorenz-Lemke, A. P. (2015) Rediscovering *Dyckia excelsa* (*Bromeliaceae*) in Mato Grosso do Sul, Brazil: Taxonomy, geographic distribution, and notes on leaf anatomy. *Syst. Bot.* 40(1): 129–135, ills., key. <https://doi.org/10.1600/036364415X686422>.
- Pinangé, D. S. B. [& al. 2017], Krapp, F., Zizka, G., Silvestro, D., Leme, E. M. C., Weising, K. & Benko-Iseppon, A. M. (2017) Molecular phylogenetics, historical biogeography and character evolution in *Dyckia* (*Bromeliaceae*, *Pitcairnioideae*). *Bot. J. Linn. Soc.* 183: 39–56, ills. <https://doi.org/10.1111/boj.12489>.

- Pompelli, M. F. & Guerra, M. P. (2004) Ex situ conservation of *Dyckia distachya*: An endangered Bromeliad from South Brazil. *Crop Breed. Appl. Biotechnol.* 4(3): 273–279, ills., maps.
- Pompelli, M. F. & Guerra, M. P. (2005) Micropropagation enables the mass propagation and conservation of *Dyckia distachya* Hassler. *Crop Breed. Appl. Biotechnol.* 5: 117–126, ills.
- Pompelli, M. F. [et al. 2006], Fernandes, D. & Guerra, M. P. (2006) Germination of *Dyckia encholirioides* (Gaudichaud) Mez var. *encholirioides* under saline conditions. *Seed Sci. Technol.* 34(3): 759–763, ills.
- Rauh, W. (1985) Bromeliestudien. I. Neue und wenig bekannte Arten aus Peru und anderen Ländern (XVII. Mitteilung). *Trop. subtrop. Pfl.-welt* 53: 1–62, ills.
- Rauh, W. & Gross, E. (1988) Bromeliestudien. I. Neue und wenig bekannte Arten aus Peru und anderen Ländern (XX. Mitteilung). *Trop. subtrop. Pfl.-welt* 65: 5–75, ills.
- Rauh, W. & Gross, E. (1991) Bromeliestudien. I. Neue und wenig bekannte Arten aus Peru und anderen Ländern (XXII. Mitteilung). *Trop. subtrop. Pfl.-welt* 79: 1–31, ills.
- Reitz, R. (1983) Bromeliáceas e a malária-bromélia endêmica. In: Reitz, R. (ed.): *Flora ilustrada catarinense, I parte as plantas, fascículo BROM.* Itajaí (BR): Herbario “Barbosa Rodrigues”.
- Rogalski, J. M. [et al. 2009], Reis, A., Reis, M. S. dos & Hmeljevski, K. V. (2009) Biologia reprodutiva da reófita *Dyckia brevifolia* Baker (*Bromeliaceae*), no Rio Itajaí-Açu, Santa Catarina, Brazil. *Revista Brasil. Bot.* 32(4): 691–702, ills. <https://doi.org/10.1590/S0100-84042009000400008>.
- Sachs, H. (2011) Auf der Suche nach/Searching for *Dyckia delicata*. *Bromelie* 2010(3): 118–121, ills.
- Santos-Silva, F. [et al. 2015], Antunes Mastroberti, A. & Araujo Mariath, E. de (2015) Capsule structure in three species of *Dyckia* (*Bromeliaceae*): Ontogenetic and taxonomic issues. *J. Torrey Bot. Soc.* 142(3): 249–257, ills. <https://doi.org/10.3159/TORREY-D-14-00002.1>.
- Saul, J. (2018) Hybriden von der Fensterbank. Hybrids from the window sill. *Bromelie* 2018(2): 65–67, ills.
- Schütz, N. [et al. 2016], Krapp, F., Wagner, N. & Weising, K. (2016) Phylogenetics of *Pitcairnioideae* s.s. (*Bromeliaceae*): Evidence from nuclear and plastid DNA sequence data. *Bot. J. Linn. Soc.* 181(3): 323–342, maps, ills. <https://doi.org/10.1111/boj.12403>.
- Silva, A. L. L. da [et al. 2007], Dornelles, E. B., Bisognin, D. A., Franco, E. T. H. & Horbach, M. A. (2007) Micropropagation of *Dyckia agudensis* Irgang & Sobral — An extinction threatened Bromeliad. *Iheringia, Bot.* 62(1–2): 39–43, ills.
- Siqueiro Filho, J. A. & Leme, E. M. C. (2007) Fragments of the Atlantic forest of Northeast Brazil: Biodiversity, conservation and the Bromeliads. Rio de Janeiro (BR): Andrea Jakobsson Estúdio.
- Smith, L. B. & Downs, R. J. (1974) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 1: *Pitcairnioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4393694>.
- Subils, R. (2009) *Bromeliaceae*, Bromeliáceas. In: Kiesling, R. (ed.): *Flora de San Juan, IV*: 340–363, ills., keys. Mendoza (AR): Zeta Editores.
- Vásquez, R. C. & Ibisch, P. L. (2012) Die Bromelien Boliviens (XI): *Dyckia barthlottii* — eine neue Art aus dem Chaco-Trockenwald Boliviens. The Bromeliads of Bolivia (XI): *Dyckia barthlottii* — a new species from the Chaco Dry Forest of Bolivia. *Bromelie* 2012(3): 123–127, ills.
- Vesprini, J. L. [et al. 2003], Galetto L. & Bernardello, G. (2003) The beneficial effect of ants on the reproductive success of *Dyckia floribunda* (*Bromeliaceae*), an extrafloral nectary plant. *Canad. J. Bot.* 81(1): 24–27, ills. <https://doi.org/10.1139/b03-003>.
- Voltoini, C. H. [et al. 2009], Reis, A. & Santos, M. (2009) Leaf morphoanatomy of the rheophyte *Dyckia distachya* Hassler (*Bromeliaceae*). *Revista Brasil. Bioci.* 7(4): 335–343, ills.
- Vosgueritchian, S. B. & Buzato, S. (2006) Reprodução sexuada de *Dyckia tuberosa* (Vell.) Beer (*Bromeliaceae*) e interação planta-animal. *Revista Brasil. Bot.* 29(3): 433–442, ills. <https://doi.org/10.1590/S0100-84042006000300010>.
- Waldemar, C. C. & Irgang, B. E. (2003) A ocorrência do mutualismo facultativo entre *Dyckia maritima* Backer [sic!] (*Bromeliaceae*) e o cupim *Cortaritermes silvestrii* (Holmgren), *Nasutitermitinae*, em afloramentos rochosos no Parque Estadual de Itapuã, Viamão, RS. *Acta Bot. Brasil.* 17(1): 37–48, ills., map. <https://doi.org/10.1590/S0102-33062003000100004>.
- Wiesbauer, M. B. (2008) Biologia reprodutiva e diversidade genética de *Dyckia distachya* Hassler (*Bromeliaceae*) como subsídio para conservação e reintrodução de populações extintas na natureza. Florianópolis (BR): Universidade Federal de Santa Catarina, Centro de Ciências Agrárias; unpublished thesis.
- Winkler, S. (1982) Die Bromeliaceae von Rio Grande do Sul (S-Brasilien). *Doc. Nat.* 3: 1–81, keys, 5 tt.



## × *Dycktia* BROMELIACEAE

N. Schütz and F. Krapp

× ***Dycktia*** D. A. Beadle (Prelim. List. Cult. Grex Bromeliad, 82, 1991). — **Distr:** Cultivated only.

= *Dyckia* × *Hechtia*. The only known cross is *D.* ‘Dark Chocolate’ × *H. epigyna*, obtained by

O. Ferris; it remained unnamed and appears to have first been mentioned in an unpublished manuscript (L. B. Smith, Manuscript of Bromeliad Hybrids and Cultivars, 1984).

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## Encholirium BROMELIACEAE

F. Krapp

**Encholirium** Martius ex Schultes & Schultes *fil.* (in Roemer & Schultes, *Syst. Veg.* 7(2): lxxviii, 1233, 1830). **Type:** *Encholirium spectabile* Martius ex Schultes & Schultes *fil.* — **Pitcairnioideae** — **Lit:** Smith & Downs (1974: 191–199, *Fl. Neotropica*); Forzza (2005: monograph); Forzza & Zappi (2011: partial key); Krapp & al. (2014: phylogeny). **Distr:** E Brazil. **Etym:** Gr. ‘enchos’, spear; and Gr. ‘leirion’, lily; presumably for the long slender inflorescence of some species.

**Incl.** *Encholirion* hort. (*nom. inval.*, ICN Art. 61.1).

Perennial terrestrial rosette plants; **Ros** solitary or more frequently forming clumps; rhizome short, erect, sometimes with lateral branches; **L** densely rosulate, sheath wide and imbricate, **L** lamina green, yellowish, reddish or nigrescent, often cinereous, triangular-lanceolate, marginal **Sp** usually well developed, rarely margins serrate or entire; **Inf** terminal, tall, unbranched or rarely few-branched; peduncular **Bra** numerous, lower ones foliaceous, upper ones small and often withering; **Fl** pedicellate, hermaphrodite, not very conspicuous; **Ped** usually distinct to very long in the *longipedicellatum*-complex; **Sep** green to yellowish-green, yellow, vinaceous or pinkish, convolute

or imbricate, symmetrical or sometimes asymmetrical, usually glabrous, free; **Pet** cream, cream-green, green, green-yellow, yellow or slightly vinaceous, imbricate or not, symmetrical or slightly asymmetrical, free; **St** inserted or exerted; **Fil** free or connate at the base, rarely adnate to the petals; **Ov** completely superior or partly inferior; **Sty** exerted or included; **Sti** conduplicate-spiral with either laminar or compact lobes; **Fr** globose stout capsules with usually persistent floral remains; **Se** numerous, brown, flattened, surrounded by a continuous membranous margin, with a single rounded, truncate, long-caudate or falciform wing.

A genus of 35 species, of which c.  $\frac{1}{3}$  were described subsequently to the taxonomic revision of Forzza (2005). No formal infrageneric classification has been published, but 8 species form the so called *longipedicellatum*-complex, characterized by long pedicels (short in *E. biflorum* and *E. reflexum*), imbricate petals and included stamens.

*Encholirium* species are typically strongly xeromorphic plants occurring in rocky habitats. They are distributed in E Brazil, from Piauí in the N to Mato Grosso do Sul in the S. Half of all species are restricted to the Serra do Espinhaço. The diversity centre is on the Diamantina plateau and in the Serra do Cipó. Nearly all species are restricted to rock outcrops in Cerrado and Caatinga vegetations; only *E. gracile* and *E. horridum* occur on inselbergs within the Atlantic Forest, while the widespread *E. spectabile* is also found in the transition zone between savanna and Atlantic Forest. Compared with the typically

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narrowly endemic and rare species of *Dyckia*, many *Encholirium* species are more common and occur in larger populations.

**Evolution and phylogeny:** A dated phylogeny based on plastid DNA sequence data shows a common origin of *Encholirium* plus *Dyckia*, and this clade separated from *Deuterocohnia* 5.6 mybp (Krapp & al. 2014). The monophyletic genus *Dyckia* is imbedded within what is currently treated as *Encholirium* and arose 4–4.6 mybp. This topology with *Encholirium* as a grade at the base of a paraphyletic *Dyckia* is also supported by nuclear DNA data (Krapp & al. 2014, Schütz & al. 2016) as well as by morphological characters (Forzza 2005). Up to now, no single synapomorphic morphological character has been described for *Encholirium*, although it is easily distinguished morphologically from *Dyckia*. Strictly speaking, the two genera would have to be merged into a single genus *Dyckia*. This merger is, however, not advocated for the time being due to insufficient sampling in the molecular studies, esp. for *Encholirium*, and the possibility to split up *Encholirium* must also be explored.

**Ecology:** *Encholirium* species are commonly pollinated by hummingbirds (Forzza 2005, Leal & al. 2006: 383, Aguilar-Rodríguez & al. 2014: 159). Some species are also or exclusively pollinated by bats, e.g. *E. subsecundum* or *E. splendidum*. Queiroz & al. (2016) recorded a mixed pollination system in *E. spectabile*, involving primarily bats, an opossum and hummingbirds, with occasional visits by passerine birds and hawkmoths. Christianini & al. (2013) regard hummingbird pollination as ancestral for the genus.

The following names are of unresolved application but are referred to this genus: *Encholirium diamantinae* Rauh (s.a.) (*nom. inval.*, ICN Art. 29.1); *Encholirium sabinae* Rauh (s.a.) (*nom. inval.*, ICN Art. 29.1); *Encholirium sanguinolentum* Hort. Paris ex C. Chevalier (1930) (*nom. inval.*, ICN Art. 36.1c).

**E. agavoides** Forzza & Zappi (Kew Bull. 66 (2): 282, ills. (p. 283, 285), 2011). **Type:** Brazil,

Minas Gerais (Forzza & al. 5475 [RB, CEPEC, K, MBM, SPF, US]). — **Distr:** Brazil (Minas Gerais: Serra do Cipó); quartzitic sandstones; narrowly endemic. **I:** Zappi & Taylor (2011).

Flowering plants (15–) 30–44 cm tall, forming dense mats; rhizome short; **Ros** 6–10 cm Ø; **L** suberect to patent, sheath 1.2–1.5 × 2.5–5.7 cm, entire, **L** lamina 3.2–3.7 × 2–3 cm, triangular, cinereous, densely lepidote, margins with patent **Sp** 3–4 mm long; peduncle 12–22 cm, green, erect, glabrous; peduncular **Bra** exceeding the internodes, 6–11 cm, erect, lanceolate to ovate-lanceolate, green to stramineous, apex acute to attenuate, entire to slightly serrate at the base, glabrous, clasping the peduncle; fertile part of the **Inf** 6–18 cm, simple, dense, rachis hidden by the flowers, green, glabrous; floral **Bra** exceeding the pedicels, 8–15 (–22) × 5–7 (–12) mm, glabrous, ovate-acuminate, completely stramineous or with green base, entire or slightly serrulate; **Ped** 2–3 mm, green; **Sep** 7–9 × 3–5 mm, green, ovate, acute, entire, not overlapping, symmetrical, glabrous; **Pet** 8–10 × 3–4 mm, green, elliptic, entire, not imbricate, symmetrical, glabrous, apex obtuse; **St** 11–14 mm, exserted; **Fil** free, green; **Ov** 3–5 mm, green; **Sty** 3–5 mm, exserted, green; **Sti** green; **Fr** 7–9 mm, globose, castaneous; **Se** ± 2 mm, with falciform wing.

The flowers are similar to those of *E. magalhaesii*.

**E. ascendens** Leme (Selbyana 30(2): 129–131, fig. 1, 2010). **Type:** Brazil, Minas Gerais (Leme & al. 7451 [HB, RB, SEL, VIC]). — **Distr:** Brazil (Minas Gerais); ecology not reported.

Flowering plants 2.4–3 m tall, in clumps or solitary; **L** suberect-arcuate to spreading, sheath much broader than the lamina, **L** lamina 70 × 3–4 cm, narrowly triangular, apex attenuate and long-caudate, completely greyish-green or reddish towards the apex, abaxially densely white-lepidote, adaxially inconspicuously white-lepidote to glabrescent, basally flat and apically canaliculate, armed with **Sp** 3–10 mm long; peduncle 1.1–1.6 m, erect, rigid, glabrous; peduncular **Bra** foliaceous to subfoliaceous, exceeding the internodes, long attenuate-caudate, white-lepidote mainly abaxially, laxly and coarsely spinose;

fertile part of the **Inf** 100–125 cm, compound and with 4–12 **Br** 27–55 cm long, without terminal raceme, densely many-flowered, erect, glabrous, rachis stout, straight; lower primary **Bra** subfoliaceous, long-filiform from a subtriangular base, suberect to reflexed, laxly spinose, upper primary **Bra** much reduced, narrowly triangular, attenuate, recurved, inconspicuously spinulose to subentire; floral **Bra** exceeding the sepals,  $\pm 10 \times 4$  mm, long filiform-caudate from a suborbicular-triangular base, glabrous, inconspicuously crenulate to entire, recurved; **Fl** subspreading; **Ped** indistinct, 2–3 mm; **Sep**  $\pm 7 \times 6$ –7 mm, broadly ovate, apex obtuse and apiculate, margins remotely and irregularly crenulate-denticulate mainly near the apex, partially imbricate, symmetrical, glabrous; **Pet** 12–13  $\times 7$ –8 mm, colour not described, ovate, apex obtuse, entire, partially imbricate, symmetrical, glabrous; **St**  $\pm 19$  mm, exserted; **Fil** almost free; **Ov**  $\pm 7$  mm; **Sty**  $\pm 5$  mm, slightly shorter than the anthers; **Sti** subcapitate; **Fr** 17–19  $\times 8$ –10 mm; **Se** subcuneate.

Similar to the poorly known *E. belemii*, but distinguished by taller stature, different floral bracts, shorter pedicels and smaller flowers.

**E. belemii** L. B. Smith & Read (Bradea 5(27): 301–302, fig. 5, 1989). **Type:** Brazil, Minas Gerais (*Belem* 3797 [US, CEPEC, IAN, NY, UB]). — **Distr:** Brazil (Minas Gerais); on limestone rocks.

A dubious name, only reliably known from two herbarium specimens, and without recent collections. The original description is based on very young inflorescences and is inadequate for positive identification (Forzza 2005).

**E. biflorum** (Mez) Forzza (Bol. Inst. Bot. (São Paulo) 23(1): 16, ills. (p. 22), 2005). **Type:** Brazil, Minas Gerais (*Glaziou* 19919 [B, F [photo], P]). — **Lit:** Cavallari & al. (2006: genetics). **Distr:** Brazil (Minas Gerais); sandy and rocky soils, known from a single population only.

≡ *Dyckia biflora* Mez (1894).

Flowering plants 11–32 cm tall, solitary or forming small clumps; rhizome without conspicuous branches; **Ros** 4–11 cm  $\emptyset$ ; **L** secund, sheath 0.5–1.2  $\times 1$ –4.2 cm, **L** lamina 3–9.5  $\times 0.7$ –1.5 cm, abaxially cinereous, adaxially green, entire, rarely

with **Sp**  $\pm 1$  mm long; peduncle 0.7–22 cm, castaneous to slightly vinaceous, erect, glabrous; peduncular **Bra** shorter than the internodes (the basal ones rarely longer), 1–3.2 cm, erect, lanceolate to ovate-lanceolate from a broadly ovate base, acute to acuminate, entire, apex lepidote, base sparsely lepidote; fertile part of the **Inf** 2.5–8.2 cm, simple, few-flowered, lax, rachis castaneous to slightly vinaceous, glabrous; floral **Bra** shorter than the flowers but exceeding the pedicels, 11–16  $\times 8$ –12 mm, stramineous, ovate, acute to acuminate, entire, glabrous; **Fl** patent to slightly reflexed; **Ped** 4–7 mm, glabrous; **Sep** 10–14  $\times 5$ –7 mm, green, ovate, apex obtuse, entire, not imbricate, symmetrical, glabrous; **Pet** 11–15  $\times 4$ –6 mm, colour not described, obovate, apex rounded, entire, symmetrical, imbricate, glabrous; **St**  $\pm 8$  mm, included; **Fil** free, slightly adnate to the petals; **Ov**  $\pm 4$  mm; **Sty**  $\pm 1$  mm, included; **Fr** 12–14 mm; **Se** 3–4 mm, with rounded wings.

Belongs to the *longipedicellatum*-complex. The species is characterized by the very small stature and inflorescences with only 2–5 flowers.

**E. brachypodium** L. B. Smith & Read (Bradea 5(27): 302, fig. 8, 1989). **Type:** Brazil, Bahia (*Read & Daniels* 3442 [RGB, US]). — **Distr:** Brazil (Bahia); granite outcrops in Caatinga or less frequently in Campo Rupestre vegetations. **I:** Forzza (2005: 35).

Flowering plants 1.5–2.3 m tall, forming large clumps; rhizome branched; **Ros** 70–100 cm  $\emptyset$ ; **L** erect-patent, sheath 4.2–4.7  $\times 5.4$ –6.5 cm, **L** lamina 44–82  $\times 2.3$ –4.2 cm, both faces cinereous, margins armed with **Sp** 4–10 mm; peduncle 0.9–1.5 m, green or castaneous, erect, sparsely lepidote to glabrescent; middle peduncular **Bra** exceeding the internodes, 8.7–17.5 cm, erect, patent or reflexed, cinereous, triangular-lanceolate to lanceolate from a broad-ovate base, apex awned, margins spinose, lepidote, upper peduncular **Bra** shorter than the internodes, 2.6–5.2 cm, erect to patent or reflexed, stramineous to slightly cinereous, lanceolate, acute to acuminate, entire to slightly serrate, sparsely lepidote to glabrescent; fertile part of the **Inf** 11–37 cm, simple, many-flowered, dense, rachis covered by the flowers, green to brown, glabrous; floral **Bra** equalling or

shorter than the flowers, 8–15 × 8–12 mm, castaneous to nigrescent, broadly ovate to obovate, rarely lanceolate, apex rounded to acuminate, entire or minimally serrulate, glabrous; **Ped** almost none; **Fl** patent, subsessile; **Sep** 7–14 × 6–8 mm, greenish-cream, ovate, apex rounded, entire, not imbricate, symmetrical, glabrous; **Pet** 13–20 × 6–7 mm, greenish-cream, ovate, apex rounded, entire, partially imbricate, symmetrical, glabrous; **St** 18–22 mm, exserted; **Fil** connate, adnate to the petals; **Ov** 12–14 mm; **Sty** 7–11 mm, exserted; **Sti** lobes laminar; **Fr** 22–27 mm; **Se** 3–4 mm, with falciform wings.

Easily identified by the sessile flowers.

**E. bracteatum** P. J. Braun & Esteves (Bromelie 2017(3): 105–111, ills., 2017). **Type:** Brazil, Bahia (*Esteves Pereira* 403 [UFG 18175]). — **Distr:** Brazil (Bahia: Wanderley); bare bambui limestone outcrops.

Flowering plants to 1.85 m tall, clump-forming with short rhizomes; **Ros** to 50 cm Ø; **L** evenly spreading to somewhat laterally upcurved, stiff and succulent, to 6 mm thick, sheath 5.5 × 8 cm, not further described, **L** lamina to 35 × 3.4 cm, narrowly triangular with narrow tip-region, green but both faces densely silvery grey-white-lepidote, **Sp** retrorse, spreading or antrorse, dark green to dark brown, pungent, 6 × 4 mm, 0.9–2.7 cm distant; peduncle 0.95–1.5 m, green, erect, glabrous, branched but branches sometimes abortive; peduncular **Bra** similar to foliage leaves but increasingly smaller upwards, to 23 cm, densely grey-silvery-lepidote, uppermost bracts chestnut-brown to straw-coloured; fertile part of the **Inf** 48 cm, with several erect branches, very densely many-flowered, fertile parts almost cone-like before anthesis because of the imbricate floral bracts; floral **Bra** very obvious, broadly obovate, stiff and succulent, carinate, ±23 × 17 mm, glossy dark brown; **Fl** ± 35 × 11 mm, ascending to porrect, widely open at anthesis; **Ped** ± 7 mm, cream-coloured, maculate; **Sep** 19 × 22 mm, dark brown to reddish-rose, maculate, oblong-ovate, fused for ±½ of their length, glabrous; **Pet** ± 26 × 5 mm, pale cream-coloured changing to dark brown towards the tips, dorsally brown-maculate, oblong-ovate, obtuse, tips spreading to

recurved at full anthesis; **St** ± 23 mm, exserted; **Fil** white-greenish, maculate; **Anth** ± 7 mm, fleshy, yellow; **Ov** ± 18 × 5 mm, pale green; **Sty** ± 20 mm, green to whitish; **Sti** connivent, dirty greenish-white; **Fr** size not described, pale cream-brown to brown, becoming stramineous with age; **Se** not described.

Similar to *E. erectiflorum*, *E. fragae* and *E. horridum*, esp. because of the inflorescence structure. — [U. Eggli].

**E. bradeanum** L. B. Smith (Smithsonian Misc. Collect. 126: 26, 41, fig. 2, 1955). **Type:** Brazil, Minas Gerais (*Smith & Brade* 5652 [US, RB]). — **Distr:** Brazil (Minas Gerais); ecology not described.

Flowering plants >70 cm tall; **L** sheath small and inconspicuous, **L** lamina 24 × 0.4 cm, both faces covered with pale appressed scales, margins laxly armed with mostly opposite slender curved **Sp** 5 mm long; peduncle 8 mm in Ø, glabrous at least with age; peduncular **Bra** suberect, lower ones foliaceous, much exceeding the internodes, upper ones small, shorter than the internodes, entire; fertile part of the **Inf** 20 cm, simple, many-flowered, dense except near the base, rachis glabrous at least with age; floral **Bra** much exceeding the pedicels, narrowly triangular; **Fl** spreading; **Ped** 6 mm, stout, sulcate; **Sep** 5 mm, broadly ovate; **Pet** and **St** probably free, colour not described; **Fr** 9 mm, ovoid, stout, dark castaneous; **Se** with falciform wings.

Insufficiently known and not found again in the wild.

**E. ctenophyllum** Forzza & Zappi (Kew Bull. 66(2): 286, ills. (p. 284–285), 2011). **Type:** Brazil, Minas Gerais (*Forzza & al.* 5455 [RB, CEPEC, K, MBM, NY, SPF, US]). — **Distr:** Brazil (Minas Gerais: Serra do Cipó); quartzitic sandstones; narrowly endemic.

Flowering plants 50–70 cm tall; rhizome short; **Ros** 15–28 cm Ø; **L** patent to recurved, sheaths 1.5–2.5 × 2–2.7 cm, entire, **L** lamina 7–16 × 0.4–1 cm, narrowly lanceolate, greyish to vinaceous, lepidote, armed with mostly patent **Sp** 6–8 mm long; peduncle 35–45 cm, green, erect, glabrous; lower peduncular **Bra** foliaceous,



exceeding the internodes, erect, lanceolate, apex acute to attenuate, cinereous to vinaceous, strongly spinose, lepidote, upper peduncular **Bra** exceeding the internodes, erect, broadly ovate, apex acute, stramineous, margins serrate, glabrous; fertile part of the **Inf** 16–25 cm, simple, dense, rachis green, glabrous; floral **Bra** exceeding the pedicels, 12–32 × 5–10 mm, broadly ovate, apex long attenuate, completely stramineous or with green base, margins serrulate, glabrous; **Ped** 2–3 mm; **Sep** 8–12 × 3–5 mm, green, ovate, acute, entire, not imbricate, symmetrical, glabrous; **Pet** 10–13 × 3–5 mm, green, elliptic, crenate at the apex, entire, not imbricate, symmetrical, glabrous; **St** 14–16 mm, exserted; **Fil** free, green; **Ov** 3–5 mm, green; **Sty** 5–8 mm, green, exserted; **Sti** green; **Fr** 10–12 mm, globose, castaneous; **Se** ± 3 mm, with falciform wings.

Similar to *E. magalhaesii* and *E. subsecundum*.

**E. diamantinum** Forzza (Nordic J. Bot. 30: 157, figs. 2, 3F–H, 2012). **Type:** Brazil, Minas Gerais (Forzza & al. 4858 [RB, K, MBM, NY, SPF]). — **Distr:** Brazil (Minas Gerais: Diamantina plateau); rock outcrops; only known from 2 populations.

Flowering plants 0.8–1.3 m tall, solitary or in small clumps; rhizome short; **Ros** 15–30 cm Ø; **L** reflexed, sheaths 2.5–3.2 × 3.8–5.2 cm, entire, **L** lamina 13–24 × 1.5–2.7 cm, lanceolate, cinereous, densely lepidote, with **Sp** 5–8 mm; peduncle 45–62 cm, green, erect, glabrous; lower peduncular **Bra** foliaceous, equalling to exceeding the internodes, 6–10 cm, erect, upper peduncular **Bra** shorter than the internodes, 1.7–2.6 cm, lanceolate, apex acute to attenuate, stramineous, entire, glabrous, erect and clasping the peduncle; fertile part of the **Inf** 28–55 cm, simple, lax, rachis green, glabrous; floral **Bra** exceeding the pedicels, 11–25 × 4–7 mm, lanceolate or ovate-lanceolate, apex acute to attenuate, completely stramineous or with green base, entire, glabrous; **Fl** suberect; **Ped** 8–10 mm; **Sep** 8–10 × 5–6 mm, with green base and castaneous apex, lanceolate, acute, entire, not imbricate, symmetrical; **Pet** 11–13 × 3–4 mm, green, narrowly elliptic, apex rounded, entire, not imbricate, symmetrical; **St** 14–16 mm, exserted; **Fil** free, green; **Ov** 5–8 mm, green; **Sty** 3–5 mm,

green, exserted; **Sti** green; **Fr** 10–13 mm, globose, castaneous; **Se** ± 3 mm, with falciform wings.

Closely related to *E. reflexum*.

**E. disjunctum** Forzza (Bol. Inst. Bot. (São Paulo) 23(1): 15–16, figs. 7, 16 (pp. 19, 39), 2005). **Type:** Brazil, Goiás (Forzza & al. 1570 [SPF]). — **Distr:** Brazil (Goiás); on sandstone.

Flowering plants 47–65 cm tall, solitary or forming small clumps; rhizome long, branched; **Ros** 15–22 cm Ø; **L** erect-patent, sheath 2.8 × 3.7 cm, **L** lamina 12–17 × 1.2–1.7 cm, both faces green, only the abaxial-proximal region cinereous, margins with **Sp** 1–2 mm long; peduncle 44–47 cm, erect, glabrous; middle peduncular **Bra** exceeding the internodes, erect, lanceolate, acute to attenuate, margins spinose, glabrous, upper peduncular **Bra** shorter than the internodes and entire; fertile part of the **Inf** ± 15 cm, simple, few-flowered, lax, rachis glabrous; floral **Bra** shorter than the pedicels, 12–18 mm, stramineous, lanceolate, glabrous, acute to attenuate, entire; **Fl** (only faded flowers seen) patent to reflexed; **Ped** 12–36 mm, glabrous; **Sep** 17–19 × 5–7 mm, ovate, glabrous, not imbricate, symmetrical, apex obtuse, entire; **Pet** 10–12 × 16–19 mm, colour not described, obovate, glabrous, imbricate, symmetrical, apex rounded, entire; **St** 15–18 mm, free, included; **Ov** ± 8 mm; **Sty** ± 9 mm, included; **Sti** lobes compact, ± 1 mm; **Fr** 13–17 mm, dark brown, brilliant, with persistent perianth remains; **Se** ± 4 mm, with rounded wings.

A member of the *longipedicellatum*-complex, and similar to *E. pedicellatum*.

**E. eddie-estevesii** Leme & Forzza (Selbyana 23: 200, fig. 1a–f, 2002). **Type:** Brazil, Goiás (Esteves Pereira 346 [HB, UFG]). — **Distr:** Brazil (Bahia, Goiás); limestone outcrops. **I:** Braun (2005); Forzza (2005: 38).

Flowering plants 0.9–2.2 m tall, forming large clumps; rhizome branched; **Ros** 60–100 cm Ø; **L** erect-patent, sheath 3.5–6.7 × 6.5–9.3 cm, **L** lamina 20–56 × 2.5–4.2 cm, both faces strongly cinereous, green to slightly reddish, armed with **Sp** 6–10 mm long; peduncle 45–120 cm, brownish-green, erect, glabrous; peduncular **Bra** exceeding the internodes, 4–12.5 cm, erect to slightly patent,

base cinereous, stramineous towards the apex, triangular-lanceolate to lanceolate, acute to long-attenuate, margins spinose, lepidote to glabrescent; fertile part of the **Inf** 22–38 cm, simple or rarely with a small branch near the base, multi-flowered, lax, rachis brown to greenish-brown, glabrous; lower floral **Bra** similar to the peduncular bracts, exceeding the pedicels, 17–25 × ±7 mm, cinereous, lanceolate, acute, margins serrate, lepidote, upper floral **Bra** very small, shorter than the pedicels, 1–4 × 2–3 mm, stramineous, ovate-triangular, acute to acuminate, entire to slightly serrate, lepidote to glabrescent; **Fl** patent; **Ped** 3–4 mm, brown, glabrous; **Sep** 6–8 × 4–5 mm, yellow, abaxially with scattered pinkish blotches, ovate-triangular, acute, margins inconspicuously crenate, imbricate, symmetrical or slightly asymmetrical, glabrous; **Pet** 15–23 × 5–7 mm, yellow, abaxially with scattered pinkish blotches, elliptic, apex acute to obtuse, margins inconspicuously crenate, partially imbricate, slightly asymmetrical, glabrous; **St** 10–18 mm, exserted; **Fil** connate, not adnate to the petals; **Ov** 6–10 mm; **Sty** 5–10 mm, exserted; **Sti** lobes laminar; **Fr** 12–16 mm; **Se** 3–4 mm, with falciform wings.

**E. erectiflorum** L. B. Smith (Phytologia 20: 180, t. 2: figs. 15–16, 1970). **Type:** Brazil, Piauí (*Andrade-Lima* 66–4800 [US, IPA]). — **Distr:** Brazil (Ceará, Piauí); on rocks in Caatinga and transitions to Cerrado vegetations. **I:** Forzza (2005: 44).

Flowering plants 1.5–2 m tall, forming large clumps; rhizome not described; **Ros** 80–100 cm Ø; **L** erect-patent, sheath ±7 × 5.5 cm, **L** lamina 50–75 × 2.5–3.8 cm, both faces green to slightly cinereous, sparsely lepidote, armed with **Sp** 6–10 mm long; peduncle ±1.5 m, green, erect, glabrous; middle peduncular **Bra** exceeding the internodes, 20–28 cm, cinereous to stramineous, triangular-lanceolate from a broad-ovate base, apex awned, margins spinose, reflexed, lepidote, upper peduncular **Bra** shorter than or slightly exceeding the internodes, 4.5–7.5 cm, erect or apex reflexed, stramineous, lanceolate, apex attenuate to awned, entire, lepidote; fertile part of the **Inf** compound with up to 9 **Br** 32–72 cm long, without terminal raceme, multi-flowered, subdense, rachis green, glabrous; floral **Bra** shorter than

the pedicels, 7–9 × ±1 mm, green, lanceolate, apex acute to attenuate, entire, glabrous; **Fl** secund; **Ped** 8–19 mm, green, glabrous; **Sep** 6–8 × 4–6 mm, yellow, ovate-triangular, acute, entire, not imbricate, symmetrical, glabrous; **Pet** 18–20 × 5–7 mm, yellow, elliptic, apex obtuse, entire, symmetrical, not imbricate, glabrous; **St** 22–25 mm, exserted; **Fil** free, not adnate to the petals; **Ov** 10 mm; **Sty** 10 mm, exserted; **Sti** lobes laminar; **Fr** 16–21 mm; **Se** 3–4 mm, with falciform wings.

**E. fragae** Forzza (Phytotaxa 227: 14, figs. 1–2 (pp. 15–16), 2015). **Type:** Brazil, Bahia (*Fraga & al.* 2735 [RB, HUEFS, US]). — **Distr:** Brazil (Bahia: São Desidério, Sertaneja); limestone outcrops.

Flowering plants 2.2–3 m tall, solitary or forming clumps; **Ros** 60–100 cm Ø; **L** erect, sheath 4–4.7 × 7–7.5 cm, **L** lamina 56–75 × 3–3.4 cm, densely lepidote, greyish, armed with **Sp** 2–5 mm long; peduncle ±1 m, greenish-brown, erect, glabrous or sparsely lepidote; peduncular **Bra** exceeding the internodes, 16–47 cm, cinereous, green at the base, densely lepidote, lanceolate, spinose, erect; fertile part of the **Inf** ± 1.1 m, lax, branched with **Br** to 63 cm, without terminal raceme, rachis green, sparsely lepidote; floral **Bra** longer than the pedicels, 12–20 × 1–2 mm, green at the base, becoming stramineous, linear-triangular, entire or inconspicuously spinose, glabrous; **Fl** polystichous, spreading; **Ped** 5–12 mm, brown; **Sep** 18–22 × 5–7 mm, vinaceous, lanceolate, long-attenuate, acute, entire, not imbricate, symmetrical; **Pet** 28–32 × 6–7 mm, vinaceous, narrowly ovate, obtuse, forming a tube with only the tips recurved, entire, imbricate, symmetrical; **St** 26–27 mm, included or slightly exserted; **Fil** free; **Ov** 10–12 mm; **Sty** 16–18 mm, exserted, vinaceous; **Sti** vinaceous; **Fr** 15–25 mm, globose, chestnut-brown; **Se** ± 3 mm, with falciform wings.

The species shares the inflorescence architecture (heterothetic, i.e. without terminal raceme) with *E. erectiflorum*, *E. ascendens*, *E. bracteatum* and *E. horridum*, but is easily distinguished by the deep vinaceous corolla. — [F. Krapp & U. Eggli].

**E. gracile** L. B. Smith (Phytologia 16: 69, t. 1: figs. 2–4, 1968). **Type:** Brazil, Minas Gerais

(*Belem* 1620 [US, CEPEC, NY, UB]). — **Distr:** Brazil (Espírito Santo, Minas Gerais); limestone outcrops. **I:** Forzza (2005: 23).

Flowering plants 80–100 cm tall, solitary or forming clumps; **Ros** 30–40 cm Ø; **L** erect-patent, sheath 1.3–2.2 × 1.8–3.3 cm, **L** lamina 20–35 × 1.6–2.2 cm, both faces cinereous, green or reddish-green, armed with **Sp** 3–5 mm long; peduncle 33–72 cm, light brown, erect, glabrous; middle peduncular **Bra** shorter than the internodes, 3.5–5.2 cm, erect or reflexed, cinereous to slightly reddish, lanceolate, apex attenuate to awned, entire to serrate, lepidote, upper peduncular **Bra** shorter than the internodes, light brown, lanceolate, acute, entire, erect, glabrous; fertile part of the **Inf** 10–35 cm, simple or rarely with 1–3 **Br** at the base, few-flowered, lax, rachis yellow-green, glabrous; floral **Bra** shorter than the pedicels, 3–9 × 1–6 mm, brown, ovate-triangular, acute, entire, glabrous; **Fl** patent; **Ped** 5–22 mm, white to slightly yellowish, glabrous; **Sep** 7–11 × 5–7 mm, yellow, ovate, apex acute to obtuse, entire, not imbricate, symmetrical, glabrous; **Pet** 14–18 × 4–5 mm, yellow, elliptic to ovate, acute, entire, not imbricate, symmetrical, glabrous; **St** 14–20 mm, exserted; **Fil** free, not adnate to the petals; **Ov** 5–7 mm; **Sty** 3–5 mm, exserted; **Sti** lobes laminar; **Fr** 7–8 mm; **Se** 1–2 mm, with long-caudate wings.

Closely related to *E. horridum*, but much smaller in habit. The two species share a unique seed morphology with long-caudate wings.

**E. heloisae** (L. B. Smith) Forzza & Wanderley (Bol. Bot. Univ. São Paulo 17: 264, 1998). **Type:** Brazil, Minas Gerais (*Smith & al.* 6698 [US, R]). — **Lit:** Christianini & al. (2013: pollination biology). **Distr:** Brazil (Minas Gerais: Serra do Cipó); sandy and rocky soils in Campo Rupestre vegetation. **I:** Forzza (2005: 14).

≡ *Dyckia heloisae* L. B. Smith (1955); **incl.** *Encholirium sazimae* Rauh (1987).

Flowering plants 25–50 cm tall, solitary or in small clumps; **Ros** 6–18 cm Ø; inner **L** erect-patent, outer slightly reflexed, sheath 1.5–2.2 × 2.8–4.2 cm, **L** lamina 4.5–9.5 × 1–1.7 cm, both faces cinereous on young leaves, later pale green to ±black and only cinereous at the base, margin entire or rarely with **Sp** 1–2 mm long; peduncle

13–30 cm, green or yellowish-green, erect, glabrous; peduncular **Bra** mostly shorter than the internodes, 1.5–4.5 cm, green with stramineous apex, lanceolate to ovate-lanceolate, acute, attenuate, entire, lepidote to glabrescent; fertile part of the **Inf** 9–15 cm, simple, few-flowered, lax, rachis yellow to greenish-yellow, glabrous; floral **Bra** 15–20 mm, stramineous to slightly greenish, lanceolate, acute to attenuate, glabrous; **Fl** patent; **Ped** 10–22 mm, greenish to yellowish-green, glabrous; **Sep** yellowish-green, to 12–15 × 6–8 mm, green, ovate, obtuse, entire, not imbricate, symmetrical, glabrous; **Pet** 10–16 × 8–10 mm, green, obovate, apex rounded, entire to slightly eroded, overlapping, symmetrical, glabrous; **St** 8–12 mm, included; **Fil** shortly connate, not adnate to the petals; **Ov** 5–7 mm; **Sty** ± 2 mm, included; **Sti** lobes compact; **Fr** 9–12 mm; **Se** ± 3 mm, with truncated wings.

Belongs to the *longipedicellatum*-complex, and grows sympatrically with *E. vogelii*. Flowers are pollinated by hummingbirds, a local endemic bat, and an unidentified sphingid (Christianini & al. 2013).

**E. horridum** L. B. Smith (Contr. Gray Herb. 129: 32, t. 3: figs. 1–3, 1940). **Type:** Brazil, Espírito Santo (*Foster & Foster* 193 [GH]). — **Lit:** Hmeljevski & al. (2015: population biology). **Distr:** Brazil (Espírito Santo, Minas Gerais); inselbergs in the Atlantic Forest biome. **I:** Forzza (2005: 41); Miller (2009).

Flowering plants 1.8–2.1 m tall, generally solitary and monocarpic; **Ros** 60–100 cm Ø; **L** strongly reflexed, sheath 3–4.2 × 5–6.7 cm, **L** lamina 60–95 × 3–3.5 cm, green to yellowish-green, margins armed with **Sp** 6–15 mm long; peduncle 40–80 cm, brown, erect, glabrous; middle peduncular **Bra** exceeding the internodes, 8.7–15 cm, reflexed, green becoming castaneous, triangular-lanceolate to lanceolate from a broad-ovate base, apex attenuate to long-attenuate, margins spinose, glabrous, upper peduncular **Bra** shorter than the internodes, 3–3.4 cm, erect, light brown, lanceolate, apex acute to attenuate, entire, glabrous; fertile part of the **Inf** 80–130 cm, compound with 10–12 pendulous **Br** 44–82 cm long, without terminal raceme, multi-flowered, lax to

subdense, rachis brown to greenish-brown, glabrous; floral **Bra** shorter than the pedicels, 3–7 × 2–3 mm, greenish-brown, ovate-triangular, acute, entire, glabrous; **Fl** patent; **Ped** 10–15 mm, white to slightly yellowish, glabrous; **Sep** 6–10 × 5–6 mm, yellow, ovate, apex acute to obtuse, entire, not imbricate, symmetrical or slightly asymmetrical, glabrous; **Pet** 15–22 × 6–8 mm, yellow, ovate, apex obtuse, entire, not imbricate, symmetrical, glabrous; **St** 15–22 mm, exserted; **Fil** free, not adnate to the petals; **Ov** 5–7 mm; **Sty** 7–8 mm, exserted; **Sti** lobes laminar; **Fr** 10–15 mm; **Se** 2–3 mm, with long-caudate wings.

Closely related to *E. gracile* but much larger in habit. The two species share a unique seed morphology with long-caudate wings. Hmeljevski & al. (2015) found that pollen dispersal distances are low (mean 45.5 m, maximum 156 m) and pollination is mostly within populations. The plants are almost always monocarpic, and clonal growth is a rare event.

**E. irwinii** L. B. Smith (Phytologia 19: 284, t. 1: fig. 12, 1970). **Type:** Brazil, Minas Gerais (*Irwin & al.* 23573 [US, NY, UB]). — **Distr:** Brazil (Minas Gerais: Grão Mogol); on rocks in Campo Rupestre vegetation. **I:** Forzza (2005: 27).

Flowering plants 80–100 cm tall, forming large clumps; **Ros** 20–30 cm Ø; **L** secund or rarely erect-patent, sheaths 3.8–4 × 1.7–2.5 cm, **L** lamina 22–35 × 0.7–1.1 cm, both faces dark green, red to nigrescent, adaxially slightly cinereous, margins with **Sp** 2–4 mm long; peduncle 43–90 cm, brownish-green, erect, glabrous; middle peduncular **Bra** generally exceeding the internodes, 3.2–9 cm, erect, stramineous, lanceolate from a broad-ovate base, acute, attenuate to awned, margins spinose, glabrous or sparsely lepidote, upper peduncular **Bra** shorter than the internodes, 1.3–2.5 cm, erect, stramineous, lanceolate, acute to acuminate, entire, glabrous; fertile part of the **Inf** 29–40 cm, simple, lax, few-flowered, rachis green, glabrous; floral **Bra** smaller or slightly exceeding the pedicels, 6–11 × 2–3 mm, stramineous, lanceolate, acute to attenuate, entire, glabrous; **Fl** patent; **Ped** 5–9 mm, green, glabrous; **Sep** 5–8 × 3–5 mm, green, ovate-triangular, acute to acuminate, entire,

not imbricate, symmetrical, glabrous; **Pet** 7–9 × 3–4 mm, green, elliptic, acute to acuminate, entire, not imbricate, symmetrical, glabrous; **St** 9–13 mm, exserted; **Fil** free, not adnate to the petals; **Ov** ± 5 mm; **Sty** 5–6 mm, exserted; **Sti** lobes compact; **Fr** 13–18 mm; **Se** 2–4 mm, with truncated wings.

Narrowly endemic to the Grão Mogol area, and the only species of *Encholirium* there.

**E. josinoi-narcisae** P. J. Braun & Esteves (Bromelie 2018(1): 33, ill. (pp. 32–38), 2018). **Type:** Brazil, Goiás (*Esteves Pereira* 788 [UFG]). — **Distr:** Brazil (N Goiás: Mun. Monte Alegre de Goiás); bambui limestone outcrops, 570 m; only known from the type locality.

Flowering plants 1.5–1.9 m tall, forming small clumps to 60 cm Ø, with short rhizome; **Ros** 23–47 cm Ø; **L** lax, spreading regularly or somewhat falcately upcurved, sheath broadly ovate, 2.5–3.8 × 4.2–5.1 cm, stiff, esp. towards the lamina succulent, in part cinereous-lepidote, otherwise glabrous, glossy, bright brown, **L** lamina 9–28 (–34) × 2.5–5.2 cm broad at the base, (pale) green, cinereous-lepidote on both faces, margins spinose, **Sp** predominantly latrorse, brilliant blackish to brown, 7 mm, 15 mm distant; peduncle to 110 cm, green-brown, erect, peduncular **Bra** triangular-lanceolate, caudate, spinose, 4.6–23 cm, green-brown, cinereous-lepidote; fertile part of the **Inf** ± 75 cm, simple, laxly flowered, glabrous; floral **Bra** minute; **Fl** semi-erect; **Ped** 42–55 mm, bright green to brown, sulcate, glabrous; **Sep** 8–11 × 7–8 mm, basally fused 1–4 mm, yellowish-green dotted with tiny brown-pink spots, triangular, obtuse to emarginate, glabrous; **Pet** 31–38 × 5–7 mm, pale yellow, narrowly lanceolate, free, glabrous, dorsally with tiny brown-pink dots; **St** to 32 mm, just visible in the throat; **Fil** free, 25 mm, pale yellow; **Anth** 6–7 mm, yellow with whitish apex; **Ov** trigonous, 7–19 × 3–3.7 mm at the base, bright green; **Sty** ± 32 mm, green; **Sti** slightly exserted, 4 mm, spirally conduplicate; **Fr** 28–31 × 9–14 mm, oblong, bright dark brown; **Se** 3 × 1 mm, dark brown, surrounded with a falcate white-cream wing.

Compared with *E. eddie-estevesii* and *E. longiflorum* in the protologue. — [U. Eggli].

**E. kranzianum** Leme & Forzza (Phytotaxa 227: 14, 17, figs. 3–4 (pp. 18–19), 2015). **Type:** Brazil, Minas Gerais (*Kranz* 393 [RB]). — **Distr:** Brazil (Minas Gerais); quartzitic rocks and sandy soil.

Flowering plants 95 cm tall, solitary or forming clumps; **Ros** 10–14 cm Ø; **L** spreading-recurved, sheath 1.5–2 × 2.5–2.8 cm, **L** lamina 6.5–8.5 × 0.8–1.2 cm, densely white-lepidote, sparsely towards the apex, bronze-coloured, margins densely to subdensely spinose with triangular **Sp** 1.5–2.5 mm long; peduncle 65–68 cm long, dark greenish to dark purple, erect, glabrous, covered by a thin layer of white wax; peduncular **Bra** shorter than the internodes except the lowest, stramineous, soon glabrous, narrowly subtriangular-lanceolate, acute-attenuate, inconspicuously spinose, recurved; fertile part of the **Inf** ± 24 cm, lax, simple, rachis dark purple, glabrous; floral **Bra** shorter than the pedicels, 5–8 × 1–3 mm, stramineous, narrowly subtriangular-lanceolate, caudate, entire or inconspicuously spinose, glabrous; **Fl** polystichous, campanulate, spreading; **Ped** 25–35 mm, dark purple; **Sep** 7–8 × 5–6 mm, dark purple, broadly oblong-ovate, subacute to obtuse, denticulate near the apex, not imbricate, symmetrical; **Pet** ± 11 × 11 mm, green except the dark purple centre of the apex, broadly obovate to orbicular, apex broadly rounded, irregularly crenulate, imbricate, symmetrical; **St** ± 12 mm, exserted; **Fil** free; **Ov** ± 5 mm; **Sty** ± 6 mm, slightly exserted, green; **Sti** green; **Fr** and **Se** unknown.

Closely related to *E. pulchrum* and *E. scrutor* from which it can be easily distinguished by the unique campanulate flowers and some other characters.

**E. longiflorum** Leme (Selbyana 16: 110, fig. 1, 1995). **Type:** Brazil, Minas Gerais (*Teixeira & Carvalho* 380 [MBM, HB]). — **Distr:** Brazil (Bahia, Minas Gerais); limestone outcrops in Cerrado and transitions to Caatinga vegetations. **I:** Forzza (2005: 4, 43).

Flowering plants 3–3.5 m tall; **Ros** > 100 cm Ø; **L** sheath 6.8–7.5 × 9.2–14 cm, **L** lamina 53–83 × 5–8.3 cm, both faces strongly cinereous, margins with **Sp** 3–5 mm long; peduncle

(fragment known only) glabrous; middle peduncular **Bra** exceeding the internodes, 12–30 cm, cinereous, lanceolate, apex acute to awned, margins spinose, lepidote, upper peduncular **Bra** exceeding the internodes, ±2.8 cm, stramineous, lanceolate, apex acute to awned, entire, sparsely lepidote; fertile part of the **Inf** 49–62 cm, simple, multi-flowered, lax (dense according to Braun & Esteves Pereira 2018), rachis glabrous; floral **Bra** reduced, much shorter than the pedicels, 2–5 × 2–3 mm, ovate-triangular, sometimes linear-lanceolate in basal flowers, apex usually acute to acuminate, rarely attenuate, margins entire or minimally serrate, glabrous; **Fl** patent; **Ped** 27–35 (–52) mm, glabrous; **Sep** 8–19 × 3–7 mm, green, ovate-triangular, apex acute to obtuse, entire, not imbricate, symmetrical, glabrous; **Pet** 22–38 × 5–12 mm, greenish-white, elliptic, apex acute to obtuse, entire, not imbricate, symmetrical, glabrous; **St** 23–34 mm, exserted; **Fil** connate, adnate to the petals; **Ov** 9–12 mm; **Sty** 5–12 mm (25 mm according to Braun & Esteves Pereira l.c.), exserted; **Sti** lobes laminar; **Fr** 22–25 mm; **Se** 3–4 mm, with falciform wings.

Identified by long pedicels and petals. The description was completed from the comparison in the protologue of the similar *E. josinoi-narcisae* (Braun & Esteves Pereira 2018). — [F. Krapp & U. Eggl].

**E. luxor** L. B. Smith & Read (Bradea 5(27): 229, fig. 1, 1989). **Type:** Brazil, Minas Gerais (*Anderson & al.* 9259 [US, HB, IAN, MO, NY, UB]). — **Distr:** Brazil (Distrito Federal, Goiás, Minas Gerais); limestone outcrops, usually in open Cerrado vegetation, rarely in dense forests. **I:** Forzza (2005: 29).

**Incl.** *Encholirium piresianum* L. B. Smith & Read (1989).

Flowering plants 1.6–2.2 m tall, generally forming large clumps; rhizome branched; **Ros** 80–110 cm Ø; **L** erect-patent, sheath 3.5–5.7 × 6–11 cm, **L** lamina 25–73 × 2.4–7.2 cm, both faces dark green to cinereous, margins with **Sp** 3–6 mm long; peduncle 70–120 cm, green, erect, glabrous; middle peduncular **Bra** exceeding the internodes, 16–34 cm, erect or apex reflexed, base vinaceous, apex cinereous or stramineous,



lanceolate to triangular-lanceolate from a broad-ovate base, apex attenuate and awned, spinose, lepidote, upper peduncular **Bra** equalling or exceeding the internodes, 2.6–9.2 cm, erect, base vinaceous, stramineous at the apex, lanceolate, acute or acuminate, entire with slightly serrate apex, sparsely lepidote; fertile part of the **Inf** 45–85 cm, simple, multi-flowered, lax to subdense, rachis green, glabrous; floral **Bra** shorter than the pedicels, 5–16 × 2–4 mm, stramineous, slightly greenish or vinaceous, lanceolate to ovate, acute to acuminate, entire, glabrous; **Fl** patent to erect-patent; **Ped** 11–25 mm, green or vinaceous, glabrous; **Sep** 7–12 × 4–6 mm, vinaceous or green, ovate, apex rounded or slightly acute to apiculate, entire, not imbricate, symmetrical, glabrous; **Pet** 19–29 × 5–9 mm, green to slightly vinaceous, elliptic, apex acute to obtuse, entire, valvate, not imbricate, symmetrical, glabrous; **St** 16–27 mm, exserted; **Fil** connate, not adnate to the petals; **Ov** 8–12 mm; **Sty** 9–13 mm, exserted; **Sti** lobes laminar; **Fr** 12–25 mm; **Se** 3–4 mm, with rounded wings.

**E. lymanianum** E. Pereira & Martinelli (Bradea 3(32): 252, t. 2: photo 2, 1982). **Type:** Brazil, Mato Grosso do Sul (*Martinelli* 400 [RB, GUA, HB, K, US]). — **Distr:** Brazil (Mato Grosso, Mato Grosso do Sul); sandstone in flat parts of the Cerrado. **I:** Forzza (2005: 4, 35).

Flowering plants 1.2–2 m tall, forming large clumps; rhizome branched; **Ros** 80–100 cm Ø; **L** erect-patent, sheath ±3.5 × 5.5 cm, entire or slightly spinose distally, **L** lamina 52–65 × 2.2–4.5 cm, both faces green to cinereous, margins with **Sp** 10–12 mm long; peduncle 60–100 cm, erect, lepidote to glabrescent; middle peduncular **Bra** exceeding the internodes, 5.5–9.5 cm, erect, cinereous to slightly vinaceous, triangular-lanceolate to lanceolate, acute, margins spinose, lepidote, upper peduncular **Bra** shorter than the internodes, 2.2–3.7 cm, erect, stramineous, lanceolate, acute, entire or serrate, lepidote to glabrescent; fertile part of the **Inf** 24–57 cm, simple, multi-flowered, lax to subdense, rachis castaneous, densely lanate, with ferruginous trichomes; floral **Bra** 5–15 × 4–7 mm, castaneous, triangular-lanceolate to ovate-triangular, acute to acuminate, entire, densely lanate;

**Fl** patent, subsessile; **Ped** none at anthesis, short after the start of fruit development; **Sep** 9–12 × 6–8 mm, ovate, apex acute to obtuse, entire, imbricate, symmetrical, lanate; **Pet** 17–25 × 11–14 mm, ovate, apex acute to rounded, margins entire to ciliate, partially imbricate, symmetrical, lanate in the centre, glabrous towards the margins; **St** 23–35 mm, exserted; **Fil** free, not adnate to the petals; **Ov** 10–14 mm; **Sty** 7–18 mm, exserted; **Sti** lobes laminar; **Fr** ± 25 mm; **Se** 5–6 mm, with falciform wings.

Disjunct from all other *Encholirium* species.

**E. magalhaesii** L. B. Smith (Phytologia 13: 152, t. 7: fig. 17, 1966). **Type:** Brazil, Minas Gerais (*Magalhães* 18056 [IAN]). — **Distr:** Brazil (Minas Gerais: Chapada Diamantina); directly on rocks in Campo Rupestre vegetation, rarely on sandy and rocky soils. **I:** Forzza (2005: 27). — Fig. 1.



**Fig. 1** *Encholirium magalhaesii* (Supthut 8843: Brazil; Minas Gerais, near Consolo Mata). (Copyright: U. Eggli)

**Incl.** *Encholirium suzannae* Rauh (1988); **incl.** *Encholirium crassiscapum* E. Gross (1997).

Flowering plants 45–100 cm tall, solitary or in clumps; rhizome without conspicuous branches; **Ros** 8–10 cm Ø; **L** erect-patent, sheath 1.2–2.8 × 2.7–3.9 cm, **L** lamina 8–23 × 0.5–0.9 cm, both faces slightly cinereous, green or sometimes slightly reddish, margins with **Sp** 2–5 mm long; peduncle 28–70 cm, brownish-green, erect, glabrous; peduncular **Bra** shorter than the internodes, 2–3.8 cm, erect or reflexed, green at the base, stramineous towards the tip, lanceolate to ovate-lanceolate, acute to acuminate, margins serrate or entire, glabrous or apex lepidote; fertile part of the **Inf** 10–40 cm, simple, lax, few-flowered, rachis green, glabrous; floral **Bra** exceeding the pedicels, 11–21 × 3–6 mm, green at the base, stramineous towards the tip, ovate-lanceolate, acute to acuminate, entire or slightly serrate, glabrous; **Fl** patent to erect; **Ped** 5–8 mm, green, glabrous; **Sep** 6–8 × 3–4 mm, green or apex sometimes slightly brown, ovate, apex obtuse, entire, not imbricate, symmetrical, glabrous; **Pet** 7–9 × 2–3 mm, green, elliptic, apex obtuse, not imbricate, symmetrical, glabrous; **St** 14–18 mm, exserted; **Fil** free, not adnate to the petals; **Ov** 5–6 mm; **Sty** 4–5 mm, exserted; **Sti** lobes compact; **Fr** 7–11 mm; **Se** ± 3 mm, with rounded wings.

Similar to *E. subsecundum*, from which it differs by the smaller habit and smaller flower parts.

**E. maximum** Forzza & Leme (Selbyana 23: 202, fig. 1 g–n, 2002). **Type:** Brazil, Bahia (Forzza & al. 1234 [SPF, CEPEC, HB, K, MBM, NY, SP, US]). — **Distr:** Brazil (Bahia); directly on rocks; only known from the type locality. **I:** Forzza (2005: 38); Braun & Esteves Pereira (2006).

Flowering plants 1.5–3.8 m tall, generally forming large clumps; rhizome without conspicuous branches; **Ros** 70–120 cm Ø; **L** erect-patent, sheath 3.2–4 × 4.5–7.2 cm, **L** lamina 30–65 × 1.8–2.5 cm, both faces cinereous, rarely reddish, margins with **Sp** 5–9 mm long; peduncle 60–130 cm, green, erect, glabrous; middle peduncular **Bra** far exceeding the internodes, 12.5–23 cm, reflexed, cinereous, triangular-lanceolate to lanceolate, attenuate to long-attenuate, base broad-ovate, margins spinose, densely lepidote, upper

peduncular **Bra** shorter than the internodes, 2.2–4.5 cm, erect to slightly reflexed, castaneous, lanceolate, apex acute, entire to slightly serrate, glabrous; fertile part of the **Inf** 60–150 cm, simple, multi-flowered, lax to subdense, rachis bright green, glabrous; floral **Bra** shorter than the flowers, 13–22 × 13–17 mm, brown, broadly ovate to obovate, apex acuminate, margins inconspicuously serrate, glabrous; **Fl** patent, subsessile; **Sep** 9–13 × 9–13 mm, yellow, greenish-yellow or apex slightly brown, obovate, apex rounded to retuse, entire or minutely crenate, imbricate, symmetrical or inconspicuously asymmetrical, glabrous; **Pet** 21–25 × 11–15 mm, vivid yellow, ovate, apex rounded, entire, partially imbricate, symmetrical, glabrous; **St** 30–32 mm, exserted; **Fil** free, not adnate to the petals; hypanthium reduced; **Ov** 20–22 mm; **Sty** 7–11 mm, exserted; **Sti** lobes laminar; **Fr** 27–33 mm; **Se** 3–4 mm, with rounded wings.

The largest species of the genus.

**E. pedicellatum** (Mez) Rauh (Trop. subtrop. Pfl.-welt 60: 15, ills. (pp. 14–16), 1987). **Type:** Brazil, Minas Gerais (*Schwacke* 8413 [B, RB]). — **Lit:** Cavallari & al. (2006: genetics). **Distr:** Brazil (Minas Gerais: Diamantina plateau); Campo Rupestre vegetation, sandy and rocky soils; known from a single population only. **I:** Forzza (2005: 4, 17). — Figs. 2 and 3.

≡ *Dyckia pedicellata* Mez (1896).

Flowering plants 65–70 cm tall, solitary or in clumps; rhizome without conspicuous branches; **Ros** 9–16 cm Ø; **L** patent to reflexed, sheaths 1.5–1.8 × 2.5–3.5 cm, **L** lamina 6.5–10 × 1.8–2.5 cm, both faces strongly cinereous, margins with **Sp** 3–5 mm long; peduncle 27–40 cm, green, erect, glabrous; peduncular **Bra** shorter than the internodes, ±3.5 cm, erect, base stramineous, apex cinereous, lanceolate, acute to acuminate, entire to slightly serrate, glabrous but the upper ones with lepidote apex; fertile part of the **Inf** 22–25 cm, simple, few-flowered, lax, rachis green, glabrous; floral **Bra** shorter than the pedicels, 9–18 × 2–3 mm, stramineous, lanceolate, acute to attenuate, entire, glabrous; **Fl** patent to slightly reflexed; **Ped** 22–55 mm, green, glabrous; **Sep** 11–14 × 5–8 mm, green,

**Fig. 2** *Encholirium pedicellatum* (Rauh 56195: Brazil; Minas Gerais, near Diamantina). (Copyright: U. Eggli)



**Fig. 3** *Encholirium pedicellatum* (same as previous illustration). (Copyright: U. Eggli)

ovate, apex obtuse, entire, not imbricate, symmetrical, glabrous; **Pet** 14–17 × 12 mm, green, obovate, apex rounded or obtuse, entire, imbricate, symmetrical, glabrous; **St** ± 12 mm, included; **Fil** connate,

not adnate to the petals; **Ov** ± 11 mm, **Sty** 4–6 mm, included; **Sti** lobes compact; **Fr** ± 14 mm; **Se** ± 3 mm, with rounded wings.

Belonging to the *longipedicellatum*-complex.

**E. pierre-braunii** Esteves (Bromelie 2017(2): 83–87, ills., 2017). **Type:** Brazil, Bahia (*Esteves-Pereira* 489 [UFG 50.535]). — **Distr:** Brazil (W Bahia: Serra do Ramalho); exposed karstic bambuí limestone, 740 m, only known from the type locality.

Flowering plants to 2.9 m tall, solitary or offsetting and group-forming; **Ros** to 90 cm Ø, dense; **L** very succulent and stiff, sheath 5.5 × 8.5 cm, broadly concave, dark brown, glossy, glabrous, **L** lamina long attenuate, sometimes sinuously curved, to 50 × 3.8 cm, upper face dark brownish-ruby to brownish-green to almost black, with large silver-grey to whitish areas around the spine bases, lower face dull greyish, finely veined, **Sp** laxly disposed, variously oriented but often retrorse, rigid, ±9 mm, basally 3–17 mm wide, ±2.5 cm distant, densely silvery-white-lepidote; peduncle 1.1–2 m, glabrous, erect, pale green; peduncular **Bra** similar to rosette leaves bud rapidly becoming smaller, to 27 cm, longer than the internodes; fertile part of the **Inf** to 85 cm, simple, laxly many-flowered; lower floral **Bra** triangular, long-attenuate, ±11 mm, uppermost only 2 mm or rudimentary; **Fl** horizontally patent; **Ped** to 27 mm, slender, pale green; **Sep** 10 × 6 mm, erect, pale green with minute reddish-brown

spots, ovate-triangular, glabrous; **Pet** 35 × 7 mm, somewhat flaring, pale green with minute reddish-brown spots giving the flowers an overall brownish-dull appearance, triangular-lanceolate, slightly succulent, glabrous; **St** exerted; **Fil** ± 30 mm, cream-coloured; **Anth** ± 8 mm, dark green; **Ov** conical, 23 × 4.6 mm Ø, dark green, glossy; **Sty** ± 8 mm, bright green basally, creamy with reddish-brown streaks above; **Sti** somewhat irregularly laminar, ±7 mm, cream-yellowish, with reddish-brown spots, glabrous; **Fr** size not described but probably ±25 mm, pale cream to chestnut-brown, paler with age; **Se** incl. the wing 4.3 × 4 mm, seed proper medium brown, papery wing pale creamy-ochre. — [U. Eggli].

**E. pulchrum** Forzza & al. (Nordic J. Bot. 30: 153, figs. 1, 3A–C, 2012). **Type:** Brazil, Minas Gerais (*Ribeiro & Paula* 48 [RB]). — **Distr:** Brazil (Minas Gerais: Diamantina plateau); flat granitic rock outcrops; known from a single site only.

Flowering plants 70–78 cm tall, solitary or in small clumps; rhizome short; **Ros** ± 40 cm Ø; **L** spreading to slightly reflexed, sheath not described, **L** lamina 20–25 × 2.5 cm, narrowly triangular to lanceolate, green to reddish, glabrous except the inconspicuously white-lepidote adaxial margins, abaxially lustrous, margins with **Sp** 3–8 mm long; peduncle 30–35 cm, green, erect, glabrous; lower peduncular **Bra** foliaceous, equalling or exceeding the internodes, 8–10 cm, erect, upper peduncle **Bra** shorter than the internodes, 3–4.5 cm, erect and amplexicaul, completely stramineous or with green base, lanceolate, apex acute to attenuate, entire, glabrous; fertile part of the **Inf** 37–45 cm, simple, lax, erect, rachis green, glabrous; floral **Bra** shorter than the pedicels, 8–22 × 1–6 mm, completely stramineous, lanceolate to ovate or filiform, apex acute to attenuate, entire to slightly serrulate, glabrous; **Fl** suberect to spreading; **Ped** 25–57 mm, green; **Sep** 6–10 × 4–6 mm, green, ovate to broadly oblong-elliptic, apex rounded or crenate, entire or remotely and irregularly denticulate near the apex, imbricate, symmetrical; **Pet** 9.5–12 × 8–10 mm, green, oblong to orbicular, apex rounded to obtuse-emarginate, entire, imbricate, symmetrical; **St** 10–11 mm, included; **Fil** free, green; **Ov** 7–8 mm,

green; **Sty** 2–4 mm, green, included; **Sti** green; **Fr** and **Se** not described.

Belonging to the *longipedicellatum*-complex, and similar to *E. pedicellatum*.

**E. reflexum** Forzza & Wanderley (Novon 11 (1): 40–42, Fig. 1, 2001). **Type:** Brazil, Minas Gerais (*Forzza & al.* 800 [SPF, BHC, US]). — **Distr:** Brazil (Minas Gerais); Campo Rupestre vegetation, directly on rocks. **I:** Forzza (2005: 22).

Flowering plants 60–100 cm tall, solitary or in clumps; rhizome without conspicuous branches; **Ros** 15–30 cm Ø; **L** reflexed, sheath 4.2–6 × 1.8–2.5 cm, **L** lamina 13–24 × 1.5–2.7 cm, both faces cinereous, rarely reddish, margins with **Sp** 4–7 mm long; peduncle 25–62 cm, green, erect, glabrous; middle peduncular **Bra** shorter than or equalling the internodes, 6–10 cm, glabrous and becoming stramineous at the base, apex cinereous and lepidote, lanceolate from a long-ovate base, attenuate, margins spinose, apex erect or slightly reflexed, upper peduncular **Bra** shorter than the internodes, 1.7–2.6 cm, lanceolate, stramineous, attenuate and acute, entire, erect, glabrous; fertile part of the **Inf** 22–33 cm, simple, few-flowered, lax, rachis green, glabrous; floral **Bra** shorter than the flowers, 11–15 × 4–5 mm, stramineous, lanceolate, acute to attenuate, entire, glabrous; **Fl** patent; **Ped** 3–4 mm, green, glabrous; **Sep** 5–7 × 5–7 mm, green, obovate, apex rounded, sometimes inconspicuously apiculate, entire, imbricate, symmetrical, glabrous; **Pet** 7–9 × 7–9 mm, green, obovate, apex rounded, entire, symmetrical, imbricate, glabrous; **St** ± 10 mm, included or slightly exerted; **Fil** connate, not adnate to the petals; **Ov** 5–6 mm; **Sty** ± 4 mm, included; **Sti** lobes compact; **Fr** 11–18 mm; **Se** ± 3 mm, with rounded wings.

Belonging to the *longipedicellatum*-complex.

**E. scrutor** (L. B. Smith) Rauh (Trop. subtrop. Pfl.-welt 60: 94, 1987). **Type:** Brazil, Minas Gerais (*Cordeiro & Simonis* 4048 [SPF, U]). — **Distr:** Brazil (Minas Gerais: around Diamantina); Campo Rupestre vegetation, sandy and rocky soils. **I:** Forzza (2005: 4, 14).



≡ *Dyckia scrutator* L. B. Smith (1987); **incl.** *Encholirium carmineoviridiflorum* Rauh (1987); **incl.** *Encholirium inerme* Rauh (1987).

Flowering plants 19–56 cm tall, solitary or in clumps; rhizome without conspicuous branches; **Ros** (4-) 8–15 cm Ø; **L** secund to slightly secund, rarely erect, sheath 1.2–1.7 × 1.9–2.5 cm, **L** lamina 2–11 × 0.6–1.3 cm, both faces green to cinereous, sometimes black-vinaceous when flowering, margins entire or rarely spinose with **Sp** ± 1 mm long; peduncle 12–28 cm, rose to slightly vinaceous, delicate, glabrous or sparsely lepidote; peduncular **Bra** shorter than the internodes, 0.7–1.6 cm, erect, stramineous or slightly pinkish, lanceolate to ovate-lanceolate, long-attenuate, acute, entire, basal ones with densely lepidote apex, upper ones glabrous; fertile part of the **Inf** 3–16 cm, simple, few-flowered, lax, rachis pink, glabrous; floral **Bra** shorter than the pedicels, 4–11 × 2–4 mm, pinkish, ovate-triangular, acute to acuminate, entire, glabrous; **Fl** patent to slightly reflexed; **Ped** 15–51 mm, pink, glabrous; **Sep** 6–15 × 4–9 mm, carmine to pinkish near the base, dark green above, ovate, obtuse, entire, not imbricate, symmetrical, glabrous; **Pet** 8–13 × 6–9 mm, cream-green at the base, (dark) green towards the apex, obovate, apex rounded, entire, imbricate, symmetrical, glabrous; **St** 6–10 mm, included; **Fil** connate, adnate to sepals and petals; **Ov** 6–7 mm; **Sty** ± 1 mm, included; **Sti** lobes compact; **Fr** 10–13 mm; **Se** 4–5 mm, with roundish wings.

Belonging to the *longipedicellatum*-complex.

**E. spectabile** Martius ex Schultes & Schultes *fil.* (in Roemer & Schultes, Syst. Veg. 7(2): lxxviii, 1233, 1830). **Type:** Brazil, Bahia (*Martius* 2483 [M]). — **Lit:** Siqueiro Filho & Leme (2007: 318–320, with ill., 320–323, as *E. pernambucanum*); Queiroz & al. (2016); Gonçalves-Oliveira & al. (2017: population genetics); **Distr:** Brazil (Bahia, Ceará, Distrito Federal, Paraíba, Piauí, Pernambuco, Rio Grande do Norte, Sergipe); rocky habitats (inselbergs) in Caatinga vegetation. **I:** Forzza (2005: 32).

≡ *Dyckia spectabilis* (Martius ex Schultes & Schultes *fil.*) Baker (1889); **incl.** *Puya saxatilis* Martius (1828) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Encholirium densiflorum* Ule (1908); **incl.**

*Encholirium rupestre* Ule (1908); **incl.** *Encholirium hoehneanum* L. B. Smith (1943); **incl.** *Encholirium lutzii* L. B. Smith (1958); **incl.** *Encholirium patens* L. B. Smith (1972); **incl.** *Encholirium bahianum* L. B. Smith & Read (1989); **incl.** *Encholirium harleyi* L. B. Smith & Read (1989); **incl.** *Encholirium paraibae* L. B. Smith & Read (1989); **incl.** *Encholirium pernambucanum* L. B. Smith & Read (1989).

Flowering plants 1.2–2.5 m tall, forming large clumps; rhizome branched; **Ros** 50–110 cm Ø; **L** erect-patent, sheath 2.8–4.7 × 3.8–6.7 cm, **L** lamina 25–84 × 2.2–4.7 cm, both faces very variable in colour, light green, green-red, green-yellow, yellow or yellow-red, margins with **Sp** 6–12 mm long; peduncle 80–150 cm, green to castaneous, erect, glabrous; middle peduncular **Bra** exceeding the internodes, 12–25 cm, erect or apically reflexed, base vinaceous, towards the apex cinereous or stramineous, triangular-lanceolate to lanceolate from a broad-ovate base, apex awned, spinose, lepidote, upper peduncular **Bra** smaller, equalling or exceeding the internodes, 2.4–9.5 cm, vinaceous base with stramineous apex to completely stramineous, lanceolate, acute to acuminate, entire to slightly serrate, erect, usually glabrous or sparsely lepidote; fertile part of the **Inf** 35–88 cm, simple or rarely with partially undeveloped branches at the base, multi-flowered, lax, subdense to dense, rachis green or greenish-brown, glabrous; lower floral **Bra** equalling or exceeding the pedicels but not the flowers, 5–22 × 1–6 mm, castaneous to nigrescent, in young inflorescences slightly greenish with vinaceous apex, filiform, lanceolate, triangular, ovate-lanceolate, acute, acuminate to attenuate, entire, glabrous; **Fl** erect-patent; **Ped** 3–15 mm, green to brown, glabrous; **Sep** 7–12 × 3–8 mm, green, yellowish-green or green with vinaceous apex, ovate, apex acute to obtuse or rarely slightly retuse, margins entire to slightly crenulate, not imbricate, symmetrical, glabrous; **Pet** 9–22 × 4–10 mm, green or cream-green, apex vinaceous in buds, elliptic, apex obtuse, entire, not imbricate, symmetrical, glabrous; **St** 15–32 mm, exserted; **Fil** free; **Ov** 8–13 mm; **Sty** 12–15 mm, exserted; **Sti** lobes laminar; **Fr** 12–27 mm; **Se** 2–4 mm, with falciform wings.



By far the most widespread and morphologically most variable species of the genus. Many formerly distinct species were synonymized by Forzza (2005). According to Braun & Esteves-Pereira (2017), the species also occurs in Alagoas and Maranhão.

Nascimento & al. (2012) report that the leaf bases (grated, sun-dried, sieved) were used to produce a bitter-tasting flour for couscous preparation during times of famine in Pernambuco.

Queiroz & al. (2016) found a mixed pollination system: The flowers open in mid-afternoon and last for  $\pm 20$  hours. They are effectively visited by 3 species of bats and the opossum *Didelphis albiventris* during the night, and 3 species of hummingbirds during the day; hawkmoths and passerine birds are recorded as sporadic further visitors. Hummingbirds were also recorded as flower visitors by Las-Casas & al. (2012). The population genetic study of Gonçalves-Oliveira & al. (2017) indicates that gene flow via bat pollination is higher than that through seed dispersal. Each inselberg population has a unique genetic composition, but two population groups (one from the SE Caatinga, the other from the remaining range in the SW Caatinga, the N Espinhaço Range, and the Borborema Plateau) have been found, indicating the possible presence of a cryptic species. — [F. Krapp & U. Egli].

**E. splendidum** Forzza (Phytotaxa 227: 17, 23, figs. 5–7 (pp. 20–22), 2015). **Type:** Brazil, Bahia (Forzza & al. 4078 [RB, B, HUEFS, K, NY, SPF, US]). — **Distr:** Brazil (Bahia); limestone outcrops.

Flowering plants 1.4–1.6 m tall, propagating by long stolons; **Ros** 20–40 cm  $\varnothing$ ; **L** spreading to slightly reflexed, sheath 3.5–4.5  $\times$  4.2–5.7 cm, **L** lamina 28–33  $\times$  1.8–2.2 cm, glabrous, inconspicuously lepidote, green to reddish, armed with broadly triangular **Sp** 3–5 mm long; peduncle 70–95 cm, green, erect, glabrous; lower peduncular **Bra** exceeding the internodes, 18–32 cm, upper peduncular **Bra** exceeding or shorter than the internodes, 5.5–9.5 cm, green at the base or completely stramineous, glabrous or inconspicuously white-lepidote, lanceolate, attenuate, spinose, erect to spreading; fertile part of the **Inf** 48–62 cm, lax, simple, rachis green, glabrous; floral **Bra**

much shorter than the pedicels, 2–3  $\times$  1–2 mm, stramineous or green, lanceolate to ovate, acute, entire, glabrous; **Fl** polystichous, spreading; **Ped** 2.2–4.2 mm, green; **Sep** 7–11  $\times$  4–6 mm, green, sometimes with purplish-vinaceous spots, ovate-lanceolate, apex narrowly rounded, entire, not imbricate, symmetrical; **Pet** 30–35  $\times$  5–7 mm, green, sometimes with purplish-vinaceous spots, oblong-lanceolate, apex narrowly rounded, curled, entire, not imbricate, symmetrical; **St** 28–32 mm, exceeding the petals; **Fil** free; **Ov** 10–12 mm; **Sty** 7–9 mm, exserted, pale green; **Sti** pale green; **Fr** 15–25 mm, globose, chestnut-brown; **Se** 3–4 mm, with falciform wings.

Closely related to *E. longiflorum* but much smaller. Bat pollination was observed for this species.

**E. subsecundum** (Baker) Mez (in A. & C. de Candolle, Monogr. Phan. 9: 540, 1896). **Type:** Brazil, Minas Gerais (*St. Hilaire* E-496 [P]). — **Lit:** Sazima & al. (1989: pollination ecology, as *E. glaziovii*); Cavallari & al. (2006: genetics). **Distr:** Brazil (Minas Gerais); on rocks.

$\equiv$  *Dyckia subsecunda* Baker (1889); **incl.** *Encholirium glaziovii* Mez (1894).

Flowering plants 1.5–2 m tall, usually in large clumps; rhizome branched; **Ros** 60–100 cm  $\varnothing$ ; **L** erect-patent, sometimes slightly arching, sheath 4–6.3  $\times$  4.2–5.8 cm, **L** lamina 46–73  $\times$  1.8–4 cm, both faces green or cinereous, margins with **Sp** 5–15 mm long; peduncle 70–150 cm, green or brown, erect or recurved, glabrous; peduncular **Bra** generally exceeding the internodes, middle ones 12–35 cm, erect to reflexed, stramineous, lanceolate from a broad-oval base, apex awned, margins spinose, glabrous, upper peduncular **Bra** 4.3–5.5 cm, erect or apex reflexed, vinaceous or brown when young, later stramineous, lanceolate, acute-attenuate, serrate, glabrous; fertile part of the **Inf** 15–40 cm, simple, multi-flowered, dense or rarely lax, rachis green to slightly grey, glabrous; floral **Bra** exceeding the flowers, 20–35  $\times$  8–16 mm, stramineous or base slightly greenish, ovate-lanceolate, acute, attenuate, entire or serrate, glabrous; **Fl** erect; **Ped** 5–10 mm, green, glabrous; **Sep** 12–18  $\times$  5–7 mm, green, triangular-lanceolate, acute, entire, not imbricate,

symmetrical, glabrous; **Pet** 15–22 × 2–4 mm, green, elliptic, apex obtuse, not imbricate, symmetrical, glabrous; **St** 15–25 mm, exerted; **Fil** free; **Ov** 5–7 mm; **Sty** 7–10 mm, exerted; **Sti** lobes laminar; **Fr** 15–25 mm; **Se** ± 5 mm, falciform.

Usually growing as solitary clumps, not in large populations as most other species.

**E. viride** P. J. Braun & Esteves (Bromelie 2017 (1): 5, ills. (pp. 6–10), 2017). **Type:** Brazil, Minas Gerais (*Esteves-Pereira* 472 [UFG]). — **Distr:** Brazil (Minas Gerais: Matias Cardoso); on limestone in transition of Campo Cerrado/Caatinga vegetation, 500 m.

Flowering plants 1.8–2.7 m tall, offsetting with thick short rhizomes and forming groups; **Ros** 35 cm tall, 75–95 cm Ø; **L** mostly arching-spreading, firm, succulent, sheath ± 8 × 9 cm, almost globosely curved and amplexicaul, dark brown, both faces glabrous and glossy, margins with a few minute teeth apically, **L** lamina 35–80 × 6.5–11 cm, long triangular-attenuate, often ± contorted, palish green, with pungent brown tip, both faces veined, densely grey-lepidote, margins with antrorse **Sp** 6–11 mm long, with broad green deltoid base, ± 21 mm apart; **Inf** erect, simple; peduncle to 1.05 m, first remaining short for a long time and rapidly elongating just before anthesis, glabrous; peduncular **Bra** erect to contorted, the largest to 76 cm, coriaceous, margins slightly spinose; fertile **Inf** part 0.85–1.34 cm, rather densely many-flowered, green, glabrous; floral **Bra** minute, triangular, succulent, green; **Fl** spreading; **Ped** 13 mm, pale green; **Sep** 8 × 5 mm, triangular, obtuse, succulent, green, glabrous; **Pet** 17 × 7 mm, linear to oblong-ovate, obtuse, bright green, with or without pinkish-violet speckles, glabrous; **St** ± 17 mm, exerted; **Fil** free, white; **Anth** 5 mm, sagittate, green; **Ov** 5 × 5 mm, 3-sulcate, glossy (dark) green; **Sty** ± 15 mm, bright green; **Sti** 3 mm, green-yellow, somewhat spirally contorted; **Fr** brown changing to straw-coloured with age, size not described; **Se** irregularly shaped, ± 4.3 × 4 mm, cream-coloured with bright brown testa, papery.

Compared with the widespread and variable *E. spectabile*, but with smaller rosettes, distinctly

green and broader leaves and conspicuously green flowers. — [U. Eggl].

**E. viridicentrum** Leme & O. B. C. Ribeiro (Phytotaxa 177(2): 86–89, ills., 2014). **Type:** Brazil, Minas Gerais (*Ribeiro & Leme* 282 [RB, HB]). — **Distr:** Brazil (Minas Gerais); quartzitic outcrops in Campo Rupestre vegetation.

Flowering plants 25–30 cm tall; **Ros** 12–15 cm Ø; **L** spreading, recurved, sheath 1.4 × 1–1.8 cm, **L** lamina 5.5–5.7 × 0.5–0.8 cm, white-lepidote except the glabrous adaxial apex, dark purple with green or yellowish-green base, armed with narrowly triangular **Sp** 1.5–2 mm long; peduncle 14–16 cm, green, erect, glabrous; peduncular **Bra** longer than the internodes, stramineous, lower ones leaf-like, upper ones broadly ovate, caudate, serrulate, glabrous; fertile part of the **Inf** 6.5–9 cm, dense, simple, rachis green, glabrous; floral **Bra** ± equalling the flowers, 12–15 × 4–6 mm, green, soon stramineous, ovate-lanceolate, acuminate, entire, glabrous; **Fl** suberect; **Ped** 2 mm, green, glabrous; **Sep** 7–8 × 3–4 mm, green, narrowly ovate, acute, apiculate, entire, not imbricate, symmetrical, glabrous; **Pet** 9 × 2–2.5 mm, green, narrowly ovate-lanceolate, apex narrow and emarginate, entire, not imbricate, symmetrical, glabrous; **St** 12–13 mm, exerted; **Fil** free or nearly so; **Ov** 3–4 mm; **Sty** 4–5 mm, exerted; **Sti** green; **Fr** and **Se** unknown.

Closely related to *E. ctenophyllum*, but much smaller.

**E. vogelii** Rauh (Trop. subtrop. Pfl.-welt 60: 95–98, ills., 1987). **Type:** Brazil, Minas Gerais (*Vogel & Sazima* 209 [HEID, UEC]). — **Lit:** Christianini & al. (2013: pollination ecology). **Distr:** Brazil (Minas Gerais: Serra do Cipó); sandy or rocky soils, between rocks. **I:** Forzza (2005: 17).

Flowering plants 1.4–2.5 m tall, forming large clumps; rhizome without conspicuous branches; **Ros** 80–100 cm Ø; inner **L** erect, outer **L** patent, sometimes secund, sheath 4.8–7.4 × 7.2–9.3 cm, **L** lamina 34–65 × 3–4 cm, both faces green or slightly reddish, margins with **Sp** 5–10 mm long; peduncle 70–80 cm, green, erect, glabrous; peduncular **Bra** exceeding the internodes, 12–35 cm, erect or with reflexed apex, green but

withering stramineous, triangular-lanceolate from a broad-ovate base, attenuate, spinose, glabrescent; fertile part of the **Inf** 30–50 cm, simple, many-flowered, lax, apex sometimes somewhat arching, rachis green, glabrous; floral **Bra** exceeding the pedicels but not the flowers, 15–70 × 20–40 mm, castaneous or slightly greenish, lanceolate, acute to long-attenuate, entire, lanuginose with white trichomes, simple; **Fl** patent; **Ped** 23–34 mm, green, glabrous; **Sep** 8–15 × 5–7 mm, green, ovate, apex obtuse, margins densely white-lanuginose, slightly eroded, not imbricate, symmetrical, glabrous or sparsely lanuginose; **Pet** 9–15 × 6–9 mm, green, obovate, apex rounded, with slightly eroded margins, sparsely white-lanuginose, imbricate, symmetrical, glabrous; **St** 9–13 mm, included; **Fil** connate, not adnate to the petals; **Ov** ± 10 mm; **Sty** ± 1 mm, included; **Sti** lobes compact; **Fr** 12–15 mm; **Se** ± 5 mm, falciform.

Belonging to the *longipedicellatum*-complex, and occurring sympatrically with *E. heloisae*. Pollination is exclusively by hummingbirds (Christianini & al. 2013).

## References

- Aguilar-Rodríguez, P. A. [& al. 2014], Krömer, T. & MacSwiney G., M. C. (2014) The secrets of night-blooming bromeliads and bats. *J. Bromeliad Soc.* 64(3): 156–165, ills.
- Braun, P. J. (2005) Reise zum Fundort von *Encholirium eddie-estevesii* (Bromeliaceae) in Zentral-Brasilien. *Kakt. and. Sukk.* 56(2): 50–53, ills.
- Braun, P. J. & Esteves Pereira, E. (2006) Succulent and xeromorphic Bromeliads of Brazil. Part 3. *Encholirium maximum*, *Orthophytum burle-marxii* and *Dyckia goehringii*. *Cact. Succ. J. (US)* 78(4): 160–164, ills. [https://doi.org/10.2985/0007-9367\(2006\)78\[160:SAXBOB\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[160:SAXBOB]2.0.CO;2)
- Braun, P. J. & Esteves Pereira, E. (2017) Ein [sic!] neue felsbewohnende Art der Gattung *Encholirium* aus dem äussersten Norden von Minas Gerais, Brasilien/A new rupicolous species of *Encholirium* from the uppermost north of Minas Gerais, Brazil: *Encholirium viride*. *Bromelie* 2017(1): 4–10, ills.
- Braun, P. J. & Esteves Pereira, E. (2018) Eine neue, isoliert wachsende *Encholirium* Art aus dem Norden von Goiás (Zentral-Brasilien)/A new isolated growing species of *Encholirium* from northern Goiás (central Brazil): *Encholirium josinoi-narcisae*. *Bromelie* 2018(1): 32–38, ills.
- Cavallari, M. M. [& al. 2006], Forzza, R. C., Veasey, E. A., Zucchi, M. I. & Oliveira, G. C. X. (2006) Genetic variation in three endangered species of *Encholirium* (Bromeliaceae) from Cadeia do Espinhaço, Brazil, detected using RAPD markers. *Biodivers. & Conservation* 15: 4357–4373. <https://doi.org/10.1007/s10531-005-3741-5>
- Christianini, A. V. [& al. 2013], Forzza, R. C. & Buzato, S. (2013) Divergence on floral traits and vertebrate pollinators of two endemic *Encholirium* bromeliads. *Pl. Biol. (Stuttgart)* 15(2): 360–368, ills. <https://doi.org/10.1111/j.1438-8677.2012.00649.x>
- Forzza, R. C. (2005) Revisão taxonômica de *Encholirium* Mart. ex Schult. & Schult. f. (Pitcairnioideae — Bromeliaceae). *Bol. Bot. Univ. São Paulo* 23(1): 1–49, ills., keys. <https://doi.org/10.11606/issn.2316-9052.v23i1p1-49>
- Forzza, R. C. & Zappi, D. C. (2011) Side by side: Two remarkable new species of *Encholirium* Mart. ex Schult. & Schult. f. (Bromeliaceae) found in the Cadeia do Espinhaço, Minas Gerais, Brazil. *Kew Bull.* 66(2): 281–287, ills., key. <https://doi.org/10.1007/s12225-011-9283-y>
- Gonçalves-Oliveira, R. C. [& al. 2017], Wöhrmann, T., Benko-Iseppon, A. M., Krapp, F., Alves, M., Wanderley, M. G. L. & Weising, K. (2017) Population genetic structure of the rock outcrop species *Encholirium spectabile* (Bromeliaceae): The role of pollination vs. seed dispersal and evolutionary implications. *Amer. J. Bot.* 104(6): 868–878, map. <https://doi.org/10.3732/ajb.1600410>
- Hmeljevski, K. V. [& al. 2015], Reis, M. S. dos & Forzza, R. C. (2015) Patterns of gene flow in *Encholirium horridum* L. B. Sm., a monocarpic species of Bromeliaceae from Brazil. *J. Heredity* 106(1): 93–101. <https://doi.org/10.1093/jhered/esu067>
- Krapp, F. [& al. 2014], Pinangé, D. S. de B., Benko-Iseppon, A. M., Leme, E. M. C. & Weising, K. (2014) Phylogeny and evolution of *Dyckia* (Bromeliaceae) inferred from chloroplast and nuclear sequences. *Pl. Syst. Evol.* 300(7): 1591–1614, ills., maps. <https://doi.org/10.1007/s00606-014-0985-0>
- Las-Casas, F. M. G. [& al. 2012], Azevedo Júnior, S. M. & Dias Filho, M. M. (2012) The community of hummingbirds (*Aves: Trochilidae*) and the assemblage of flowers in a Caatinga vegetation. *Brazil. J. Biol.* 72(1): 51–58.
- Leal, F. C. [& al. 2006], Lopes, A. V. & Machado, I. C. (2006) Polinização por beija-flores em uma área de caatinga no Município de Floresta, Pernambuco, Nordeste do Brasil. *Revista Brasil. Bot.* 29(3): 379–389. <https://doi.org/10.1590/S0100-84042006000300005>
- Miller, L. J. (2009) There's more than just cacti in eastern Brazil: Some bromeliads we encountered. *Cact. Succ. J. (US)* 81(3): 122–125, ills. <https://doi.org/10.2985/015.081.0305>
- Nascimento, V. T. do [& al. 2012], Vasconcelos, M. A. da S., Maciel, M. I. S. & Albuquerque, U. P. (2012) Famine foods of Brazil's seasonal dry forests: Ethnobotanical and nutritional aspects. *Econ. Bot.* 66(1): 22–34, ills. <https://doi.org/10.1007/s12231-012-9187-2>

- Queiroz, J. A. [et al. 2016], Quirino, Z. G. M., Lopes, A. V. & Machado, I. C. (2016) Vertebrate mixed pollination system in *Encholirium spectabile*: A bromeliad pollinated by bats, opossum and hummingbirds in a tropical dry forest. *J. Arid Environm.* 125: 21–30, ills. <https://doi.org/10.1016/j.jaridenv.2015.09.015>
- Sazima, I. [et al. 1989], Vogel, S. & Sazima, M. (1989) Bat pollination of *Encholirium glaziovii*, a terrestrial bromeliad. *Pl. Syst. Evol.* 168(3–4): 167–179, ills. <https://doi.org/10.1007/BF00936097>
- Schütz, N. [et al. 2016], Krapp, F., Wagner, N. & Weising, K. (2016) Phylogenetics of *Pitcairnioideae* s.s. (*Bromeliaceae*): Evidence from nuclear and plastid DNA sequence data. *Bot. J. Linn. Soc.* 181(3): 323–342, maps, ills. <https://doi.org/10.1111/boj.12403>
- Siqueiro Filho, J. A. & Leme, E. M. C. (2007) Fragments of the Atlantic forest of Northeast Brazil: Biodiversity, conservation and the Bromeliads. Rio de Janeiro (BR): Andrea Jakobsson Estúdio.
- Smith, L. B. & Downs, R. J. (1974) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 1: *Pitcairnioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4393694>
- Zappi, D. C. & Taylor, N. P. (2011) A new species of *Pilosocereus* subgenus *Gounellea*, *P. frewenii*, from SE Brazil. *Bradleya* 29: 131–136, ills. <https://doi.org/10.25223/brad.n29.2011.a16>



## × *Enchotia* BROMELIACEAE

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× ***Enchotia*** Lemiaux (J. Bromeliad Soc. 61(3): 140, 2011). — **Distr:** Cultivated only.

= *Encholirium* × *Hechtia*. The only known hybrid ('Ruby') is a cross between *H. rosea* (male)

× *E. horridum* (female), and was obtained by a Florida-based nursery. The leaves of the hybrid are described as spineless, which is surprising in view of the leaf morphology of both parental species.

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## Fascicularia BROMELIACEAE

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**Fascicularia** Mez (in Martius, Fl. Bras. 3(3): 627, 1891). **Type:** *Bromelia bicolor* Ruiz & Pavón. — **Bromelioideae** — **Lit:** Zizka & al. (1999: monograph). **Distr:** C-S Chile (Región V to Región X: 34–42° 24' S, and probably even further S to 45° 17' S); neophyte in W Europe. **Etym:** Lat., clustered, bundled; not explained, and presumably for the densely rosulate leaves.

**Incl.** *Hechtia* Rivière (1871) (*nom. illeg.*, Art. 53.1). **Type:** not typified.

Perennial terrestrial or less often epiphytic rosette plants, stem none or short and stout; **Ros** solitary or in small groups; **L** numerous, densely arranged, ascending-spreading to spreading, **L** sheath broadly ovate to triangular-ovate, 3–9 × 1–4.5 cm, membranous and white at the base, coriaceous in the upper ½ and with spinose-serrate margin, ± lepidote, glabrescent and veined towards the base, **L** lamina narrowly linear, stiff, attenuate into the pungent tip, (17–) 22–113 (–133) × (0.6–) 0.8–1.8 (–2.2) cm, upper face channelled or flat, lepidote to glabrate, lower face ± densely lepidote, margin coarsely spinose, **Sp** 1–2.5 mm, antrorse or near the base spreading to retrorse, innermost **L** at flowering time bright red and

surrounding the inflorescence, with gradually reduced lamina; **Inf** terminal, simple, condensed and head-like, ± sessile in the rosette centre, 3.5–9 × 3–9.5 cm; outer **Bra** ovate to oblong, as long or longer than the flowers, serrate, lamina short or absent; floral **Bra** to 7 cm, shorter than the flowers, ovate to oblong to spatulate, membranous, apically serrate, apical ⅓ densely lepidote on the outer face; **Fl** numerous, densely arranged, sessile or shortly pedicellate, with a conspicuous epigynous tube, (2.2–) 3.3–6.5 (–7.5) × 0.6–0.9 (–1.2) cm, hermaphrodite, actinomorphic; **Sep** free, carinate, 10–24 × 3.5–8 mm, coriaceous, retuse to praemorse, with a short inconspicuous mucro, outer face lepidote-tomentose; **Pet** free, obtuse, ± fleshy, 15–26 × 4–8 mm, deep to light blue (or occasionally almost white), with 2 small scales at the base; **St** included; **Fil** free, broadened at the base; **Ov** inferior, dorsally compressed, obconical; **Sty** elongate, included; **Sti** not contorted; **Fr** dry berries, to 7.4 cm (incl. perianth remains); **Se** ovoid to fusiform, 2.2–3 × 1–1.2 mm, dark brownish, rugose, without appendages.

Similar to *Ochagavia* (see there for differences), and difficult to distinguish when not in flower. Traditionally regarded as having five species (Smith & Downs 1979: 1711–1715), the recent monograph by Zizka & al. (1999) concluded that only a single variable species (divided in two subspecies) can be recognized. *Fascicularia*

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is amongst the most distinctly water-storing *Bromelioideae* (Horres & Zizka 1995). The leaves have a strongly developed water-storage tissue that makes up as much as 60% of leaf cross-sectional area.

*Fascicularia* groups with *Ochagavia* and *Greigia* in recent molecular phylogenies, and this group is amongst the earliest diverging genera of *Bromelioideae*, together with *Deinacanthon* (Schulte & al. 2005, Schulte & Zizka 2008, Schulte & al. 2009, Givnish & al. 2011). Silvestro & al. (2014) and Evans & al. (2015) found *Fascicularia* to be embedded in *Ochagavia*.

The genus is not widely cultivated, but is fairly winter-hardy in the mild climate of S England. Roguenant & al. (2016: with ill.) report it as subsynchronous neophyte from S Ireland, S England and W France (Bretagne and several islands).

**F. bicolor** (Ruiz & Pavón) Mez (in A. & C. de Candolle, Monogr. Phan. 9: 9, 1896). **Type** [neo]: Chile, Región VII Maule (*Ochsenius* s.n. [BR]). — **Distr:** As for the genus.

≡ *Bromelia bicolor* Ruiz & Pavón (1802) ≡ *Billbergia bicolor* (Ruiz & Pavón) Schultes fil. (1830) ≡ *Rhodostachys bicolor* (Ruiz & Pavón) Bentham & Hooker fil. (1883).

Description as for the genus.

**F. bicolor** ssp. **bicolor** — **Distr:** C to S Chile (Región V to Región X [N Chiloé]); mostly on rocks near the coast; neophyte in W Europe

(Ireland, England, W France). **I:** Rauh (1990: 120: fig. 92, as *F. pitcairniifolia*); Nelson & Zizka (1997: 233); Roguenant & al. (2016: 568). — Fig. 1.

**Incl.** *Bromelia joinvillei* E. Morren (1876) ≡ *Rhodostachys joinvillei* (E. Morren) Bentham (1883); **incl.** *Rhodostachys micrantha* Philippi (1895) ≡ *Fascicularia micrantha* (Philippi) Mez (1934); **incl.** *Fascicularia parviflora* Mez (1896).

**L** succulent esp. towards the base, lamina (1–) 1.2–1.8 (–2.2) cm wide, upper face flat or slightly convex, margins not recurved; floral **Bra** (3.2–) 4–5.8 (–7) cm; **Fl** 3.7–6.5 (–7.5) cm.

**F. bicolor** ssp. **canaliculata** E. C. Nelson & Zizka (New Plantsman 4(4): 238, 1997). **Type:** Chile, Región X Valdivia (*Sparre* 3546 [S]). — **Distr:** S Chile (Región VII to Región X [Chiloé]); usually epiphytic in temperate evergreen forests. **I:** Roguenant & al. (2016: 569).

**Incl.** *Bromelia albobracteata* Steudel (1857) (*nom. inval.*, Art. 32.1c) ≡ *Rhodostachys albobracteata* (Steudel) Baker (1889) (*nom. inval.*, Art. 32.1c); **incl.** *Hechtia joinvillei* Rivière (1871); **incl.** *Pourretia joinvillei* hort. ex Chantin ex Rivière (1871); **incl.** *Rhodostachys pitcairniifolia* var. *kirchhoffiana* Wittmack (1890) ≡ *Fascicularia kirchhoffiana* (Wittmack) Mez (1919).

**L** not markedly succulent towards the base, lamina (0.6–) 0.8–1.1 (–1.4) cm wide, upper face channelled, margins distinctly recurved; floral **Bra** (2.2–) 3–3.8 cm; **Fl** (2.2–) 3.3–4.4 cm.

**Fig. 1** *Fascicularia bicolor* ssp. *bicolor*. (Copyright: E. J. Gouda)



## References

- Evans, T. M. [ & al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>.
- Givnish, T. J. [ & al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ill., maps. <https://doi.org/10.3732/ajb.1000059>.
- Horres, R. & Zizka, G. (1995) Untersuchungen zur Blattsukkulenz bei *Bromeliaceae*. *Beitr. Biol. Pfl.* 69(1): 43–76, ill.
- Nelson, E. C. & Zizka, G. (1997) *Fascicularia* (*Bromeliaceae*): Which species are cultivated and naturalized in northwestern Europe? *New Plantsman* 4(4): 232–239, ill.
- Rauh, W. (1990) *Bromelien*. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Roguenant, A. [ & al. 2016], Lecoufle, M. & Raynal-Roques, A. (2016) Les Broméliacées. Approche panoramique d'une grand famille "américaine". Paris (FR): Belin.
- Schulte, K. & Zizka, G. (2008) Multi locus plastid phylogeny of *Bromelioideae* (*Bromeliaceae*) and the taxonomic utility of petal appendages and pollen characters. *Candollea* 63(2): 209–225. [http://www.ville-ge.ch/cjb/publications\\_candollea\\_632.php](http://www.ville-ge.ch/cjb/publications_candollea_632.php)
- Schulte, K. [ & al. 2005], Horres, R. & Zizka, G. (2005) Molecular phylogeny of *Bromelioideae* and its implications on biogeography and the evolution of CAM in the family. *Senckenberg. Biol.* 85(1): 113–125, maps.
- Schulte, K. [ & al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromeliaceae*) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylogen. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>.
- Silvestro, D. [ & al. 2014], Zizka, G. & Schulte, K. (2014) Disentangling the effects of key innovations on the diversification of *Bromelioideae* (*Bromeliaceae*). *Evolution* 68(1): 163–175. <https://doi.org/10.1111/evo.12236>.
- Smith, L. B. & Downs, R. J. (1979) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>
- Zizka, G. [ & al. 1999], Horres, R., Nelson, E. C. & Weising, K. (1999) Revision of the genus *Fascicularia* Mez (*Bromeliaceae*). *Bot. J. Linn. Soc.* 129(4): 315–332, map, key. <https://doi.org/10.1111/j.1095-8339.1999.tb00507.x>.







## Fosterella BROMELIACEAE

U. Eggli

**Fosterella** L. B. Smith (Phytologia 7: 171, t. 1, 1960). **Type:** *Pitcairnia micrantha* Lindley. — **Pitcairnioideae** — **Lit:** Smith & Downs (1974: 199–209, Fl. Neotropica); Rex & al. (2007: molecular phylogeny); Ibsch & al. (2008: key to species); Rex & al. (2009: molecular phylogeny); Peters (2009: monograph); Wagner & al. (2013: evolution); Lima Silva & al. (2016: cytology). **Distr:** N, C & S America (S Mexico, El Salvador, Guatemala, Brazil, Peruvian Andes to Bolivia, Paraguay and N Argentina), 100–2750 m. **Etym:** For Mulford Bateman Foster (1888–1978), US-American horticulturist and plant collector, and co-founder and first president of the US-American Bromeliad Society; and Lat. diminutive suffix, for the small flowers.

Perennial terrestrial or saxicolous rosette plants, mesophytic to xerophytic, acaulescent or shortly caulescent, offsetting; **L** 5–30, flat or ± ascending, sheath broadly ovate to triangular, entire or slightly serrate, glabrous or upper face slightly lepidote, somewhat succulent, lamina linear, narrowly triangular or narrowly to broadly lanceolate or oblanceolate, rarely basally much narrowed and petiolate, 10–100 × 1–8 cm, thin or basal part somewhat succulent, entire or

serrate near the base, rarely somewhat undulate, upper face glabrous or sparsely lepidote towards the base, lower face ± densely covered with pel-tate or stellate hairs; **Inf** pedunculate, indeterminate, racemose to panicle with up to 30 branches with up to 3.-order branching, axis green or reddish, glabrous, villous or cobwebby, rarely glaucous; peduncular **Bra** ± appressed, narrowly triangular, the lower often leaf-like, shorter than the internodes and sometimes imbricate, entire or slightly serrate, green, reddish or straw-coloured; floral **Bra** broadly ovate to triangular, acute, shorter or longer than the pedicels, lower face glabrous or variously hairy to lepidote; **Fl** spreading or secund, erect or pendent, inconspicuous, mostly whitish, hermaphrodite, actinomorphic, sessile or with **Ped** to 15 mm; **Sep** 3, free, convolute, much shorter than the petals, to 9 mm, glabrous or hairy, rarely glaucous; **Pet** 3, free, 3–24 mm, straight, recurved during anthesis and straight afterwards, or revolute during anthesis and afterwards, without appendage; **St** in 2 whorls, exserted, the outer free, the inner adnate to the petals; **Anth** basifixed, linear, coiled at anthesis; **Ov** superior, deeply grooved; **Sty** short to long; **Sti** complex simple-erect or conduplicate-spiral; **Fr** basically septicial capsules; **Se** numerous, filiform or fusiform, 2–4 mm, brown with white membranous appendage, bicaudate. — **Cytology:** 2n = 50, polyploids (to 2n = 150) comparatively common (Peters 2009: 20, summarizing earlier studies by several authors).

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A genus of 31 species (Peters 2009), traditionally placed in *Pitcairnioideae*, where it is placed as sister to a clade that includes *Encholirium*, *Dyckia* and *Deuterocohnia* in the molecular phylogenies of Givnish & al. (2007), Rex & al. (2009) and Schütz & al. (2016). Rex & al. (2009) found a basal dichotomy in 2 major clades, and a total of 6 major lineages, which are only informally named (clade 1: *albicans* group, *rusbyi* group, *micrantha* group, *weberbaueri* group; clade 2: *penduliflora* group, *weddelliana* group (Peters 2009).

The genus originated in the late miocene ( $\pm 9.6$  mybp) during the last rapid Andean uplift, and the ancestral habitat has been reconstructed as seasonally deciduous tropical forest and azonal lowland sites (Wagner & al. 2013). The same authors found that the disjunct occurrence of 2 species in S Mexico, C America and Amazonia is due to 2 recent long-distance dispersal events. Speciation is proposed to have been mostly allopatric. The diversification rate is low, and Andean uplift did not enhance speciation rate. Many of the species are narrow rare endemics esp. in the arid to semihumid habitats of the NE Andean slopes of Bolivia. Wagner & al. (2015) found that at least some species are partially self-fertile, and that hybrids are easily formed amongst the majority of the 4 taxa studied, indicating that reproduction barriers are weak or absent. A possible important role for hybridization in the evolution of the genus was also suggested by Lima Silva & al. (2016) on the base of chromosomal features. The same authors found that polyploidization events could be comparatively recent, at least in some taxa.

Succulence is present in the vast majority of the species, but usually confined to the midvein-areas of the basal-most parts of the lamina. In some taxa from arid or semi-arid places, succulence is more pronounced, and these are covered below. The account is based entirely on the data presented in the monograph by Peters (2009), where illustrations of all taxa can also be found.

**F. albicans** (Grisebach) L. B. Smith (Phytologia 7: 171, 1960). **Type:** Argentina, Salta (*Lorentz & Hieronymus* 502 [GOET, B, CORD]). — **Lit:** Peters (2009: 27–34, with ills.). **Distr:** S & W Bolivia (La Paz, Cochabamba, Santa Cruz, Chuquisaca,

Tarija), N Argentina (Jujuy, Salta, Tucumán); clearings in Yungas vegetation, 550–2650 m. — Fig. 1.

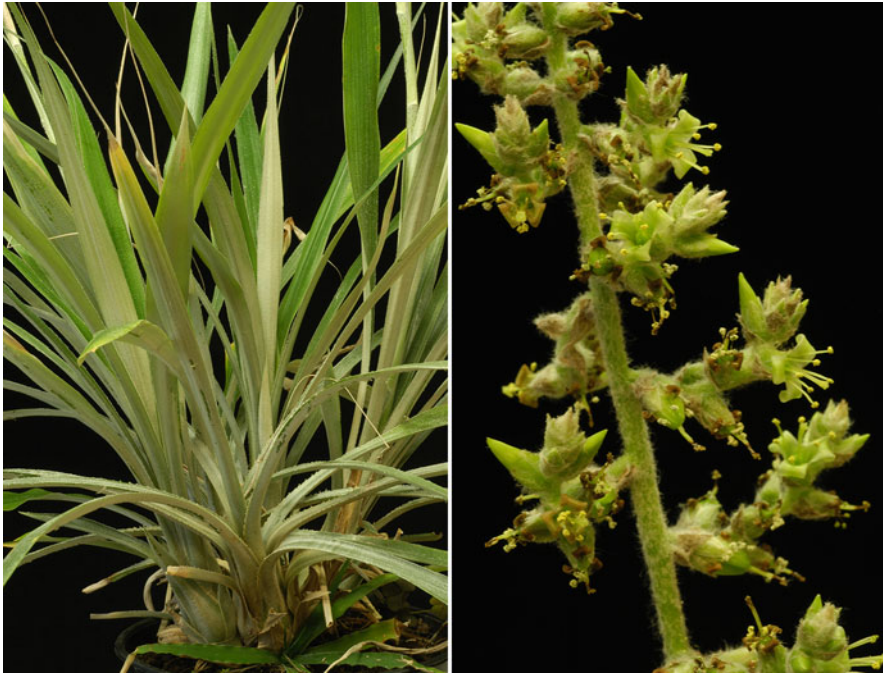
≡ *Cottendorfia albicans* Grisebach (1879)  
 ≡ *Lindmania albicans* (Grisebach) Mez (1896);  
**incl.** *Fosterella fuentessii* Ibisch & al. (2002).

Subcaulescent, colony-forming, flowering to 100 (–180) cm tall; **L** 20–30, irregularly erect to spreading, sheath 5–7 cm wide, entire, glabrous, lamina narrowly oblanceolate, acuminate, basally narrowing, 40–100 × 2–3 (–4) cm, succulent, serrate towards the base, upper face sparsely lepidote, lower face completely covered by interwoven peltate hairs; **Inf** 70–180 cm, erect, paniculate with 1.- and 2.-order branches, peduncle 50–120 cm, densely cobwebby; peduncular **Bra** 4–12 cm, longer than the internodes, entire; primary **Bra** 2–3 cm, longer than the sterile branch base; **Br** 8–20, inclined, arcuate, to 18 cm, to 50-flowered, with 2–5 cm long secondary branches; floral **Bra** 4–5 mm; **Fl** spreading, suberect, subsessile; **Sep** 3–4 mm, green, sparsely cobwebby; **Pet** 6–8 mm, white, recoiled like a watchspring.

The species is both morphologically and ecologically variable and similar to the more mesophytic *F. caulescens* (not treated here).

**F. cotacajensis** M. Kessler & al. (Revista Soc. Boliv. Bot. 2(2): 111, 1999). **Type:** Bolivia, Cochabamba (*Kessler* 9620 [LPB, SEL]). — **Lit:** Peters (2009: 56–60, with ills.). **Distr:** C-W Bolivia (La Paz, Cochabamba); inter-Andean dry semi-deciduous forests, sunny dry rocky slopes, 1150–2200 m.

Caulescent, flowering to 100 cm tall; stems to 30 cm, sparsely offsetting; **L** 15–25, densely spreading-arching at the top parts of the stems, sheath to 3 cm wide, entire, glabrous, lamina lanceolate, 15–45 × to 2 cm, succulent, serrate towards the base, upper face sparsely lepidote, lower face thickly covered with interwoven peltate trichomes; **Inf** to 100 cm, erect, paniculate with 1.- and 2.-order branches, peduncle 20–50 cm, glabrous, glaucous; peduncular **Bra** 3–5 cm, longer than the internodes, slightly serrate; primary **Bra** 1–3 cm, as long as or longer than the sterile branch base; **Br** 10–15, ascending, straight, to 30 cm, to 25-flowered, with 2–3 cm long secondary branches; floral **Bra** 4–7 mm; **Fl** secund, pendulous; **Ped** 3–4 mm; **Sep** 5 mm, green, glabrous; **Pet** 8 mm, white, recoiled like a watchspring.



**Fig. 1** *Fosterella albicans*. (Copyright: E. J. Gouda)

Closely related to the morphologically similar *F. weddelliana* from lower and less arid habitats, but differing in narrower leaves and longer floral bracts and sepals.

**F. penduliflora** (C. H. Wright) L. B. Smith (Phytologia 7: 172, 1960). **Type:** Peru (*Forget* s.n. [K]). — **Lit:** Peters (2009, 105–113, with ills.). **Distr:** Peru?, Bolivia (La Paz, Cochabamba, Santa Cruz, Chuquisaca, Tarija), N Argentina (Jujuy, Salta), Yungas vegetation and deciduous to evergreen inter-Andean dry forests and montane Chaco vegetation, 200–2650 m. **I:** Rauh (1990, 272, fig. 341). — Fig. 2.

≡ *Catopsis penduliflora* C. H. Wright (1910) ≡ *Lindmania penduliflora* (C. H. Wright) Stapf (1924); **incl.** *Fosterella chiquitana* Ibisch & al. (1999); **incl.** *Fosterella latifolia* Ibisch & al. (1999).

Acaulescent, flowering to 120 cm tall; **Ros** open, flat, sparsely offsetting; **L** 8–15, sheath 2–5 cm wide, entire, glabrous, lamina lanceolate, acuminate, narrowed towards the base, 20–40 × 2.5–8 cm, succulent, entire, upper face glabrous, lower face often flushed reddish, sparsely lepidote; **Inf** to 120 cm,

erect, paniculate, with 1- and 2-order branches, peduncle 25–60 (–85) cm, glabrous, often glaucous; peduncular **Bra** 1–3 cm, as long as the internodes, often reddish, sparsely lepidote; primary **Bra** 0.5–1.5 cm, shorter than the sterile branch base; **Br** 10–15, inclined, arcuate, 8–22 cm, to 35-flowered, with 3–5 cm long secondary branches; floral **Bra** 2–4 (–10) mm, entire, often reddish; **Fl** secund, pendulous; **Ped** 2–6 mm; **Sep** 2–3 mm, green or often reddish, glabrous; **Pet** 7–10 mm, white, recurved.

The most common species, both in the field and in cultivation. The type was reported from Peru, but apart from a second collection from Peru, also without locality, the taxon is only known from Bolivia and N Argentina, and its occurrence in Peru is doubtful.

**F. rexiae** Ibisch & al. (Selbyana 23(2): 213, 2002). **Type:** Bolivia, La Paz (*Vásquez & Gerlach* 3673 [LPB]). — **Lit:** Peters (2009: 119–122, with ills.). **Distr:** W Bolivia (La Paz: near Caranavi); evergreen Yungas vegetation, 800–1300 m; known from the type locality only.

Caulescent, flowering to 90 cm tall; **Ros** open, semiglobose, sparsely offsetting; **L** 10–15, sheath



**Fig. 2** *Fosterella penduliflora*. (Copyright: E. J. Gouda)

2.5 cm wide, entire, glabrous, lamina linear to narrowly lanceolate, acuminate, narrowed towards the base, 20–30 × 1.7 cm, succulent, serrate towards the base, upper face towards the base and lower face entirely with dense appressed peltate trichomes; **Inf** to 90 cm, erect, paniculate, with 1.- and 2.-order branches, peduncle to 55 cm, slightly cobwebby becoming glabrescent; peduncular **Bra** 5 cm, as long or longer than the internodes, entire, lower face slightly cobwebby; primary **Bra** 1.5 cm, longer than the sterile branch base, slightly cobwebby; **Br** 15–18, inclined, arcuate, 8–10 cm, to 20-flowered, with 3–5 cm long secondary branches; floral **Bra** 2 mm, entire, slightly cobwebby; **Fl** spreading, erect, sessile; **Sep** 3 mm, green to reddish, sparsely long-hairy, glabrescent; **Pet** 5 mm, white, recoiled like a watchspring.

Closely related to the similar *F. albicans*, but with flatter rosette, less tomentose leaves, and less densely flowered inflorescences.

**F. rusbyi** (Mez) L. B. Smith (Phytologia 7: 172, 1960). **Type:** Bolivia, La Paz (*Bang* 2571 [B, BM, F, G, GH, K, MO, NY, US]). — **Lit:** Peters (2009: 132–138, with ills.). **Distr:** W

Bolivia (La Paz, Cochabamba); evergreen to deciduous Yungas and inter-Andean dry forests, terrestrial or saxicolous, 700–1900 m. **I:** Rauh (1990: 272, fig. 342). – Fig. 3.

≡ *Lindmania rusbyi* Mez (1901); **incl.** *Fosterella elata* H. Luther (1981).

Acaulescent, flowering to 200 cm tall; **Ros** open, flat, sparsely offsetting; **L** 10–15, sheath 5–6 cm wide, entire, glabrous, lamina linear to narrowly lanceolate, acuminate, narrowed towards the base, 20–45 × 1–6 cm, succulent, serrate towards the base, undulate, upper face lepidote towards the base, lower face densely white-hairy with peltate trichomes; **Inf** to 200 cm, erect, paniculate, with 1.- and 2.-order branches, peduncle 30–120 cm, glabrous; peduncular **Bra** 4–10 cm, longer than the internodes, entire, lower face cobwebby; primary **Bra** 0.6–1 (–2.5) cm, shorter than or as long as the sterile branch base, lepidote, glabrescent; **Br** 10–15, inclined, arcuate, 8–15 cm, to 15-flowered, with 5–8 cm long secondary branches; floral **Bra** 2–3 mm, entire, glabrous; **Fl** secund, pendulous; **Ped** 1.5–2 mm; **Sep** 2–3 mm, green, glabrous; **Pet** 7 mm, greenish, cream or rose-coloured, recoiled like a watchspring.

Similar and closely related to *F. vasquezii*, but with broader, serrate and undulate leaves, larger inflorescences and longer petals.

**F. vasquezii** E. Gross & Ibsch (J. Bromeliad Soc. 47(5): 212, ills. (pp. 214–215, 1997). **Type:** Bolivia, Santa Cruz (*Ibsch & al.* 93.0652 [HEID, LPB]). — **Lit:** Peters (2009: 148–151, with ills.). **Distr:** E Bolivia (Santa Cruz); transition between humid and Chiquitano dry forests, 200–850 m.

Acaulescent, flowering to 50 cm tall; **Ros** open, flat, sparsely offsetting; **L** 10–15, sheath 5 cm wide, obscurely serrate, glabrous, lamina lanceolate, 25–45 × 1.5–3.5 cm, succulent, obscurely serrate towards the base, undulate, upper face glabrous, lower face with a dense thick layer of peltate hairs; **Inf** to 50 cm, erect, paniculate, with 1.- and 2.-order branches, peduncle 20–30 cm, glabrous; peduncular **Bra** 3 cm, longer than the internodes, entire, lower face with interwoven hairs; primary **Bra** 1 cm, shorter than the sterile branch bases, glabrous; **Br** 10–20, ascending, straight, 10–15 cm, to 10- to 25-flowered, with 3–5 cm long secondary branches; floral **Bra** 2–3 mm, entire, glabrous; **Fl** secund,



**Fig. 3** *Fosterella rusbyi*.  
(Copyright: E. J. Gouda)



pendulous; **Ped** 2–3 mm; **Sep** 2 mm, green, glabrous; **Pet** 5 mm, white, recoiled like a watchspring.

Closely related to *F. rusbyi* (see there for differences).

**F. weddelliana** (Brongniart ex Baker) L. B. Smith (Phytologia 7: 172, 1960). **Type:** Bolivia, La Paz (*Weddell* 4233 [P, B]). — **Lit:** Peters (2009: 162–167, with ills.). **Distr:** W-C Bolivia (La Paz), evergreen to deciduous Yungas and inter-Andean dry forests, terrestrial or saxicolous, 750–2750 m.

≡ *Cottendorfia weddelliana* Brongniart ex Baker (1889) ≡ *Lindmania weddelliana* (Brongniart ex Baker) Mez (1896); **incl.** *Fosterella nowickii* Ibisich & al. (2002).

Caulicent, flowering to 150 cm tall; **Ros** open, very sparsely offsetting; **L** 8–15, irregularly spreading to arching, sheath 5–7 cm wide, serrate, glabrous, lamina narrowly lanceolate, acuminate to acute, 15–50 × 2–3.5 cm, succulent, serrate towards the base, upper face lepidote towards the base, lower face with a thick layer of interwoven peltate hairs; **Inf** to 150 cm, erect, paniculate, with 1.- and 2.-order branches, peduncle 30–80 cm, green to reddish, glabrous, glaucous, peduncular **Bra** 5–8 cm, longer than the internodes, serrate, with interwoven hairs, primary **Bra** 2.5–5 cm, as long as or longer than the sterile branch base, entire to obscurely serrate, hairy, glabrescent; **Br** 8–25, ascending to

inclined, 10–15 cm, to 30-flowered, with up to 5 cm long secondary branches; floral **Bra** 2–3 mm, entire, glabrous; **Fl** secund, pendulous; **Ped** 2–4 mm; **Sep** 2–3 mm, green to reddish, glabrous; **Pet** 4–5 mm, white to greenish or reddish, recoiled like a watchspring; **Fr** 4–5 × 2–3 mm.

Originally incorrectly described as acaulescent. Closely related to *F. cotacajensis* (see there for differences).

**F. windischii** L. B. Smith & Read (Bradea 6(15): 137, 1992). **Type:** Brazil, Mato Grosso (*Windisch* 2044 [US, HB]). — **Lit:** Peters (2009: 168–171, with ills.). **Distr:** E Bolivia (Santa Cruz), adjacent Brazil (Mato Grosso); dry rock slopes of Caparús table mountain in evergreen humid lowland forest, 300–550 m.

Acaulescent, flowering to 60 cm tall; **Ros** open, sparsely offsetting; **L** 6–12, arching-spreading, sheath to 2.5 cm wide, entire, glabrous, lamina narrowly lanceolate, acuminate, narrowed towards the base, 30–50 × 1.5–2.5 cm, succulent towards the base, entire or obscurely serrate towards the base, upper face glabrous, lower face with a thick layer of interwoven hairs; **Inf** to 60 cm, erect, compound-racemose, peduncle to 30 cm, glabrous; peduncular **Bra** 2 cm, longer than the internodes, entire, lower face with interwoven hairs; primary **Bra** 0.5 cm, shorter than the sterile branch base,



lepidote; **Br** 6–15, ascending, straight, 6–10 cm, to 20-flowered; floral **Bra** 1–2 mm, entire, glabrous; **Fl** secund, pendulous; **Ped** 2–3 mm; **Sep** 2–3 mm, green, glabrous; **Pet** 4–5 mm, white, recoiled like a watchspring.

According to molecular data part of a group that includes *F. vasquezii* and *F. yuvinkae*.

**F. yuvinkae** Ibsch & al. (Selbyana 23(2): 216, 2002). **Type:** Bolivia, Santa Cruz (*Reichle* P-SR1 [LPB]). — **Lit:** Peters (2009: 172–176, with ills.). **Distr:** Bolivia (Santa Cruz); Chiquitano dry deciduous forest, steep rock slopes or sandy ground, 400–1200 m.

Acaulescent, flowering to 100 cm tall, sparsely offsetting; **Ros** open, flat; **L** 15–20, sheath 2–3 cm wide, entire, villous, lamina linear to narrowly oblanceolate, acuminate, narrowing towards the base, 20–35 × 1.5–3 cm, succulent towards the base, entire, upper face glabrous, lower face densely tomentose with stellate hairs; **Inf** to 60 cm, erect, paniculate, with 1.- and 2.-order branches, peduncle 30–50 cm, glabrous, glaucous; peduncular **Bra** 2–4 cm, longer than the internodes, entire, lower face long-hairy; primary **Bra** 0.5–1 cm, shorter than the sterile branch base, long-hairy, glabrescent; **Br** to 15, inclined, arcuate, 8–20 cm, to 20-flowered, with 5–7 cm long secondary branches; floral **Bra** 2 mm, entire, glabrous; **Fl** secund, pendulous; **Ped** 2–4 mm; **Sep** 3–4 mm, green, glabrous; **Pet** 7–9 mm, only 1.5 mm wide, white, recurved.

Similar to *F. penduliflora* but with the leaves densely tomentose on the lower face. The species is unique in the genus because of the very narrow petals. Molecular data shows a close relationship to *F. vasquezii* and *F. windischii*, which all occur on the Brazilian Shield.

## References

Givnish, T. J. [ & al. 2007], Millan, K. C., Berry, P. E. & Systsma, K. J. (2007) Phylogeny, adaptive radiation, and

- historical biogeography of *Bromeliaceae* inferred from ndhF sequence data. In: Columbus, J. T. & al. (eds.): Monocots. Comparative biology and evolution: Poales. *Aliso* 23: 3–26. <https://doi.org/10.5642/aliso.20072301.04>
- Ibsch, P. L. [ & al. 2008], Read, R. & Peters, J. (2008) Key to the species of the genus *Fosterella* (*Bromeliaceae*). *Selbyana* 29(2): 195–198. <http://www.jstor.org/stable/41760333>
- Lima Silva, H. M. de [ & al. 2016], Vasconcelos, E. V., Benko-Iseppon, A. M., Wagner, N., Weising, K. & Brasileiro-Vidal, A. C. (2016) Chromosomal features of *Fosterella* species (*Bromeliaceae*, *Pitcairnioideae*). *Bot. J. Linn. Soc.* 181(3): 532–541, ills. <https://doi.org/10.1111/boj.12390>
- Peters, J. (2009) Revision of the genus *Fosterella* (*Bromeliaceae*). Kassel (DE): Universität Kassel, Fachbereich Naturwissenschaften, unpublished Ph.D. thesis. <http://nbn-resolving.de/urn:nbn:de:hebis:34-2009081429441>
- Rauh, W. (1990) Bromelien. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Rex, M. [ & al. 2007], Patzold, K., Schulte, K., Zizka, G., Vásquez, R., Ibsch, P. L. & Weising, K. (2007) AFLP analysis of genetic relationships in the genus *Fosterella* L. B. Smith (*Pitcairnioideae*, *Bromeliaceae*). *Genome* 50(1): 90–105. <https://doi.org/10.1139/g06-141>
- Rex, M. [ & al. 2009], Schulte, K., Zizka, G., Peters, J., Vásquez, R., Ibsch, P. L. & Weising, K. (2009) Phylogenetic analysis of *Fosterella* L. B. Sm. (*Pitcairnioideae*, *Bromeliaceae*) based on four chloroplast DNA regions. *Molec. Phylog. Evol.* 51(3): 472–485. <https://doi.org/10.1016/j.ympev.2009.01.001>
- Schütz, N. [ & al. 2016], Krapp, F., Wagner, N. & Weising, K. (2016) Phylogenetics of *Pitcairnioideae* s.s. (*Bromeliaceae*): Evidence from nuclear and plastid DNA sequence data. *Bot. J. Linn. Soc.* 181(3): 323–342, maps, ills. <https://doi.org/10.1111/boj.12403>
- Smith, L. B. & Downs, R. J. (1974) Flora Neotropica. Monograph No. 14 [*Bromeliaceae*]. Part 1: *Pitcairnioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4393694>
- Wagner, N. D. [ & al. 2015], Wöhrmann, T., Öder, V., Burmeister, A. & Weising, K. (2015) Reproduction biology and chloroplast inheritance in *Bromeliaceae*: A case study in *Fosterella* (*Pitcairnioideae*). *Pl. Syst. Evol.* 301(9): 2231–2246, map, ills. <https://doi.org/10.1007/s00606-015-1226-x>
- Wagner, N. D. [ & al. 2013], Silvestro, D., Brie, D., Ibsch, P. L., Zizka, G., Weising, K. & Schulte, K. (2013) Spatio-temporal evolution of *Fosterella* (*Bromeliaceae*) in the Central Andean biodiversity hotspot. *J. Biogeogr.* 40(5): 869–880. <https://doi.org/10.1111/jbi.12052>



## × *Hechcohnia* BROMELIACEAE

N. Schütz and F. Krapp

× ***Hechcohnia*** G. H. Anderson *ex* J. Grant (Selbyana 19: 117, 1998). — **Distr:** Cultivated only.

= *Hechtia* × *Deuterocohnia*. The only known cross (*D. schreiteri* (female) × *H. glomerata*) remained unnamed (Anderson 1986: 103). The plants and the leaf spines are more delicate than in either parent, and

the plant colour varies from green to light rose.

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### References

Anderson, G. H. (1986) Hybrids by design and by chance. *J. Bromeliad Soc.* 36(3): 99–103, 109, ills.

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## Hechtia BROMELIACEAE

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**Hechtia** Klotzsch (Allg. Gartenzeitung 3: 401, 1835). **Type:** *Hechtia stenopetala* Klotzsch. — **Hechtioideae** — **Lit:** Mez (1896: synopsis); Mez (1935: 351–360, synopsis); Smith & Downs (1974: 577–604, Fl. Neotropica); McVaugh (1989: Fl. Novo-Galiciana); Utley & Burt-Utley (1994: Fl. Mesoamericana); Espejo-Serna & al. (2005: Fl. Veracruz); Espejo-Serna & al. (2010a: Fl. Bajío); Ramírez Morillo & al. (2014a: growth patterns). **Distr:** S USA (Texas), Mexico (widespread) and N C America (Guatemala, Honduras, El Salvador, Nicaragua, Belize). **Etym:** For Julius Gottfried Conrad Hecht (1771–1837), German botanist and counselor to the King of Prussia.

**Incl.** *Bakeria* André (1889) (*nom. illeg.*, Art. 53.1). **Type:** *Bakeria tillandsioides* André.

**Incl.** *Bakerantha* L. B. Smith (1934). **Type:** *Bakeria tillandsioides* André.

**Incl.** *Niveophyllum* Matuda (1965). **Type:** *Niveophyllum caeruleum* Matuda.

Perennial xerophytic rosette plants, dioecious, polycarpic or monocarpic, caespitose or rarely solitary, terrestrial and frequently saxicolous;

**Ros** stemless or sometimes shortly to distinctly caulescent (*H. mooreana*, *H. myriantha*), rarely rhizomatous (*H. caulescens*) or more rarely stoloniferous (*H. pretiosa*); **Ros** small to medium or rarely very large (*H. myriantha*), dense; **L** long-lived, succulent and xeromorphic, narrowly triangular to linear, lepidote throughout or only abaxially, tip pungent, rarely soft (*H. lundelliorum*, *H. purpusii*, *H. tillandsioides*); **L** margins strongly spiny or more rarely minutely serrate (*H. lundelliorum*, *H. purpusii*, *H. tillandsioides*); **Sp** uncinatate, retrorse, antrorse and/or divaricate; **Inf** erect or ascending to rarely pendent, paniculate, rarely racemose, 0.5–4 m (= overall size, i.e. peduncle and floriferous part), 1–3× branched, terminal or seemingly lateral by reduction of the floriferous rosette; lower peduncular **Bra** similar to innermost rosette leaves, diminishing in size upwards; peduncle long to short, cylindrical to complanate; **Inf** branches long racemose to capitate; **Fl** actinomorphic, unisexual (and plants dioecious), sessile to long pedicellate; **Ped** frequently articulated with the rhachis; **Per** campanulate, very rarely tubular (*H. pretiosa*), usually white, greenish or yellowish, rarely rose, lilac, red or reddish; **Sep** 3, free, sepaloïd; **Pet** 3, free or rarely basally connate (*H. pretiosa*), petaloïd, naked; **male Fl** with **St** longer or shorter than the petals, equal to subequal, **Fil** white, rarely greenish, filiform or linear to triangular and flattened, **Anth** dorsifixed, oblong, **Ov** vestigial; **female Fl** with **Ov** superior to  $\frac{3}{4}$  inferior, rarely inferior (*H. epigyna*, *H. malvernii*), ovoid to long ovoid or ellipsoid, glabrous to lepidote, 3-locular, ovules numerous, **Sty** absent or rarely present

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(*H. guatemalensis*), **Sti** 3-branched erect to recurved branches, **Fil** of the staminodes flattened, triangular, antheroids present or sometimes absent; **Fr** dehiscent septicidal and loculicidal capsules, ellipsoid to ovoid, sometimes triquetrous, sepals, petals and stigma branches persistent at the apex; **Se** numerous, fusiform, circuncumulate and bicaudate.

A genus with 69 species, 63 (92.5%) of them endemic to Mexico (Espejo-Serna 2012), and entirely endemic to the region termed “Mega-mexico 3” by Rzedowski (1991). The genus is still not well known, and not less than 17 species (28% of the genus) have been described in the past 7 years, and several more remain to be described. No subgeneric classification has been established, and no phylogenetic analysis is available at this time, even though some subgroups like the *H. podantha*, *H. glomerata*, *H. tillandsioides*, and *H. zamudioi* complexes, can be circumscribed.

Dioccy, as exhibited by *Hechtia*, is unique in the family with the exception of andromonoecy in *Cryptanthus* and a few isolated taxa of *Aechmea*, *Androlepis* and *Catopsis*, and gynomonoccy in a few isolated taxa of *Dyckia*. There is no sexual dimorphism in the vegetative characters, but the male and female flowers can appear quite different (e.g. *H. confusa*).

Flowering is always terminal, but the flowering rosette is pushed into a seemingly lateral position in some species, and appears completely lateral when the flowering rosette is prematurely overtopped by the offset it produces before starting to flower. Truly lateral flowering, as discussed by Ramírez Morillo & al. (2014a), does not occur in the genus.

All taxa exhibit  $\pm$  succulent leaves, varying from rigid (*H. podantha*, *H. roseana*) to soft and flexible (*H. tillandsioides*), and the genus is thus covered in its entirety below. *Hechtia* species inhabit xeric vegetation from arid shrublands to tropical deciduous and semideciduous forests, with few taxa from humid places such as oak forests or canyons and river sides.

The following names are of unresolved application but are referred to this genus: *Bromelia antiacantha* Bertoloni (1824)  $\equiv$  *Agallostachys antiacantha* (Bertoloni) Beer (1856); *Hechtia*

*cordylinoides* Baker (1881); *Hechtia longifolia* hort. ex Baker (1889); *Hechtia striata* Lemaire (1846); *Hechtia suaveolens* E. Morren ex Mez (1896).

**H. aquamarina** I. Ramírez & Jiménez (Phytotaxa 2012(33): 1, 2012). **Type:** Mexico, Puebla (Ramírez & Carnevali 1689 [CICY, B, G, K, MEXU, MO, SEL, UAMIZ, XAL, WU]). — **Lit:** Espejo-Serna & al. (2007: as *Hechtia* sp. 3); Ramírez Morillo & Jimenez-Nah (2012: as *H. pueblensis*). **Distr:** C Mexico (SE Puebla, NW Oaxaca); xerophytic shrublands, >900 m.

$\equiv$  *Hechtia pueblensis* I. Ramírez & Jiménez (2012) (*nom. illeg.*, Art. 53.1).

Caespitose, flowering  $\pm$ 80 cm tall; **Ros** 35–60 cm  $\varnothing$ ; **L** 12–16, sheaths pale brown, transversely oblong, 3–3.5  $\times$  3.5–5 cm, entire, glabrous, **L** lamina glaucous, 22–30  $\times$  2–2.5 cm, densely white-lepidote abaxially and white-lepidote adaxially, **Sp** antrorse, 4–5 mm, 1–1.5 cm apart; **male Inf** 2  $\times$  branched, with  $\pm$ 55 primary **Br** 10–23 cm long, secondary **Br** 2, basal, present only on the basal primary branches; floral **Bra** brownish, ovate, 2.2–2.4  $\times$  1.1–1.3 mm, acuminate, shorter than the sepals; **Ped** 1.2–1.4 mm; **Fl** fragrant; **Sep** green, ovate oblong, 2.1–2.2  $\times$  1.8–2 mm, acute; **Pet** pale green, elliptic, 4–5  $\times$  2.3–2.5 mm; **St** subequal, longer than the petals; **Fil** 4.3–5 mm; **Anth** green, 1.8–2 mm, mucronate; **female Inf** 1  $\times$  branched, with  $\pm$ 15 primary **Br** 18–20 cm long; floral **Bra** brownish, widely triangular, 1–1.4  $\times$   $\pm$ 1.4 mm, minutely serrate, shorter than the sepals; **Ped** 15–17  $\times$  6–7 mm  $\varnothing$ ; **Fl** fragrant; **Sep** pale green, triangular,  $\pm$ 2.2  $\times$   $\pm$ 2 mm, obtuse; **Pet** green, long triangular, 3.7–4.5  $\times$   $\pm$ 2 mm; **Ov** pale rose, ellipsoid,  $\pm$ 7  $\times$   $\pm$ 2.8 mm; **Fr** light brown, 6–9  $\times$  3.5–5.8 mm; **Se** brown, 2.8–5.7  $\times$  0.87–1.2 mm.

**H. bracteata** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 550, 1896). **Type:** Mexico, Veracruz (Müller 813 [W?, B, NY]). — **Lit:** Espejo-Serna & al. (2005); Burt-Utley & Utley (2011). **Distr:** C Mexico (Puebla, Veracruz); shrubland and tropical deciduous forests on calcareous soils, 1880–2050 m.

Caespitose, flowering 2–3 m tall; **Ros** globose, to 70 cm high and 50 cm  $\varnothing$ ; **L** numerous, sheaths



pale yellow to light brown, widely ovate to square or transversely elliptic, 6–7.5 × 6.6–12 cm, serrate, densely lepidote at the apical portion on both faces, **L** lamina light green, 37.6–60 × 1–3.5 cm, glabrous adaxially, white-lepidote abaxially, **Sp** dark brown to black, uncinatae, antrorse, 3–4 mm, 1.5–2 cm apart; **Inf** floccose-tomentose, 2 × branched; **male Inf** with ±21 primary **Br** 2.5–8 cm long, secondary **Br** 2, basal; floral **Bra** light brown, ovate to widely ovate, 4–8 × ±2.4 mm, acuminate, erose, glabrous, longer than the sepals; **Fl** polystichous, divaricate, 3.6 × 1.9–3.1 mm, densely arranged; **Ped** 2–2.5 mm, lepidote; **Sep** brown, ovate to broadly ovate, 2.5–4 × 1.2–2 mm, entire, glabrous, acute; **Pet** shortly connate at the base, yellowish, oblong to elliptic, 3.5–5 × 1.6–2 mm, entire, rounded; **St** equal, shorter than the petals; **Fil** 3–3.1 mm; **Anth** yellow, 1–2 mm; **female Inf** with 60 or more primary, short to capituliform primary **Br** 2–3.5 cm long; secondary **Br** 2, basal; floral **Bra** brown, ovate, 4.5–6.9 × 1.1–4.2 mm, acute, entire, glabrous, longer than the sepals; **Ped** 2.4–4.3 mm, lepidote; **Sep** brownish, ovate, 3–4.5 × 1.4–2 mm, entire, acute; **Pet** yellowish, triangular, 3.9–4.2 × 1.4–1.6 mm, entire, acute; **Ov** green, ovoid, ±8.5 × ±6.2 mm Ø; **Fr** brownish, 7–9.9 × 4.4–6.9 mm Ø; **Se** 2.5–3 mm.

Easily distinguished on account of the caespitose growth and the tall inflorescences, as well as by the long and broad floral bracts that cover the flowers. — The type number was originally erroneously given as “Müller 803”.

**H. carlsoniae** Burt-Utley & Utley (Syst. Bot. 13(2): 276–279, ill., 1988). **Type:** Mexico, Guerrero (*Burt-Utley & Utley* 7492 [MEXU, BH, CAS, F, MICH, MO, NY, US]). — **Lit:** Pulido-Esparza & al. (2004). **Distr:** S Mexico (Guerrero: Taxco, Iguala, Buenavista de Cuéllar); tropical deciduous forest, crevices or cliffs, 800–1050 m.

Caespitose, flowering to 1.4 m tall; **L** 10–15 per rosette, frequently falcate, sheaths broadly ovate or elliptic to reniform, 2.3–4.8 × 1.9–6.4 cm, margin finely spiny, glabrous and lustrous on both faces, becoming densely lepidote for ½ their length, **L** lamina 17–62 × 1–2.1 cm, appressed cinereous-lepidote on both faces, **Sp** antrorse,

red-brown, thin, 1.5–2.5 mm, 6–10 mm apart; **male Inf** 1 × branched, with ±12–13 primary **Br** 7.5–20 cm long; floral **Bra** narrowly ovate, ovate-elliptic or ovate-triangular, 2–4.5 × 0.8–2 mm, attenuate-acuminate, entire to distally erose; **Fl** divaricate, sometimes appearing verticillate; **Ped** 0.2–1.8 mm; **Sep** white-greenish with apical purple little dots, ovate to ovate-triangular, 2.5–3.3 × 1.5–2 mm, glabrous, acute, margin distally erose; **Pet** white with apical purple little dots, elliptic to ovate-elliptic, 4.2–5 × 2–3 mm, rounded to acute, margin distally erose; **St** longer than the petals; **Fil** 4.5–5.5 mm; **Anth** green, 1–1.6 mm; **female Inf** simple or 1 × branched, with 2–7 primary **Br** 4–17.5 cm long; floral **Bra** narrowly triangular to oblong, 2–8 × 0.8–3 mm, attenuate-acuminate to apiculate, margin erose, shorter or longer than the pedicels; **Ped** 2.5–4 mm; **Sep** green, purple at the apex, narrowly ovate-triangular, 2.5–4 × 2–2.5 mm, acuminate or rarely apiculate, margin distally erose, glabrous; **Pet** white, ovate-triangular, 4.2–7.5 × 2.5–3.5 mm, acuminate; **Ov** purple, ovoid to ellipsoid, 7–8 mm × ±4 mm Ø; **Fr** nutant, 9.5–16.5 × 4.5–8 mm, triquetrous, glabrous; **Se** dark brown, 7–8 × ±1.5 mm.

**H. caudata** L. B. Smith (Phytologia 8: 5, t. 1, figs. 1–5, 1961). **Type:** Mexico, Oaxaca (*Foster & Van Hyning* 2999 [US, US]). — **Distr:** Mexico (Oaxaca: Santiago Lachiguiri, Tehuantepec); xerophytic shrubland, saxicolous, 300–400 m; known only from the type material.

Growth habit unknown, flowering to 1.3 m tall; **L** ±25, sheaths brown to dark brown, lustrous, suborbicular, 4–7 × 3–8 cm, slightly serrulate, lepidote distally, **L** lamina reddish adaxially, 50–80 × 3–5.5 cm, glabrous adaxially, appressed cinereous-lepidote abaxially, **Sp** antrorse, 2–4 mm, 5–15 mm apart; **Inf** seemingly lateral, 1 × branched, glabrous; peduncular **Bra** ovate with long linear, caudate, subentire, lepidote lamina, the upper much reduced and without lamina; lower primary **Bra** like the peduncular bracts, caudate; **male Inf** with ±30 primary **Br** 3.5–8 cm long, slightly compressed at the base; floral **Bra** stramineous, ovate, 2.6–4 mm, acuminate, as long as or slightly longer than the pedicels; **Fl** divaricate to ascending; **Ped** slender, 1–1.3 mm; **Sep** white, elliptic to

ovate,  $2.5\text{--}3 \times \pm 1.7$  mm, obtuse; **Pet** white, elliptic to ovate,  $4.3\text{--}4.6 \times 2.3\text{--}2.5$  mm, obtuse; **St** longer than the petals; **Fil**  $\pm 3.9$  mm; **Anth** green,  $\pm 1.6$  mm; **female Inf** with  $\pm 40$  primary **Br**  $4\text{--}10$  cm long; floral **Bra** stramineous, ovate,  $\pm 2$  mm, acuminate; **Fl** divaricate, laxly disposed; **Sep** triangular,  $1.3\text{--}1.4 \times 1.3\text{--}1.4$  mm, acute; **Pet** white, narrowly triangular,  $4.5\text{--}4.7 \times 1.9\text{--}2.3$  mm, acuminate; **Ov** ovoid; **Fr** light brown,  $6.4\text{--}11 \times \pm 4$  mm  $\emptyset$ ; **Se** light brown,  $3\text{--}4$  mm.

**H. caulescens** López-Ferrari & al. (Novon 19 (2): 197–200, ills., 2009). **Type:** Mexico, Puebla (Martínez & al. 58 [UAMIZ, IEB, MEXU]). — **Distr:** C Mexico (Morelos, Puebla, Oaxaca); arid scrub and tropical deciduous forests, on the ground or on rocks, 1200–1600 m.

Caespitose, flowering 0.8–1.9 m tall; stems cylindrical, long rhizomatous, prostrate or decumbent,  $3\text{--}3.7$  cm  $\emptyset$ ; **Ros** regular,  $\pm 40$  cm  $\emptyset$ ; **L** numerous, sheaths light brown, depressed ovate,  $3.2\text{--}4.7 \times 4.9\text{--}6$  cm, lustrous and white-lepidote at the apex on both faces, **L** lamina green to dark green,  $29\text{--}40 \times 1.8\text{--}3$  cm, densely white-lepidote on both faces, **Sp** brown, curved, antrorse or some retrorse,  $1.9\text{--}4$  mm,  $1.5\text{--}1.9$  cm apart; **Inf**  $2 \times$  branched; peduncle  $4\text{--}12$  mm  $\emptyset$ ; peduncular **Bra** foliaceous, entire, glabrous, becoming gradually shorter upwards; **male Inf** with  $18\text{--}20$  ascending to erect primary **Br**  $10\text{--}22$  cm long; secondary **Br** ascending,  $4.5\text{--}7$  cm long; floral **Bra** light brown, triangular,  $2.2\text{--}2.5 \times 1.3\text{--}1.7$  mm, entire, acuminate; **Fl** ascending to divaricate, sessile or subsessile, densely disposed; **Sep** light brown to brown basally, ovate-triangular,  $2.1\text{--}2.2 \times 1.6\text{--}1.8$  mm; **Pet** white, elliptic,  $3.5\text{--}4 \times 2\text{--}2.5$  mm; **St** subequal, longer than the petals; **Fil**  $2.8\text{--}3$  mm; **Anth** white to whitish-yellow,  $\pm 1$  mm; **female Inf** with  $20\text{--}30$  ascending primary **Br**  $0.6\text{--}2.3$  cm long; secondary **Br**  $2.5\text{--}9$  cm long; floral **Bra** light brown, triangular,  $\pm 2 \times \pm 1.8$  mm, slightly erose, acuminate; **Fl** ascending to appressed; **Ped**  $1.3\text{--}1.7$  mm; **Sep** greenish-brown, triangular,  $2.7\text{--}3.7 \times 1.3\text{--}1.7$  mm; **Pet** white, narrowly triangular,  $3.4\text{--}3.8 \times 1.1\text{--}1.4$  mm; **Ov** green, ovoid to long ovoid,  $3.3\text{--}3.9 \times 1.2\text{--}1.5$  mm, glabrous; **Fr**  $8.5\text{--}10 \times 3.2\text{--}4.3$  mm; **Se**  $2.8\text{--}4$  mm.

**H. chichinautzensis** Martínez-Correa & al. (Syst. Bot. 35(4): 746, ills. (pp. 747–748), 2010). **Type:** Mexico, Morelos (Martínez-Correa & al. 37 [UAMIZ, CICY, IEB, MEXU]). — **Distr:** C Mexico (Morelos: Cuernavaca, Tepoztlán), rosette-rich scrub on igneous rocks of lava flows, on rocks, 2000–2500 m.

Caespitose, flowering 0.6–1.7 m tall; **L** numerous, sheaths yellow to brown, ovate to square, glabrous basally and sparsely lepidote at the apex on both faces,  $2.5\text{--}4.3 \times 2\text{--}6.4$  cm, **L** lamina green,  $10\text{--}36 \times 1\text{--}4$  cm, glabrous adaxially, sparsely lepidote abaxially, **Sp** divaricate to antrorse,  $2\text{--}6.3$  mm,  $0.6\text{--}1.4$  cm apart; **Inf** lepidote,  $2 \times$  branched; peduncle  $4.5\text{--}15$  mm  $\emptyset$ ; peduncular **Bra** foliaceous, lepidote, serrate,  $4\text{--}12.3$  cm, gradually becoming shorter upwards; **male Inf** with up to 57 ascending primary **Br**  $0.6\text{--}5.4$  cm long; **Fl** fragrant, laxly arranged,  $3.2\text{--}4.7 \times 2\text{--}3$  mm  $\emptyset$ ; **Ped**  $1.6\text{--}2.4$  mm; floral **Bra** brown, triangular, entire, glabrous,  $1.5\text{--}3.5 \times 0.4\text{--}0.7$  mm; **Sep** brown, ovate,  $2\text{--}3.1 \times 1.3\text{--}1.7$  mm, entire, acute; **Pet** green with a longitudinal brown line abaxially, oblong,  $3\text{--}4.4 \times 1.8\text{--}2.4$  mm, rounded; **St** equal, longer than the petals; **Fil**  $3.2\text{--}4.2$  mm; **Anth** brown to black,  $0.8\text{--}1.7$  mm; **female Inf** with up to 35 ascending primary **Br**  $2.2\text{--}5.5$  cm long; floral **Bra** brown, triangular, entire, glabrous,  $1.5\text{--}2.4 \times 0.7\text{--}1.2$  mm; **Fl** fragrant, laxly arranged,  $3.8\text{--}6.8 \times 2\text{--}3.5$  mm  $\emptyset$ ; **Ped**  $1.5\text{--}4.4$  mm; **Sep** brown, triangular,  $1.6\text{--}2.8 \times 0.9\text{--}1.8$  mm, entire, acute; **Pet** green with a brown longitudinal line abaxially, triangular,  $2.2\text{--}4.4 \times 1.3\text{--}2$  mm, entire, acute; **Ov** ovoid,  $4\text{--}7 \times 2\text{--}2.4$  mm  $\emptyset$ ; **Fr**  $10\text{--}14 \times 3\text{--}7$  mm; **Se**  $2.4\text{--}5.5$  mm.

**H. colossa** Martínez-Correa & al. (Syst. Bot. 35(4): 746–747, ills. (pp. 752–753), 2010). **Type:** Mexico, Oaxaca (Espejo & al. 6872 [UAMIZ]). — **Distr:** S Mexico (Puebla, Oaxaca); tropical deciduous forest, limestone slopes, 1400–1900 m.

Caespitose, flowering 1.9–2 m tall; **L** numerous, sheaths yellow adaxially, brown abaxially, widely ovate to square,  $7.5 \times 9.7\text{--}11.3$  cm, glabrous basally and lepidote at the apex on both faces, serrulate, **L** lamina light green,  $45\text{--}55 \times 5\text{--}6.3$  cm, glabrous adaxially, sparsely lepidote abaxially, **Sp** divaricate to antrorse,  $4.3\text{--}5.5$  mm,

1.3–2 cm apart; **Inf** 2× branched; peduncle ±20 mm Ø; peduncular **Bra** foliaceous, ±14 cm, lepidote, spiny, the apical ones narrowly triangular, lepidote, entire; **male Inf** 1.25–1.94 m, with up to 60 ascending primary **Br** 9.8–12 cm long; floral **Bra** brown, triangular, 4.9–5.7 × ±0.9 mm, entire, glabrous, attenuate; **Fl** divaricate, densely disposed; **Ped** 2.1–3 mm, glabrous; **Sep** brown, triangular, 3.2–3.8 × 1.7–2.1 mm, entire, acute; **Pet** green, elliptic to oblong, 5.8–6.2 × 2.6 mm, rounded, glabrous, entire; **St** equal, longer than the petals; **Fil** 4.5–4.6 mm; **Anth** yellow, 1.1–1.2 mm; **female Inf** with ±47 ascending primary **Br** ±17.5 cm long, secondary **Br** ascending, 7.5–9.5 cm; floral **Bra** brown, triangular, ±4.8 × 1.7 mm, entire, glabrous; **Fl** divaricate to ascending, densely disposed; **Ped** ±5 mm, glabrous; **Sep** brown, ovate, 2.5 × 1.5 mm; **Pet** green, triangular, ±4.8 × ±2.1 mm, glabrous, entire; **Fr** ±15 × ±5.3 mm Ø; **Se** ±5.4 mm.

**H. complanata** Burt-Utley (Phytoneuron 2012 (69): 6–10, ill., 2012). **Type:** Mexico, Oaxaca (Utley & Utley 8823 [MEXU, BM, CAS, GH, MICH, MO, US, USF]). — **Distr:** S Mexico (Oaxaca); thorn scrub and tropical deciduous forest, on the ground or on rocks on talus slopes.

Solitary, flowering to 2.3 m tall; **Ros** 1–1.2 m Ø, forming long rhizomes to 30 cm, ±4 cm Ø; **L** numerous, reflexed in the apical portion, sometimes the tips strongly curled, sheaths stramineous to castaneous, semiorbicular to transversely elliptic, 6–7.5 × 9.5–16 cm, margins finely spinulose, floccose at the apex, glabrous and lustrous on both faces, becoming densely lepidote distally, **L** lamina green, occasionally pink-tinged, 45–75 × 5–6 cm, very densely white-lepidote on both faces, most conspicuous on the lower 1/3, glabrescent adaxially at the apical portion, **Sp** castaneous to dark brown, antrorse and retrorse, or rarely divaricate, 3.5–7.5 mm, 2.7–5.3 cm apart; **Inf** finely lepidote to glabrous; peduncle 12–30 mm Ø; peduncular **Bra** rose-greenish, linear to narrowly triangular, 31–33 cm, becoming progressively reduced distally and exceeding the internodes, pungent; **male Inf** 2× branched, with 1–14 divaricate to ascending primary **Br** (8–) 11.5–32 cm long; floral **Bra** shorter than to

equalling the sepals, ovate to narrowly triangular, 0.9–2 × 0.3–0.8 mm, finely spinulose-serrulate, attenuate-acuminate, lepidote, acute; **Fl** divaricate, sometimes appearing verticillate; **Ped** articulated, stout, conical, 0.3–1.5 mm, lepidote; **Sep** ovate to deltoid, 1.2–1.6 × 1–1.6 mm, apiculate, occasionally finely serrulate-spinulose or erose, lepidote; **Pet** pale yellow, ovate to elliptic, 2.5–4.5 × 1.3–2.2 mm, apiculate, glabrous; **female Inf** 1× or infrequently 2× branched, with up to 34 divaricate to ascending primary **Br** (8.5–) 13–23.5 cm long; floral **Bra** triangular, 1–1.5 × 0.4–0.7 mm, apiculate, finely serrulate-spinulose, lepidote to occasionally glabrous; **Fl** divaricate, laxly disposed, sometimes appearing verticillate; **Ped** articulated, stout, conical, 0.5–1 mm, lepidote to occasionally glabrous; **Sep** triangular, 0.8–1.2 × 0.8–1.2 mm, entire to irregularly finely serrulate, lepidote to occasionally glabrous; **Pet** green, triangular, 2.1–2.9 × 1–1.8 mm, entire, apiculate to acute, glabrous; **Ov** lepidote; **Fr** dark brown but drying olive-green, 7.5–8.5 × 3–4 mm Ø, finely lepidote; **Se** not known.

**H. confusa** L. B. Smith (Contr. Gray Herb. 117: 22, t. 1, figs. 71–72, 1937). **Type:** Mexico, Puebla (Pringle 7479 [GH, VT]). — **Lit:** Smith (1938); Espejo-Serna & al. (2007); Burt-Utley & Utley (2011). **Distr:** C Mexico (Puebla, Oaxaca); rosette-rich scrub and thorn scrub, limestone hills and slopes, and on calcareous bluffs on rocks, 1900–2600 m. — Figs. 1 and 2.

Caespitose, flowering to 1.3 m tall; **Ros** ±25 × ±20 cm Ø; **L** numerous, sheaths yellow to brownish, ovate, 2–6 (7–) × 1.3–6 (–9) cm, serrate, glabrous basally, lepidote on both faces, **L** lamina dark green, recurved, 9–35 (–50) × 0.35–0.9 cm, pungent, glabrous adaxially, densely cinereous-lepidote abaxially, **Sp** retrorse or divaricate, some antrorse, 1.5–8 mm, 0.5–1.7 cm apart; **Inf** 2× branched; basal peduncular **Bra** foliaceous, caudate, sparsely lepidote, serrate, 3.7–12.8 cm, the apical ones triangular, erose; **male Inf** with up to 38 primary **Br**; floral **Bra** brownish, widely ovate, 3.8–7.3 × 1.7–4.5 (–6) mm, erose, lepidote, acute; **Fl** sessile, 3–6.9 × 2.1–3.1 mm Ø; **Sep** brownish, ovate, 2.4–4.6 × 1.4–3.2 mm, entire, rounded; **Pet** green-yellowish, oblong to

**Fig. 1** *Hechtia confusa* (male flowers). (Copyright: A. Espejo-Serna)



**Fig. 2** *Hechtia confusa* (female flowers). (Copyright: A. Espejo-Serna)

elliptic, 2.5–5.7 × 1.6–4 mm, entire, rounded; **St** equal, longer than the petals, triangular, flattened; **Fil** 2.4–4.4 mm; **Anth** yellow, 0.8–2.2 (–2.8) mm; **female Inf** with up to 38 primary **Br**; floral **Bra** brownish, widely ovate, 4.3–7.9 × 1.5–4.8 mm, erose, lepidote, acute; **Fl** sessile, densely disposed,

6.6 (–9.5) × 2.4 mm Ø; **Sep** brownish, ovate, 2.7–5.1 × 1.2–3.1 mm, acute; **Pet** green-yellowish, triangular 3.5–5.1 × 1.2–3 mm, entire, rounded; **Ov** ovoid, 6–7 × 2.1–2.5 mm Ø; **Fr** brownish, 6.5–10 × 3–8 mm Ø; **Se** 2.2–3.6 mm.

***H. konzattiana*** L. B. Smith (Contr. Gray Herb. 117: 19, t. 1, fig. 56, 1937). **Type:** Mexico, Oaxaca (*Conzatti & Gómez* 3501 [US, MEXU]). — **Distr:** S Mexico (Oaxaca, Puebla); oak forest, ±1300 m.

Flowering to ±1 m tall; **L** numerous, sheaths brown, ovate, ±4 cm long, **L** lamina 15–40 × 1–1.3 cm, sparsely pale-lepidote adaxially, soon becoming glabrous, prominently nerved and lepidote abaxially, largely acuminate; **Sp** divaricate to barely antrorse, ±2 mm, 0.8–1 cm apart; **Inf** glabrous; peduncular **Bra** red with prominent hyaline margins, linear from a triangular-ovate base, lepidote, becoming progressively reduced distally; **male Inf** 1 × branched with ±35 primary divaricate **Br** 4–11 cm long; floral **Bra** brownish, elliptic, 2–2.5 mm, erose, longer than the pedicels; **Fl** divaricate, densely disposed; **Ped** ±1.5 mm; **Sep** pale brown, blackish punctate, broadly elliptic, ±2 mm, entire to faintly erose, obtuse; **Pet** white, elliptic, 2–2.3 × 2.5–4 mm, obtuse; **St** longer than the petals; **Fil** 3–3.2 mm; **Anth** yellow, ±1.5 mm; **female Inf**, **Fl** and **Fr** unknown.

***H. deceptrix*** I. Ramírez & Hornung (Phytotaxa 221(2): 158, Figs. 1, 2, 3a, 3e, 2015).

**Type:** Mexico, Hidalgo (*López-Ferrari & al.* 3309 [UAMIZ, IEB]). — **Distr:** Mexico (Hidalgo: Actopan, Atotonilco El Grande, Cardonal); xerophilous scrub on calcareous cliffs, 1700–1800 m.

Caespitose, flowering to 2.5 m tall; **Ros** 50–60 cm Ø; **L** 50–80, sheaths light brown, broadly ovate, 4–6 × 4–5 cm, margins erose, lustrous and glabrous adaxially, densely white-lepidote abaxially, **L** lamina green, narrowly triangular, 26–50 × 1–3.5 cm, densely white-lepidote abaxially, glabrous adaxially, **Sp** light green or occasionally purple, antrorse, 1.5–2.5 mm, 0.4–1 cm apart; **male Inf** 1 × branched, with ±30 **Br**, occasionally the lower ones with a pair of secondary basal branches; peduncular **Bra** foliaceous, sheaths light brown, triangular, 2.5–4 × 3–4 cm, margins entire to erose, lamina green, narrowly triangular, 4–6 × 0.6–1.2 cm, margins spinose, glabrous adaxially, densely white-lepidote abaxially; **Br** ascending, 4–17 cm; floral **Bra** green with light brown apex, ovate-elliptic, 6–7 × 2.6–3 mm, margins erose, glabrous; **Fl** polystichous; **Ped** 4–5 mm; **Sep** green with light brown apex, triangular, 3.5–3.8 × 1.8–2 mm, entire, glabrous; **Pet** light green, widely elliptic, 4.2–4.5 × 3.3–3.5 mm, rounded; **St** unequal; **Fil** 1.9–3.5 mm; **Anth** green, 0.9–1.5 mm; **female Inf** 1 × branched, with 7–16 **Br**, occasionally the lower ones with a pair of secondary basal branches; peduncular **Bra** foliaceous, sheaths green, triangular, 2.5–4 × 3–4 cm, margins entire to erose, lamina green, narrowly triangular, 7–9 × 0.6–1 cm, margins spinose, glabrous adaxially, densely white-lepidote abaxially; **Br** ascending, 5–14 cm; floral **Bra** green, ovate-elliptic, ±8 × 4–5 mm, margins erose, glabrous; **Fl** polystichous; **Ped** <1 mm; **Sep** green, triangular, 4–5 × 2–2.5 mm, entire, glabrous; **Pet** green, elliptic, 4–5.2 × 2–2.8 mm, rounded; **Ov** oblong to ellipsoid, 5–7 mm; **Fr** brown, ellipsoid, 10–14 mm; **Se** brown to reddish-brown, ±3 mm.

**H. dichroantha** Donnell Smith (Bot. Gaz. 42: 299–300, 1906). **Type:** Guatemala, Baja Verapaz (*Cook* s.n. [US]). — **Distr:** Guatemala (Baja Verapaz, Chiquimula), Honduras (Francisco Morazán, El Paraíso); ±1600 m, terrestrial.

Growth habit unknown, flowering to 1.5 m tall; **L** numerous, sheaths ample, 3.5–5 cm wide, spiny, **L** lamina 15–100 × 2.3–4 cm, lepidote to glabrous adaxially, white-lepidote abaxially, long filiform-attenuated, **Sp** yellow, divaricate to antrorse, 1–3 mm, 0.5–1 cm apart; **Inf** terminal, 1–2 × branched, glabrous; peduncle ±1 cm Ø; peduncular **Bra** red, linear-lanceolate, 7–9 cm, densely white-lepidote abaxially, serrulate; **male Inf** with numerous primary **Br** 4–20 cm long; floral **Bra** linear-lanceolate, 6–19 mm, acuminate, equalling the sepals; **Fl** divaricate, tightly arranged; **Ped** 2–4 mm; **Sep** red, ovate-lanceolate, 4–6 mm, acuminate to mucronate; **Pet** white, ovate-lanceolate to oblong-lanceolate, 5–7 mm, acute; **St** equal or slightly shorter than the petals; **female Inf** with numerous primary **Br** 2.5–7 cm long; floral **Bra** linear-lanceolate, 4–9 mm, attenuate-acuminate; **Fl** sessile; **Sep** 4–5 mm, acuminate to mucronate; **Pet** white to white-reddish, 4–6 mm; **Ov** almost wholly inferior; **Fr** 8–15 mm, glabrous; **Se** brownish.

**H. edulis** I. Ramírez & al. (Novon 21: 362–367, ill., 2011). **Type:** Mexico, Chihuahua (*Ramírez & Carnevali* 1527 [CICY, MO, UAMIZ]). — **Lit:** Kopfstein (2015). **Distr:** Mexico (Chihuahua: Uruáchi, Batopilas); tropical deciduous forest and pine-oak forest, on steep rocks, 650–1850 m.

Caespitose, flowering to 1 m tall; **Ros** small, ±25–40 cm Ø; **L** numerous, sheaths oblong, ±1.2 × ±2 cm, dentate, thin, white-lepidote on both faces, **L** lamina 14–20 × 0.9–1.2 cm, glabrous and lustrous adaxially, white-lepidote abaxially, **Sp** antrorse, retrorse or divaricate, 1.2–2 mm, 5–7 mm apart; **Inf** erect, 1 × branched, glabrous; peduncle 3–4 mm Ø; peduncular **Bra** narrowly triangular, acute to long acuminate, 3–9 × 0.8–1 cm, decreasing in length further up; **male Inf** with 11–17 ascending primary **Br** (1–) 3–7 cm long; floral **Bra** light brown, oblong, asymmetrical, 3–3.5 × 3.8–4 mm, acute, irregularly serrate; **Fl** ascending, sessile, ±11 × ±3 mm Ø; **Sep** basally connate with the petals for ±1 mm, ovate, 3–3.5 × 2.2–2.3 mm, slightly dentate at the apex, sinuose to erose; **Pet** widely elliptic, 4.5–5 × 3.4–3.5 mm, obtuse, margin irregular; **St** subequal, 3 adnate to the petals, 3 free; **Fil** ±3.8 mm; **Anth** ±1 mm; **female Inf**



with 10–16 ascending primary **Br** (2–) 4–6 cm long; floral **Bra** light brown, rectangular, asymmetrical,  $3\text{--}3.5 \times \pm 2.8$  mm, irregularly erose; **Fl** ascending, almost sessile; **Ped** green, conical, stout, 1–1.5 mm; **Sep** basally green, apically light brown, widely triangular,  $2\text{--}2.5 \times 3\text{--}3.2$  mm, obtuse, slightly erose; **Pet** green, widely elliptic to ovate,  $4\text{--}4.5 \times 2.8\text{--}3$  mm, acute; **Ov** wholly superior, green, ovoid,  $4\text{--}5 \times \pm 2.3$  mm; **Fr** dark brown,  $7\text{--}10 \times 2\text{--}3$  mm.

This species is called “chikana” by the Raramuri people from the Sierra Tarahumara. The leaves can be eaten raw after the marginal spines are removed, or they can be used to make a paste that, combined with chili pepper and salt, is eaten with tortillas (Kopfstein 2015).

**H. elliptica** L. B. Smith (Contr. Gray Herb. 117: 20, t. 1, figs. 61–62, 1937). **Type:** Mexico, Coahuila (*Palmer* 205 [GH, BM, C, F, K, NY, UC, US]). — **Distr:** Mexico (Coahuila); xerophilous scrub, on the ground or on rocks, 1000–1600 m.

Densely caespitose, flowering to 50 cm tall; **Ros**  $\pm 20$  cm  $\varnothing$ , asymmetrical; **L** numerous, sheaths yellowish to brown, ovate to subquadrate,  $2.2\text{--}2.5 \times 2\text{--}2.2$  cm, glabrous, serrulate, **L** lamina green to green tinged with rose,  $17\text{--}27 \times 1\text{--}2$  cm, glabrescent adaxially, densely appressed-lepidote abaxially, **Sp** dark brown, divaricate or rarely slightly antrorse or retrorse,  $\pm 4$  mm,  $1.5\text{--}2.3$  cm apart; **Inf** seemingly lateral, white-lepidote; peduncle basally compressed, glabrous,  $3\text{--}6.3$  mm  $\varnothing$ ; peduncular **Bra** ovate,  $1\text{--}1.7 \times 0.55\text{--}0.6$  cm, acuminate, longer than the internodes, the upper ones shorter than the internodes; **male Inf** 1  $\times$  branched, with 8–19 ascending primary **Br** 1–8 cm long; primary **Bra** stramineous, ovate, 4.5–7 mm, margins hyaline, acute; floral **Bra** brownish to rose with broad hyaline margins, suborbicular,  $\pm 4$  mm, erose, apiculate,  $\pm$  equalling the sepals; **Fl** ascending, subsessile; **Sep** brownish, with broad hyaline margins, elliptic,  $\pm 5$  mm, obtuse; **Pet** basally connate for  $\pm 3$  mm, white, elliptic,  $\pm 8$  mm, lepidote abaxially, obtuse; **St** shorter than the petals; **Fil**  $\pm 7$  mm, **Anth** yellow,  $\pm 2$  mm; **female Inf**, **Fl** and **Fr** unknown.

**H. epigyra** Harms (Notizbl. Bot. Gart. Berlin-Dahlem 12: 531–532, 1935). **Type:** Mexico,

Tamaulipas (*Viereck* 81 [B?]). — **Lit:** Espejo-Serna & al. (2010b). **Distr:** Mexico (Hidalgo, Tamaulipas); rosette-rich and juniper-palm scrub on limestone cliffs, 750–1800 m.

Caespitose, flowering to 4 m tall; **Ros** 30–80 cm  $\varnothing$ ; **L** numerous, sheaths light brown, widely ovate to square,  $4\text{--}6 \times 4.4\text{--}5$  cm, densely white-lepidote on both faces, glabrescent when mature, **L** lamina dark green,  $28\text{--}40 \times 1.2\text{--}3$  cm, glabrescent and lustrous at the apex adaxially, densely white-lepidote at the base adaxially, densely white-lepidote abaxially, **Sp** purple, triangular, antrorse, 1–2 mm, 0.4–1 cm apart; **Inf** terminal, 1  $\times$  (rarely 2  $\times$ ) branched; peduncular **Bra** green tinged with purple, foliaceous, attenuate, pungent, longer than the internodes; **male Inf** with up to 30 primary **Br**, divaricate to ascending, 4–17 cm; floral **Bra** green with brown apex, ovate-elliptic,  $6\text{--}7 \times 2.6\text{--}2.9$  mm, acute, margin slightly erose and hyaline; **Fl** divaricate; **Ped** 4–5 mm; **Sep** green with apex brown, triangular,  $3.5\text{--}3.8 \times 1.8\text{--}2$  mm, glabrous, acute, entire; **Pet** green, widely elliptic,  $4.2\text{--}4.5 \times 3.3\text{--}3.5$  mm, rounded, entire; **St** subequal, shorter than the petals; **Fil** 1.9–3.2 mm; **Anth** green,  $\pm 1$  mm; **female Inf** with up to 16 divaricate to ascending primary **Br** 6–14 cm long; floral **Bra** green, ovate-elliptic,  $\pm 8 \times 4\text{--}5$  mm, acute, margin slightly erose and hyaline; **Fl** divaricate; **Ped**  $\pm 2$  mm; **Sep** green, triangular,  $4.5\text{--}4.9 \times 2\text{--}2.4$  mm, glabrous, acute, entire; **Pet** green, elliptic,  $4.8\text{--}5.2 \times 2.8\text{--}3$  mm, rounded, entire; **Ov** inferior, green, ellipsoid,  $5\text{--}7 \times 2.5\text{--}2.8$  mm; **Fr** green, tinged with red towards the apex, brown to dark brown when mature, trigonous,  $10\text{--}14 \times 4\text{--}4.5$  mm, glabrous; **Se** brown to reddish-brown,  $\pm 3$  mm.

**H. flexilifolia** I. Ramírez & Carnevali (Phytotaxa 178(2): 116–118, ills., 2014). **Type:** Mexico, Oaxaca (*Ramírez & Carnevali* 1868 [CICY, MEXU, OAX, SEL, US]). — **Distr:** Mexico (Oaxaca); cliffs with pine-oak forest, on rocks, 1900–2000 m.

Solitary, flowering to 1.8 m tall; **Ros** 50–55 cm  $\varnothing$ ; **L** 30–40, sheaths dark brown, broadly oblong,  $3\text{--}4 \times 5\text{--}6.5$  cm, densely white-lepidote on both faces at the apex, **L** lamina narrowly triangular to linear,  $15\text{--}100 \times 1.5\text{--}3$  cm, glabrous adaxially, densely white-lepidote abaxially, **Sp** white-

yellowish, antrorse, 10–20 mm, 1–1.5 cm apart; **male Inf** 1–2× branched with 70–80 primary **Br**; peduncular **Bra** foliaceous, narrowly triangular, 2.5–20 × 1.5–2.5 cm, entire to finely serrate, acuminate; primary **Br** divaricate to ascending, 4.5–30 cm; floral **Bra** yellowish, lanceolate, 2–4.5 × 1–2 mm, erose, acute, glabrous; **Fl** polystichous, divaricate; **Ped** 1–1.5 mm; **Sep** light brown, ovate, 2–2.5 × 1.2–1.6 mm, acute; **Pet** white, elliptic, 2.4–3.5 × 1.4–2.5 mm, acute to rounded; **St** unequal; **Fil** 1.5–3 mm; **Anth** yellow, 1–1.5 mm; **female Inf** 1× branched with 14–20 **Br**; peduncular **Bra** foliaceous, narrowly triangular, 2.5–20 × 1.5–2.5 cm, entire to finely serrate, acuminate; **Br** divaricate to ascending, 4–10 cm; floral **Bra** yellowish, ovate, 2–3 × 1.5–2 mm, acute, glabrous; **Fl** polystichous; **Ped** 1–1.5 mm; **Sep** light brown, ovate, 1.5–2.2 × 1.2–1.6 mm, acute; **Pet** white, triangular, 2.5–3 × 1–1.5 mm, acute; **Fr** dark brown, narrowly ovoid, 5–6 mm; **Se** 3.5–5 mm.

**H. fosteriana** L. B. Smith (Phytologia 8: 8, t. 1, figs. 10–11, 1961). **Type:** Mexico, Oaxaca (*Foster & Van Hynning* 2935 [US, US]). — **Distr:** Mexico (Oaxaca); tropical deciduous forest, on the ground or on rocks, 100–600 m.

Solitary, flowering to 1.5 m tall; **L** numerous, sheaths very dark castaneous and lustrous on both faces, transversely oblong to transversely reniform, ±10 cm wide, glabrous except at the apex, **L** lamina green tinged with red adaxially, >1 m × ±7 cm, glabrous above, appressedly cinereous-lepidote abaxially, **Sp** antrorse, ±6 mm; **Inf** seemingly lateral, 1× branched; peduncular **Bra** broadly triangular, exposing almost the whole peduncle but the linear mostly entire laminae equalling or exceeding the internodes; **male Inf** with ±15 slender primary **Br** 6.5–25 cm long; floral **Bra** narrowly triangular to ovate, 4.2–4.4 × ±1.7 mm, acuminate, longer than the pedicels; **Fl** ascending, some appearing verticillate; **Ped** slender, 1–1.3 mm; **Sep** white, ovate-triangular, 2.3–2.4 × 1.7–2 mm, glabrous, acute; **Pet** white tinged with red at the base adaxially, ovate-elliptic, 4.8–5 × 3.2–3.3 mm, glabrous, acute; **St** shorter than the petals; **Fil** 3.5–3.6 mm; **Anth** yellow, ±1.6 mm; **female Inf** 1× branched; floral **Bra** broadly ovate, 4 mm, acute, much exceeding the stout obconic pedicels; **Fl** divaricate; **Sep**

hyaline with a thickened brown base, ovate-oblong, 3 mm, obtuse; **Pet** white, ±4 mm; **Fr** brown, ±8 mm, acute, sharply trigonous, smooth, lustrous.

**H. fragilis** Burt-Utley & Utley (Brittonia 39 (1): 40–42, ill., 1987). **Type:** Mexico, Oaxaca (*Burt-Utley & Utley* 6980 [MEXU, MO, US]). — **Distr:** Mexico (Oaxaca, Puebla); tropical deciduous forest and thorn scrub, on the ground or on limestone cliffs, 600–1200 (–1800?) m.

Caespitose in small groups, flowering 40–100 cm tall; **L** 20–25, brittle, sheaths yellow to light brown, transversely oblong, 1.6–4 × 3.8–5.6 cm, margin finely spiny, **L** lamina light green with red spots, 10–21 × 1–3 cm, glabrous adaxially, appressedly cinereous-lepidote abaxially, **Sp** retrorse to divaricate, green to red-brown, 1.3–4 mm; **Inf** 1× branched, sparsely tomentose; **male Inf** with ±40 primary **Br**; floral **Bra** ovate-triangular, 2–3.1 × 0.7–1 mm, sparsely tomentose-lepidote, acuminate, occasionally apiculate, finely erose; **Ped** 1.5–2.3 mm; **Sep** green tinged purple, ovate to ovate-elliptic, 1.3–2.5 × 1.9–2.1 mm, glabrous, acute to obtuse; **Pet** greenish-white tinged purple, broadly elliptic to oblong, 4.5–5 × 2.9–3.1 mm, glabrous; **St** as long as the petals; **Fil** 3–5 mm; **Anth** green, 1.5–2 mm; **female Inf** with ±20 primary **Br**; floral **Bra** narrowly ovate to ovate-triangular, 1.6–4.5 × 1–2 mm, acuminate, margin distally erose, sparingly tomentose to lepidote; **Ped** 1.5–2.5 mm; **Sep** brownish-green, ovate-triangular to triangular, 2–2.9 × 1.3–1.6 mm, glabrous to sparingly tomentose, acute, margin hyaline, entire, sometimes distally erose; **Pet** green tinged purple, ovate to ovate-elliptic, 3.6–4.7 × 2.3–2.5 mm, glabrous, acuminate; **Ov** wholly superior, green, purplish at the apex, ovoid, 4.5–5.1 × 3.4–3.6 mm; **Fr** dark brown, 5.5–8 × 3.5–5 mm; **Se** brown, 5.5–6 mm.

**H. galeottii** Mez (Repert. Spec. Nov. Regni Veg. 16: 71–72, 1919). **Type** [lecto]: Mexico, Oaxaca (*Pringle* 6703 [B, B, BR, ENCB, G, GH, HBG, M, MEXU, P, UC, VT, WU, Z]). — **Lit:** Espejo-Serna & al. (2013). **Distr:** S Mexico (Oaxaca: Asunción Nochixtlán, San Jerónimo Sosola); oak forest and transitions to tropical

deciduous forests, terrestrial on calcareous hills, 1500–2000 m.

Solitary; flowering to 2 m tall; **L** numerous, sheaths light brown, oblong to suborbicular, 5.2–6 × 5–5.5 cm, glabrous and lustrous basally, becoming densely white-lepidote distally on both faces, **L** lamina green, 30–40 × 3.5–4.5 cm, glabrous adaxially, finely appressedly white-lepidote abaxially, **Sp** stout, dark to light brown or green, curved, antrorse, with a conspicuous triangular base, ±4 mm, 2–4 cm apart; **Inf** very sparsely floccose-lepidote, glabrescent; peduncle dark brown, cylindrical, ±2 cm Ø basally; peduncular **Bra** light brown, linear-triangular to triangular, pungent; **male Inf** 2× branched, with numerous divaricate to ascending primary **Br** 16–35 cm long, with 2 short (2.5–13 cm) secondary branches at the base; floral **Bra** light brown, ovate-triangular, ±1 mm, sparsely lepidote, acute, erose, shorter than the sepals; **Fl** ascending, sometimes appearing verticillate, subsessile or very shortly pedicellate; **Ped** stout, conical, ±1.5 mm; **Sep** broadly ovate, ±1.5 × 1.4–1.6 mm, obtuse; **Pet** densely black-punctate, elliptic to ovate-elliptic, 2.5–2.8 × 1.9–2 mm, rounded; **St** longer than the petals; **Fil** 2.5–2.8 mm; **Anth** greenish, ±1 mm; **female Inf** 1× branched, with numerous divaricate to ascending primary **Br** 12.5–28 cm long; floral **Bra** light brown, dark brown towards the base, ovate-triangular, ±1.5 mm, lepidote, erose, shorter than the sepals; **Fl** ascending, densely to laxly disposed, sometimes appearing verticillate, subsessile; **Sep** ovate to triangular, 1.8–2 × 1.4–1.5 mm, acute; **Pet** narrowly triangular to deltoid, 3.3–3.4 × 1.4–1.5 mm, acute; **Ov** ellipsoid, ±2.5 × ±1 mm, glabrous; **Fr** dark brown, 7.5–8 mm, acute; **Se** reddish-brown, ±3.5 mm.

See Espejo-Serna & al. (2013) for details of the typification and the type locality.

**H. glauca** Burt-Utley & Utley (Brittonia 45: 220–222, fig. 1, 1993). **Type:** Mexico, Michoacán (Burt-Utley & Utley 8387 [MEXU, B, CAS, DUKE, IEB, MICH, MO, NY, US]). — **Distr:** Mexico (Michoacán: Arteaga); on exposed rocky cliffs, 300–900 m.

Usually solitary or in groups of few rosettes, flowering 0.9–1.5 m tall; **Ros** strongly spreading, to 80 cm Ø; **L** frequently falcate, sheaths stramineous to light brown, often deep pink-red distally, transversely elliptic to reniform, 4.5–6.7 × 6.5–11 cm, margins crenulate to weakly spinulose, glabrous and lustrous on both faces, **L** lamina blue-green, occasionally suffused with pink, wax-covered, strongly recurved distally, 33.5–70 × 5.8–9.3 cm, glabrous on both faces, **Sp** red-brown, antrorse, 0.8–3 mm, 0.7–3 cm apart; **Inf** glabrous; peduncular **Bra** foliaceous, becoming progressively reduced distally; **male Inf** weakly 2× branched; floral **Bra** broadly ovate, 1.2–2 × 1.5–1.7 mm, apiculate to attenuate-acuminate, very finely denticulate to erose, longer than the pedicels; **Ped** stout, 0.3–1.2 mm, articulated; **Sep** light green or green suffused with pink, ovate to broadly ovate, 1.6–2.2 × 1.5–2.3 mm, glabrous, rounded to acute or acuminate, entire or rarely somewhat erose; **Pet** white to light lavender-pink, subspatulate, 4.5–5 × 1.8–2.2 mm, rounded; **female Inf** 1× or rarely 2× branched; floral **Bra** ovate, 1–2.3 × 1–1.3 mm, acuminate to apiculate, erose distally, shorter than the pedicels; **Ped** 2–4.5 mm, articulated; **Sep** light green or green suffused with pink, triangular to ovate-triangular, 1.7–2.5 × 1.4–2 mm, apiculate to acute, entire or somewhat erose; **Pet** white to faintly or deeply suffused with dark lavender-pink, triangular, 3.5–5 × 1.3–2.1 mm, acuminate to apiculate; **Ov** largely superior, light green to light green suffused with pink; **Fr** brown, (8–) 9–12 × 3.5–5 mm, glabrous, smooth.

**H. glomerata** Zuccarini (Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 3: 240–242, t. 6, 1840). **Type:** Mexico, Hidalgo? (Karwinsky s.n. [[lecto — icono]: l.c., t. 6]). — **Lit:** Burt-Utley & Utley (2011). **Distr:** Mexico (Nuevo León, Tamaulipas, San Luis Potosí, Aguascalientes, Hidalgo, Querétaro, Guanajuato, México, Chiapas), Guatemala (Guatemala, Huehuetenango, Quiché); thorn scrub vegetation and tropical deciduous forest, generally on limestone hills or cliffs, on the ground or on rocks, 200–2100 m.

**Incl.** *Dasyllirion pitcairniifolium* Karwinsky & Zuccarini ex Zuccarini (1838) (*nom. inval.*, ICN

Art. 38.3); **incl.** *Yucca pitcairniifolia* Karwinsky ex Zuccarini (1838) (*nom. inval.*, ICN Art. 38.3); **incl.** *Hechtia ghiesbreghtiana* Lemaire (1862) (*nom. inval.*, ICN Art. 38.3); **incl.** *Hechtia ghiesbreghtii* Lemaire (1863); **incl.** *Hechtia argentea* K. Koch ex Baker (1884)  $\equiv$  *Dyckia argentea* (K. Koch ex Baker) G. Nicholson (1886); **incl.** *Hechtia capituligera* Mez (1896); **incl.** *Hechtia gamopetala* Mez (1896); **incl.** *Hechtia morreniana* Mez (1896); **incl.** *Hechtia lepidophylla* I. Ramírez (2008).

Solitary or caespitose, flowering 1.4–2.5 m tall; **Ros** globose, 20–90 cm  $\varnothing$ ; **L** numerous, 50–100 per rosette, sheaths white to yellowish with a dark brown to black spot, oblong to depressed-ovate, 3–6  $\times$  3–8 cm, glabrous, lustrous, entire or sometimes minutely denticulate towards the apical portion, **L** lamina green to light or greyish, 20–85  $\times$  1–3.5 cm, densely cinerous to white-lepidote or glabrous and lustrous adaxially, densely white-lepidote abaxially, **Sp** light brown to brown or reddish, antrorse to divaricate, 4–7 mm, 0.7–2 cm apart; **Inf** seemingly lateral, 1–2 $\times$  branched, rarely simple, white-lepidote to white-tomentulose, soon glabrous; peduncle cylindrical, flattened at the base, 1–3 cm  $\varnothing$ , white-lepidote to glabrescent; peduncular **Bra** brown to light brown, triangular to narrowly triangular, 3–5.5  $\times$  0.9–1.5 cm, entire to minutely denticulate, white-lepidote to glabrescent on both faces, acute to acuminate, the basal ones imbricate and longer than the internodes, the upper shorter than the internodes; **male Inf** with 13–35 divaricate to ascending, glomerate to elongated primary **Br** 1–15 (–23) cm long; primary **Bra** brown to light brown, triangular, 8–12  $\times$  3–4 mm, acute to acuminate, margins spiny, becoming progressively reduced distally; secondary **Br**, when present, glomerate, 0.6–2.2 cm; secondary **Bra** ovate-triangular, 7–8  $\times$  3–4 mm, apiculate; floral **Bra** brownish, widely triangular-ovate, 4–7  $\times$  5–7 mm, fimbriate, lepidote abaxially, acute to apiculate; **Fl** ascending, sessile or shortly pedicellate; **Sep** white to rose-coloured, ovate, widely elliptic to oblong, 3.5–4.5  $\times$   $\pm$ 3 mm, densely white-lepidote, entire, rounded; **Pet** white, obovate to ovate or elliptic, 4.5–6  $\times$  3–3.5 mm, rounded; **St**

unequal, shorter than the petals; **Fil** 2.5–4 mm; **Anth** green, 1–1.5 mm; **female Inf** with 15–39 divaricate to ascending, glomerate to elongated primary **Br** 1–15 cm long; primary **Bra** brown to light brown, triangular, becoming progressively reduced distally; secondary **Br**, when present, glomerate,  $\pm$ 1.5 cm; secondary **Bra** ovate-triangular, 7–8  $\times$  3–4 mm, apiculate; floral **Bra** brownish, triangular-ovate to triangular, 4.5–6.5  $\times$  3–5 mm, brownish, densely white-lepidote, fimbriate, acute to apiculate, longer than the sepals; **Fl** ascending, sessile to shortly pedicellate; **Ped** stout,  $\pm$ 1 mm; **Sep** greenish or brownish to reddish, ovate to triangular-ovate, 4.2–5.8  $\times$  3–4 mm, sparsely to densely white-lepidote, margin hyaline, entire to erose, rounded to acute; **Pet** white to rose-coloured, ovate to oblong, 4.5–7  $\times$  3–4 mm, rounded to apiculate; **Ov** green, ellipsoid to oblong, 4.5–7.5  $\times$  3–3.5 mm, densely white-lepidote to light brown-floccose-lepidote; **Fr** light to dark brown, 6.5–10  $\times$  4–5 mm, densely white-lepidote to glabrescent; **Se** brown to reddish, 4.5–5 mm.

Smith & Downs (1974) cite a Karwinski specimen in the Munich herbarium as type, but this specimen was only prepared 1853 from cultivated descendants of the original collection, i.e. 13 years after the publication of the name. According to the nomenclatural rules, this material cannot be the type. Therefore, the detailed figure (plate 6) in the protologue of *H. glomerata* is **here designated as lectotype** of the name.

*H. glomerata* is a highly variable species with a wide distribution in Mexico and Guatemala. The populations show variation in some characters, particularly in the size of the plants and inflorescences, in the pubescence of the leaves, and in the form of the floral structures. *H. argentea* (accepted as separate species by Siekkinen (2015)), *H. ghiesbreghtii* and *H. lepidophylla* are here listed as synonyms since we consider them to represent only forms of this variation. More detailed studies at the level of populations are needed for a better understanding of the *H. glomerata* complex, however.

**H. guatemalensis** Mez (Repert. Spec. Nov. Regni Veg. 3: 14, 1906). **Type:** Guatemala,

Guatemala (*Pittier* 137 [US, B]). — **Distr:** Guatemala, Honduras, El Salvador, Nicaragua, Belize; tropical deciduous forest, thorn scrub and pine-oak forest, on the ground or on rocks, 200–1500 m.

Caespitose, flowering to 2 m tall; **Ros** 60–100 cm Ø; **L** numerous, sheaths light brown, widely ovate to suborbicular, 3.5–4 × 4.5–6 cm, glabrous, lustrous, margins weakly spinulose, **L** lamina 30–80 × 2–5.3 cm, lepidote to glabrous adaxially, densely white-lepidote abaxially, long caudate, **Sp** red-brown, antrorse, 3–4.5 mm, 0.7–1.7 cm apart; **Inf** glabrous; peduncle pale brown, cylindrical, 1–2 cm Ø, basally slender, glabrous; peduncular **Bra** light brown, linear to linear-triangular, margins spiny; **male Inf** 2 × branched, laxly flowered; primary **Bra** light brown, triangular, 1.7–3 cm × 4–7 mm, margins minutely spiny; primary **Br** slender, 23–30 cm; secondary **Bra** narrowly triangular, 5–7 mm; secondary **Br** 6–16 cm; floral **Bra** narrowly ovate, 1.3–1.5 mm long, scarious, acuminate, ±equalling the pedicels; **Fl** polystichous, reflexed; **Ped** slender, ±1.5 mm; **Sep** triangular, 2–2.2 × ±2 mm, obtuse; **Pet** white, elliptic, 4–4.5 × 2.4–2.7 mm, obtuse; **St** longer than the petals; **Fil** 4.6–4.9 mm; **Anth** green, 2.3–2.6 mm; **female Inf** generally 2 × branched, rarely 1 × or 3 × branched, laxly flowered; primary **Bra** light brown, triangular, 0.8–1.4 cm × 4–7 mm, entire; primary **Br** slender, 23–41 cm; secondary **Bra** narrowly triangular, 3–4 mm; secondary **Br** 7.5–15 cm; floral **Bra** triangular, ±1.5 mm, acuminate; **Fl** polystichous, reflexed; **Ped** ±1 mm; **Sep** white, triangular, 1.8–3 × 1.8–2 mm, acute; **Pet** white, elliptic, 3.5–3.7 × ±2 mm, acuminate; **Ov** almost wholly inferior, green, ellipsoid, 3–3.3 mm × 2.5–2.6 mm, glabrous; **Sty** ±1 mm; **Fr** light brown, 5–8 mm, glabrous, prominently and irregularly veined; **Se** red-brown.

**H. hernandez-sandovalii** I. Ramírez & al. (*Phytotaxa* 112(2): 34–38, ills., 2013). **Type:** Mexico, Tamaulipas (*Hernández & Martínez* 1797 [MEXU, QMEX, TEX-LL, UAT]). — **Distr:** Mexico (SW Tamaulipas: Miquihuana); *Agave-Hechtia* rosette-rich shrubland, on limestone hills or rocky exposed areas, 1550–2200 m.

Caespitose, flowering 1–1.8 m tall; **Ros** to 35 cm Ø; **L** 25–35, sheaths white-yellowish adaxially, brownish abaxially, sometimes with a darker brown area on the apical zone, transversely oblong, 2.5–3 × (2.6–) 3.7–4.8 cm, glabrous on both faces, finely dentate at the apex, **L** lamina green, 21–39 × 1.3–2.9 cm, acuminate, glabrous to sparsely white-lepidote adaxially, white-lepidote abaxially, **Sp** reddish, generally retrorse, 4–7 mm, (0.8–) 1.6–4.4 (–5.1) cm apart; **Inf** seemingly lateral; **male Inf** 1 × branched, sparsely white-lepidote but sometimes glabrous, with ±29 primary capitate **Br**; peduncular **Bra** brownish, triangular to triangular-ovate, 2.3–6.2 × 1–2.7 cm, acute and acuminate, sparsely lepidote, finely and laxly denticulate at the base, entire towards the apex; primary **Bra** brownish, triangular, 1–4 × 0.6–1.2 cm, acute, sparsely lepidote, entire; **Fl** densely clustered, covered by a thick brownish cotton-like indumentum, 6.5–7.5 × 3–3.2 mm, sessile; floral **Bra** brownish, long-ovate, 6.3–8.2 × 4–4.4 mm, acute, erose, densely white lepidote, longer than the petals; **Sep** connate for ½ their length, brownish, oblong, 4.4–5.3 × 2.3–2.5 mm, acute, erose, densely white-lepidote; **Pet** white, obovate, 5.5–6 × 2.8–3 mm, rounded, entire, densely white-lepidote; **St** adnate to the petals and pistillode base, barely longer than the petals; **Fil** 2.9–3.5 mm; **Anth** ±2.2 mm; **female Inf** 1 × branched, sparsely white-lepidote, with 11–13 capitate primary **Br**; peduncular **Bra** brownish, 1.7–6.3 × 0.7–2.6 cm, acute, sparsely lepidote, finely and laxly denticulate at the base, entire towards the apex; **Fl** densely clustered, covered with a thick, white, cotton-like indumentum, 7–7.5 × 4–4.6 mm, sessile; floral **Bra** brownish, transversely oblong to broadly elliptic, 8.7–9.4 × 5.8–6 mm, acute, margin erose, densely white-lepidote; **Sep** connate for ½ of their length, brownish, carinate, ovate, 6.2–6.5 × 4–4.2 mm, acute, margin erose, densely white-lepidote; **Pet** free, white, ovate to long ovate, 4–4.9 × 3.8–4.4 mm, acute, entire, densely white-lepidote; **Ov** white to greenish, ovoid, ±6 × 3 mm; **Fr** brown, 7.2–8 × 4–5.2 mm; **Se** brownish, 3.3–3.9 × ±1.4 mm.

**H. hintoniana** Burt-Utley & al. (*Phytoneuron* 2011(59): 2, 2011). **Type:** Mexico, México



(*Matuda & al.* 31124 [MEXU, CAS, MEXU, MO, NY, US]). — **Distr:** Mexico (México, Michoacán); tropical deciduous forest, 750–900 m.

Habit unknown, flowering to 2 m tall; **L** presumably numerous, sheaths narrow, 3.5–5.5 cm wide, marginally spiny and floccose, distally lepidote on both faces, **L** lamina straight to somewhat falcate,  $36.5\text{--}93 \times 0.6\text{--}2.2$  (–3.5) cm, lepidote on both faces, **Sp** red-brown to pale yellow, generally antrorse, 1.8–2.5 mm, 0.7–1.5 cm apart; **Inf** presumably terminal; peduncle 1.2–1.4 cm  $\varnothing$ , glabrous to glabrescent; upper peduncular **Bra** chartaceous, shorter than the internodes, rarely equal to or exceeding them, lanceolate-ovate with appressed linear-triangular lamina 1.5–3.9 cm long; **male Inf** lepidote, 2 $\times$  branched, with numerous primary **Br** 8–16 cm long and (2–) 3–6 secondary **Br**; primary **Bra** ascending to subascending, (4.5–) 7.8–22 cm; floral **Bra** shorter than to exceeding the pedicels, chartaceous, ovate-triangular to oblong or suborbicular,  $0.7\text{--}1.5 \times 0.4\text{--}1$  mm, externally lepidote, marginally finely serrulate to erose, spinulose or apiculate to praemorse; **Fl** divaricate to weakly ascending, subsessile to shortly pedicellate; **Ped** weakly articulated, stout, lepidote; **Sep** ovate-triangular to oblong,  $0.7\text{--}1.3 \times 0.7\text{--}1.3$  mm, margin entire to erose distally, lepidote to glabrous, apically praemorse; **Pet** oblong-elliptic to ovate-elliptic,  $2\text{--}3 \times 1.4\text{--}2$  mm, entire, glabrous, apically denticulate to praemorse; **St** equal, **Fil** basally briefly adnate to the petals; **female Inf** 1 $\times$  branched (or if 2 $\times$  branched then with 1–2 short secondary branches); primary **Br** ascending to subascending, (6.5–) 15–31 cm, lepidote, densely many-flowered throughout or flowers disposed in verticills; floral **Bra** shorter than to exceeding the pedicels, chartaceous, narrowly ovate-triangular,  $1.3\text{--}2.2 \times 0.8\text{--}1.5$  mm, lepidote, entire to serrulate or erose, attenuate-acuminate to praemorse; **Fl** divaricate to ascending; **Ped** articulated, stout, 0.8–1.5 mm, lepidote; **Sep** triangular to ovate-triangular,  $1.7\text{--}2.1 \times 1\text{--}1.8$  mm, glabrous to weakly lepidote, entire and hyaline at the margins, rounded to acute or praemorse; **Pet** narrowly ovate-triangular,  $3.1\text{--}4 \times 1.2\text{--}1.9$  mm, glabrous, rounded; **Ov** glabrous; **Fr**  $8\text{--}10 \times 3\text{--}4.5$  (–5.5) mm, glabrous, shiny and somewhat ridged, reticulate.

**H. huamelulaensis** I. Ramírez & Carnevali (Phytotaxa 178(2): 119–121, ills., 2014). **Type:** Mexico, Oaxaca (*Ramírez & Carnevali* 1675c [CICY]). — **Distr:** Mexico (Oaxaca); xerophytic vegetation,  $\pm 60$  m.

Caespitose in small groups, flowering to 1.5 m tall; **Ros** 50–60 cm  $\varnothing$ ; **L** 30–40, sheaths yellowish-green, transversely oblong,  $7\text{--}8 \times 10\text{--}12$  cm, glabrous on both faces, **L** lamina dull green, narrowly triangular,  $30\text{--}35 \times 6\text{--}8$  cm, glabrous adaxially, white-lepidote abaxially, long-acuminate, **Sp** red, antrorse, 3–5 mm, 1–1.5 cm apart; **male Inf** 1 $\times$  branched with 45–55 branches; peduncular **Bra** foliaceous, sheaths triangular,  $2\text{--}3 \times 4\text{--}7$  mm, lamina narrowly triangular,  $2\text{--}10 \times 0.5\text{--}0.8$  cm, margins entire to finely serrate, sparsely white-lepidote at the apex; **Br** divaricate, 2.5–13.5 cm; floral **Bra** broadly ovate,  $2.3\text{--}2.6 \times 2$  mm, margins erose, acuminate, glabrous; **Fl** polystichous; **Ped**  $\pm 1$  mm; **Sep** ovate to triangular-ovate,  $2.5\text{--}3.5 \times 1.3\text{--}2$  mm, acute; **Pet** elliptic,  $4.5\text{--}6 \times 2.5\text{--}3$  mm, rounded; **St** subequal; **Fil** 4–4.7 mm; **Anth** 1.6–2 mm; **female Inf** 1 $\times$  branched with 45–100 branches; peduncular **Bra** foliaceous, sheaths broadly triangular,  $3\text{--}5 \times 5\text{--}9$  mm, lamina narrowly triangular,  $2\text{--}12 \times 0.7\text{--}1$  cm, margins finely serrate, sparsely white-lepidote; **Br** divaricate, 1.5–13 cm; floral **Bra** basally green, apically brown, oblong to triangular,  $2.4\text{--}4.7 \times 1.5\text{--}3$  mm, margins erose, acuminate, glabrous; **Fl** polystichous; **Ped** 1.5–3 mm; **Sep** purple, triangular,  $1.3\text{--}2.6 \times 2\text{--}2.5$  mm, margins entire to erose, acute; **Pet** white with a red stripe, ovate,  $4\text{--}5.2 \times 2\text{--}2.7$  mm, acute; **Ov** light green, purple at the apex, ovoid, 3.2–3.5 mm; **Fr** narrowly ellipsoid, 9–12.5 mm; **Se** 6–8.5 mm.

**H. iltisii** Burt-Utley & Utley (Brittonia 45: 222–225, fig. 2, 1993). **Type:** Mexico, Jalisco (*Burt-Utley & Utley* 7703 [MEXU, DUKE, MICH, MO, NY, US, WIS]). — **Distr:** Mexico (Jalisco: La Huerta); thorn-scrub vegetation, on rock outcrops, 250–300 m.

Caespitose, flowering 0.93–2.1 m tall; **Ros** to 70 cm  $\varnothing$ ; **L** numerous, straight to occasionally falcate, sheaths stramineous, transversely elliptic to reniform,  $3.5\text{--}5.6 \times 5.5\text{--}9.5$  cm, glabrous becoming lepidote distally on both faces,

somewhat inflated in older leaves, spinulose, **L** lamina 42.5–62.5 cm, glabrous adaxially, lepidote abaxially, **Sp** antrorse, occasionally retrorse, 1.5–4.5 mm, 0.5–3 cm apart; **male Inf** 1× branched; primary **Br** subascending; floral **Bra** pink, broadly ovate, 5–8 × 4–6.5 mm, acuminate, lepidote, finely spinulose-serrate, longer than the pedicels; **Fl** pedicellate or occasionally sessile; **Ped** stout, 0.5–3 mm, lepidote; **Sep** pink but drying dark maroon, ovate to ovate-triangular, 4.5–8 × 3.5–4.7 mm, lepidote, rounded to acute; **Pet** green, ovate, 5.5–9 × 3–4.5 mm, glabrous abaxially, somewhat cucullate apically; **St** shorter than the petals; **female Inf** 1× or very rarely 2× branched; primary **Br** subascending; floral **Bra** pink but drying maroon, ovate to broadly ovate, 5–11 × 3–6.5 mm, attenuate-acuminate, lepidote, finely spinulose-serrate to erose, shorter or longer than the pedicels; **Fl** pedicellate; **Ped** stout, triquetrous, 2–6 mm, lepidote; **Sep** pink, triangular, 5–7 × 2.8–3.8 mm, lepidote, attenuate-acuminate, very finely erose to serrulate distally; **Pet** green, triangular, 7–10 × 2.5–4 mm, glabrous abaxially; **Fr** olive-brown, (10–) 15–21 × 6–9 (–11) mm, glabrous, smooth.

In the protologue the presence of abnormal branches and flowers that occasionally had four sepals and petals, as well as ovaries with four locules have been mentioned. Staminate flowers on normal inflorescences occasionally had five sepals and petals and up to 10 stamens. Similar variations in the number of sepals and petals were observed in other species such as *H. glomerata*, *H. montana* (described for the synonymous *H. gayorum*) or *H. tillandsioides*.

**H. isthmusiana** Burt-Utley (Phytoneuron 2012(69): 10–13, ills., 2012). **Type:** Mexico, Oaxaca (*Utley & Utley* 8491 [MEXU, CAS, GH, MO, NY, US, USF, XAL]). — **Distr:** Mexico (SE Oaxaca: Ciudad Ixtepec, Asunción Ixtaltepec, Tehuantepec); thorn scrub and tropical deciduous forests, on the ground or on rocks on low rocky hillsides and slopes, 0–300 m. **I:** Ramírez Morillo & al. (2014b).

Caespitose, caulescent, flowering 0.6–1 m tall; **Ros** 25–50 cm Ø; **L** several to many, sheaths pale

to dark castaneous, 2–4 × (2.8–) 4–8 cm, glabrous and lustrous on both faces, becoming lepidote distally, margins finely spinulose and floccose, **L** lamina bright green to pale dusty rose, straight to subfalcate, 12–32 × 1.5–3 cm, appressedly cinereous-lepidote on both faces, **Sp** generally antrorse, (0.5–) 1.8–2.5 mm, (0.6–) 0.8–1.8 cm apart; **Inf** glabrous, typically 1× branched; **male Inf** with ±14 ascending primary **Br** (1.8–) 2.5–7.5 cm long; floral **Bra** chartaceous, ovate to oblong, 2–3.5 (–5) × 1–2.5 (–3) mm, glabrous, attenuate-acuminate to apiculate, margin finely denticulate to serrulate or erose distally; **Fl** divaricate to ascending; **Ped** articulated, conical, 1.2–3.5 mm; **Sep** white to cream, ovate to ovate-triangular, 1.5–2.7 × 1–1.8 mm, apically praemorse, margin hyaline; **Pet** white to cream but often tipped rose, elliptic to ovate-elliptic, 3.5–4.5 × 1.9–3.3 mm, glabrous; **female Inf** with ±19 ascending primary **Br** (0.1–) 1.5–3.5 (–4.5) cm long; floral **Bra** chartaceous, ovate-triangular to oblong, 2–3.5 × 1.2–2 mm, apiculate to acuminate, margin erose to very finely serrulate, hyaline; **Fl** divaricate; **Ped** articulated, 1.5–2.5 mm; **Sep** white or greenish to cream, triangular, 1.8–2.5 × 1.2–1.5 mm, glabrous, acuminate to apiculate, praemorse; **Pet** white or greenish to cream but often tipped rose, triangular, 4–5 × 1.5–2.5 mm, glabrous, margin hyaline; **Fr** dark castaneous, (6–) 7.5–11 × 3–4.5 mm Ø.

**H. ixtlanensis** Burt-Utley (Phytoneuron 2012 (69): 1–5, ills., 2012). **Type:** Mexico, Oaxaca (*Utley & Utley* 7961 [MEXU, B, C, CAS, GH, M, MICH, MO, NY, US, USF, XAL]). — **Distr:** Mexico (Oaxaca); pine-oak forest, on moist steep slopes, 1650–1900 m.

Forming clumps, flowering 1.5–2.7 m tall; **Ros** to 80 cm Ø; **L** very numerous, sheaths stramineous but oldest bases brown to castaneous distally, semiorbicular to transversely elliptic, 5–8.5 × 8–12 cm, margin finely spiny and distally floccose, glabrous and lustrous on both faces, becoming densely lepidote distally, **L** lamina straight to subfalcate, 32–56 × 2–3.5 (–4.5) cm, appressedly cinereous-lepidote but occasionally glabrescent on both faces, **Sp** red-brown, antrorse

to retrorse, (1.5–) 3–6 (–8) mm, 1.5–4.5 cm apart; **Inf** lepidote; peduncular bracts foliaceous, pungent, becoming progressively reduced distally; **male Inf** 2× branched or rarely 1×, with numerous divaricate primary **Br** 8–25 cm long, and with (0–) 5–9 (–11) divaricate to ascending secondary **Br** 0.5–9.5 cm long; floral **Bra** ovate-triangular to broadly ovate, 1.2–3 × 0.8–1.8 mm, lepidote, finely spinulose-serrulate; **Fl** very numerous, divaricate; **Ped** articulated, conical, stout, 0.7–1.8 mm, glabrous to sparingly lepidote; **Sep** ovate-triangular to triangular, 1–1.6 × 0.8–1.8 mm, glabrous to sparingly lepidote, apiculate, entire to erose or very finely serrulate; **Pet** cream, ovate to elliptic, (2–) 2.5–3.2 × 1.5–2 mm, glabrous, rounded to praemorse; **female Inf** 1× or rarely 2× branched, with up to 50 primary **Br** 6–22 cm long, and with 0–2 secondary **Br** 3–6 cm long; floral **Bra** ovate-triangular, 1.3–2.5 × 1–1.6 mm, glabrous to sparingly lepidote, proximally irregularly and finely serrulate-spinulose, apiculate; **Fl** very numerous, sometimes verticillate, ascending; **Ped** stout, 0.5–1.5 mm, glabrous to lepidote; **Sep** ovate-triangular, 1–1.5 × 0.7–1.5 mm, glabrous to lepidote, apiculate, erose distally; **Pet** greenish-yellow, triangular, (1.5–) 2–3 × 1–1.5 mm, glabrous, rounded to acute; **Fr** greenish-brown, 6.5–8 × 2.8–4 mm, smooth but sparingly finely ridged, glossy.

**H. jaliscana** L. B. Smith (Phytologia 10: 482, t. 1, fig. 10, 1964). **Type:** Mexico, Jalisco (*McVaugh* 18530 [MICH]). — **Distr:** Mexico (Jalisco: Amatitán, San Cristóbal de la Barranca, Zapopan); steep moist ravines with tropical deciduous forest, on rocks, 750–1300 m.

Caespitose, flowering to 1.8 m tall; **L** numerous, sheaths elliptic, 5–6 cm, glabrous basally, serrate distally, **L** lamina 50–80 × 2.7–3 cm, glabrous adaxially, finely appressedly cinereous-lepidote abaxially, margin undulate, **Sp** divaricate to antrorse, ±3 mm, 1.7–3 cm apart; **Inf** 1× branched, sparsely pale-lepidote, becoming glabrous; **male Inf** with 10–15 primary **Br**; basal peduncular **Bra** linear, to 15 cm, margins spiny; floral **Bra** ovate, 6–9 mm, acuminate, erose; **Fl** ascending to divaricate, sessile to shortly

pedicellate; **Ped** 2.5 mm; **Sep** whitish, ovate-deltoid, 4–5 × ±4 mm, glabrous, acute; **Pet** white, oblong-elliptic, 6–7 × 3.5–4 mm, acute to rounded; **St** equalling the petals; **Fil** 5.5–6 mm; **Anth** yellow, 1.5–2 mm; **female Inf** with ±20 primary **Br** 7–20 cm long; primary **Bra** lanceolate, caudate-acuminate, 2–4 cm, serrate; floral **Bra** green towards the base and brown towards the apex, lanceolate-ovate, ±9 mm, acuminate, minutely denticulate, about equalling the sepals; **Fl** divaricate, laxly and subverticillately disposed; **Ped** stout, cylindrical, ±4 mm, subulate, articulate; **Sep** brown with prominent scarious margin, ovate, 3.5–4 mm, attenuate, irregularly erose, acute or obtuse; **Pet** white, triangular-ovate, 3.5–4 × ±3 mm, attenuate, acute; **Fr** brown, 8–11 × 4–5 mm, sparsely lepidote, glabrescent and lustrous when mature.

**H. laevis** L. B. Smith (Phytologia 10: 482–483, t. 1, figs. 11–12, 1964). **Type:** Mexico, Colima (*McVaugh* 15528 [MICH, MICH, US]). — **Distr:** Mexico (Colima); open rocky slopes with tropical deciduous forests, also reported from chalky soils, on the ground or on rocks, 400–1000 m. **I:** Ramírez-Morillo & al. (2016: 263).

Caespitose, flowering 1–2 m tall; **L** numerous, densely rosulate, sheaths stramineous to light brown, transversally oblong to oblong, 4–4.5 × 4–7 cm, glabrous, barely lepidote distally, lustrous, margins serrate, **L** lamina rigid, 20–60 × 2.5–3 cm, pale appressed-lepidote on both faces, becoming glabrous adaxially, **Sp** reddish, antrorse, 2.5–5.5 mm, 1.4–2 cm apart; **Inf** 1× branched, sparsely white-lepidote when young, glabrescent with age; peduncle straight, 4–10 mm Ø; peduncular **Bra** erect, entire or laxly spiny, the lower linear from a small triangular base, the upper narrowly triangular; **male Inf** with 30–45 divaricate to ascending primary **Br** 3–25 cm long; floral **Bra** minute, narrowly triangular, densely white-lepidote; **Fl** divaricate, laxly disposed; **Ped** filiform, 1.5–3 mm, white-lepidote; **Sep** white with the median nerve purple, oblong-ovate, 1–1.3 × ±1 mm, erose, densely white-lepidote; **Pet** white to yellowish, widely ovate to suborbicular, 2–2.4 × ±2 mm, obtuse; **St** subequal,

shorter to as long as the petals; **Fil**  $\pm 1.4$  mm; **Anth**  $\pm 1$  mm; **female Inf** with 20–40 divaricate to ascending primary **Br** 5.5–20 cm long; floral **Bra** minute,  $\pm 2 \times 0.3$ –0.5 mm, shorter than the pedicels; **Fl** divaricate, laxly disposed; **Ped** slenderly cylindrical, 2.5–3.5 mm, white-lepidote, smooth; **Sep** purplish, triangular,  $2.2$ – $2.4 \times 1.2$ – $1.5$  mm, sparsely white-lepidote, acute; **Pet** white with the median nerve purplish, narrowly triangular,  $3.5$ – $4.4 \times 1.8$ – $2$  mm, acuminate; **Ov** purple, ellipsoid,  $\pm 3.4 \times \pm 2.2$  mm; **Fr** brown,  $\pm 8$  mm, deeply sulcate between the carpels, smooth, covered at first with appressed white scales; **Se** brown, 5–6 mm.

Material from Jalisco identified as this species was recently described as *H. santanae*.

**H. lanata** L. B. Smith (Phytologia 8: 5, t. 1, figs. 6–9, 1961). **Type** [neo]: Mexico, Oaxaca (*Ceja & al.* 1928 [UAMIZ, IEB]). — **Lit**: Espejo-Serna & al. (2012). **Distr**: Mexico (Oaxaca: Santiago Lachiguiri), thorn scrub and tropical deciduous forest, rocky slopes and cliffs, on rocks, 750–1300 m. **I**: Kemble (2016). — Fig. 3.

Solitary, caulescent, flowering to 1.2 m tall; **Ros** 30–40 cm  $\varnothing$ , forming long rhizomes to 30 cm and  $\pm 4$  cm  $\varnothing$ ; **L** numerous, reflexed in the apical part, sometimes the tips strongly curled,

sheaths stramineous to castaneous, suborbicular to broadly ovate,  $4$ – $6 \times 4$ – $8.5$  cm, margins finely spinulose, floccose at the apex, glabrous and lustrous on both faces becoming densely lepidote distally, **L** lamina green, occasionally pink-tinged,  $12$ – $110 \times 3$ – $8$  cm, very densely white-lepidote on both faces, most conspicuous on the lower  $\frac{1}{3}$ , glabrescent adaxially in the apical part, **Sp** green to dark brown, antrorse and retrorse, or rarely divaricate, 3–8 mm, 4–7.5 cm apart; **Inf** densely lepidote, glabrescent with age; peduncle cylindrical, 4–10 mm  $\varnothing$ ; peduncular **Bra** rose-greenish, linear to narrowly triangular, from a deltoid base, 3–18 cm, becoming progressively reduced distally and exceeding the internodes; **male Inf**  $1 \times$  or rarely  $2 \times$  branched, with 35–50 divaricate to ascending primary **Br** 2.5–17 cm long; floral **Bra** shorter than to equalling the sepals, ovate to triangular,  $2$ – $2.3 \times 0.3$ – $0.8$  mm, finely spinulose-serrulate, attenuate-acuminate, lepidote, acute; **Fl** divaricate, sometimes appearing verticillate; **Ped** articulated, stout, conical, 0.5–2 mm, lepidote; **Sep** green to light brown apically, triangular,  $1.5$ – $2 \times 1$ – $1.6$  mm, apiculate, occasionally finely serrulate-spinulose or erose esp. distally, lepidote, acute; **Pet** white, elliptic,  $3$ – $4.5 \times 2$ – $2.5$  mm, entire, rounded to acute, apiculate, glabrous; **St** longer than the petals; **Fil**  $\pm 4.5$  mm; **Anth** yellow,

**Fig. 3** *Hechtia lanata* (near Santiago Lachiguiri). (Copyright: A. Espejo-Serna)



$\pm 1$  mm; **female Inf**  $1\times$  or infrequently  $2\times$  branched, with up to 34 divaricate to ascending primary **Br** (1.5–) 4–9 cm long; floral **Bra** narrowly triangular,  $1-1.5 \times 0.4-0.7$  mm, apiculate, entire to finely serrulate-spinulose, lepidote to occasionally glabrous; **Fl** divaricate, laxly disposed, sometimes appearing verticillate; **Ped** articulated, stout, conical, 1.5–2.5 mm, lepidote to occasionally glabrous; **Sep** green, apically brown, triangular,  $2-2.5 \times 2-2.3$  mm, entire to irregularly finely serrulate, lepidote to occasionally glabrous, acute; **Pet** white, with a broad green central line, ovate,  $3.1-3.5 \times 3.1$  mm, entire, apiculate to acute, glabrous; **Ov** green, ovoid,  $4.5-5 \times 1-2$  mm; **Fr** dark brown, drying olive-green,  $8-10 \times 3-4$  mm, lustrous, glabrous to finely lepidote; **Se** reddish-brown,  $2.8-3$  mm  $\times \pm 0.5$  mm.

**H. laxissima** L. B. Smith (Contr. US Nation. Herb. 29: 521–522, fig. 77, 1954). **Type:** Mexico, Michoacán (Moore & al. 5770 [US]). — **Distr:** Mexico (Michoacán: Múgica, Gabriel Zamora); on cliffs,  $\pm 400$  m.

Caespitose, flowering  $> 1.7$  m tall; **L** numerous, sheaths not described, **L** lamina  $\pm 40 \times \pm 4$  cm, glabrous adaxially, finely veined and covered with pale appressed scales abaxially, **Sp** pale brown,  $\pm 4$  mm; **Inf** seemingly lateral, glabrous; peduncle flattened at the base,  $\pm 1$  cm  $\varnothing$ ; peduncular **Bra** stramineous, triangular, acuminate, thin; **male Inf** unknown; **female Inf**  $1\times$  branched, with  $\pm 15$  divaricate or ascending, very slender primary **Br**  $\pm 20$  cm long; floral **Bra** greenish-rose, ovate, acute, mostly about  $\frac{1}{2}$  as long as the pedicels; **Fl** divaricate, very laxly disposed; **Ped** slenderly cylindrical, 2–4 mm; **Sep** dark rose with a greenish tinge, very broadly ovate,  $\pm 3$  mm, acute; **Pet** green with rose tips, ovate,  $\pm 5$  mm, acute; **Ov** glabrous; **Fr** unknown.

**H. liebmannii** Mez (Bot. Jahrb. Syst. 30 (Beiblatt 67): 6, 1901). **Type:** Mexico, Puebla (Liebmann s.n. [C, B]). — **Distr:** Mexico (Puebla, Veracruz); thorn scrub on lava flows, on the ground or on volcanic rocks, 2400–2500 m.

**Incl.** *Hechtia perotensis* I. Ramírez & Martínez-Correa (2007).

Caespitose to densely caespitose, flowering 0.55–2 m tall; **Ros** compact, globose, to  $50 \times 40$  cm, sometimes slightly asymmetrical; **L** numerous, sheaths yellow to brownish, lustrous, widely ovate to subquadrate,  $3.5-5.5 \times 3.5-8.5$  cm, white-lepidote apically, **L** lamina light green,  $15.7-30.5 \times 1-1.8$  cm, glabrescent adaxially, minutely white-lepidote abaxially, **Sp** brown to dark brown, antrorse to divaricate, 5–6 mm, 1.5–2 cm apart; **Inf**  $2-3\times$  branched; peduncle cylindrical, 1–3 cm  $\varnothing$ ; peduncular **Bra** brown, triangular to narrowly triangular,  $3-20 \times 1-3.5$  cm, acute to acuminate, densely imbricate, sheaths entire, lamina erose to spiny, densely lepidote at the base abaxially, glabrescent adaxially; **male Inf** with numerous, ascending, glomerate to shortly elongate primary **Br** 2–3.5 cm long with 2 basal shorter secondary **Br**; primary **Bra** brown, ovate to narrowly ovate,  $2.5-7 \times 0.8-1$  cm, lepidote abaxially, erose, acuminate; floral **Bra** green, lanceolate to oblong,  $\pm 4$  mm; **Fl** divaricate, laxly disposed; **Ped** 2–3 mm; **Sep** green, ovate to narrowly ovate,  $4.5-5 \times 2-2.5$  mm, acute to rounded; **Pet** green to yellowish, elliptic to oblong,  $6-7 \times 3-4$  mm, rounded; **St** as long as or shorter than the petals; **Fil**  $\pm 5$  mm; **Anth** yellow, curved, 1.2–1.5 mm; **female Inf** with numerous ascending glomerate to elongate primary **Br** 1.5–8 cm long; primary **Bra** widely triangular,  $2-2.5 \times 1-1.3$  cm, acuminate to acute; floral **Bra** yellowish, triangular, 3–5 mm; **Fl** densely disposed, ascending; **Ped** obconical, 2–4 mm; **Sep** brownish, widely triangular,  $4-5 \times 2.4-2.7$  mm, acute and apiculate; **Pet** green, triangular,  $\pm 6 \times \pm 3$  mm, acute; **Ov** green, ovoid; **Fr** brown,  $9-10 \times 3.5-7$  mm, lustrous; **Se** light brown, 2.9–3.5 mm.

**H. lundelliorum** L. B. Smith (in N. L. Britton & al. (eds.), North Amer. Fl. 19: 97–98, 1938). **Type:** Mexico, San Luis Potosí (Lundell & Lundell 7265 [MICH]). — **Lit:** López-Ferrari & al. (2011). **Distr:** Mexico (San Luis Potosí, Querétaro, Hidalgo, Puebla); tropical deciduous and semideciduous forest, limestone ledges and cliffs, on rocks, 150–1250 m.

Forming large pendulous colonies, flowering 0.8–1.8 m tall; **Ros** asymmetrical in mature plants, 30–120 cm long; **L** numerous, very long and



pendent, sheaths white to yellowish, broadly oblong to oblong, 5–6 × 3–5 cm, minutely serrate esp. towards the apical portion, white-lepidote on both faces, **L** lamina light green adaxially, densely white-lepidote abaxially, long-attenuate, 60–110 × 1–2 cm, margins minutely serrate; **Inf** erect to arched and/or pendulous, 3 × branched; peduncle brown, cylindrical, 0.8–2 cm Ø, glabrous; peduncular **Bra** brown to light brown or green, foliaceous, linear to long triangular, 5–70 × ±1 cm, entire to minutely denticulate, densely lepidote abaxially, glabrous to glabrescent adaxially, attenuate; **male Inf** with numerous ascending stalked primary **Br** 25–40 cm long; primary **Bra** light brown, linear to triangular, 2–25 cm × 4–6 mm, long-attenuate to acuminate; secondary **Br** numerous, ascending to appressed, 6–13 cm long, stalked; secondary **Bra** triangular, ±2 × ±1 mm, deciduous; tertiary **Br** numerous; **Fl** numerous on each branch, polystichous; **Ped** filiform, 1.5–2.5 mm; floral **Bra** light brown, triangular, ±2 × ±2.5 mm, rounded; **Sep** brown to light brown suffused with white, slightly rose towards the margins, ovate to triangular, ±1.2 × ±1.4 mm, glabrous, entire, rounded; **Pet** white, elliptic, 3.5–4.2 × 2.1–2.4 mm, rounded; **St** subequal, shorter than the petals; **Fil** 2–3 mm; **Anth** yellow, ±1.4 mm; **female Inf** with numerous ascending stalked primary **Br** 25–35 cm long; primary **Bra** brown to light brown, linear to triangular, 3–12 cm × 4.5–5 mm, acuminate; secondary **Br** numerous, ascending to appressed, 14–17 cm long; secondary **Bra** triangular, ±2 × ±1 mm, deciduous; tertiary **Br** numerous; **Fl** numerous on each branch, polystichous; **Ped** 1.4–1.7 mm; floral **Bra** light brown, hyaline, ovate to triangular, ±1 × ±1 mm, rounded; **Sep** light brown suffused with white, ovate to triangular, ±1.5 × ±1 mm, acute; **Pet** white, oblong-elliptic, ±3.5 × ±1.7 mm, rounded; **Ov** green, ovoid, ±3 × ±2 mm, glabrous; **Fr** brown to dark brown, slightly trigonous, 5–7 × 2–3 mm, glabrous, reflexed; **Se** brown to reddish-brown, ±1.3 mm.

**H. lyman-smithii** Burt-Utley & Utley (Brittonia 39(1): 37–40, ills., 1987). **Type:** Mexico, Oaxaca (Burt-Utley & Utley 6982 [MEXU, MO, NY, US]). — **Distr:** Mexico (Puebla:

Caltepec; Oaxaca: San Antonio Nanahuatipan, Santa María Ixcatlán, Santa María Tecomavaca); thorn scrub and tropical deciduous forest, steep limestone slopes and cliffs, on rocks, 600–1150 m. — Fig. 4.

Densely caespitose, flowering to 80 cm tall; **Ros** 20–27 cm Ø; **L** few, sheaths reniform, 1.8–2.8 × 3.5–4.5 cm, margins inconspicuously spiny, glabrous and lustrous, becoming lepidote distally, **L** lamina light green, often suffused with purple, 7–17 × 1.7–3 cm, appressedly cinereous-lepidote on both faces, **Sp** antrorse or occasionally retrorse, red-brown, 2.5–4 mm, 0.6–1.1 cm apart; **Inf** 1 × branched, glabrous; peduncle 3–5.5 mm Ø; lower peduncular **Bra** exceeding the internodes, ovate with linear, erose, appressed, lepidote lamina, 1.8–5.7 cm; **male Inf** with 15–40 slender divaricate to ascending primary **Br** (0.5–) 2.2–14 cm long; floral **Bra** as long as or slightly exceeding the pedicels, ovate, 0.8–2 × 0.7–1 mm, lacerate to erose, acute to apiculate; **Fl** divaricate; **Ped** slender, 0.8–3 mm; **Sep** white, tinged with rose, ovate to broadly ovate, 1.3–2.3 × 0.9–1.8 mm, glabrous, margin hyaline and distally erose, rounded to acute; **Pet** white to rose, ovate to oblong-ovate, 3–5 × 2–3.1 mm, **St** longer than the petals; **Fil** 4–4.5 mm; **Anth** yellow-green to green, ±2 mm, mucronate; **female Inf** with 12–40 slender divaricate primary **Br** 2–8.5 cm long; floral **Bra** shorter than the pedicels, narrowly ovate to ovate-triangular, 1–2 × 0.7–0.8 mm, margin hyaline, erose, acuminate; **Fl** divaricate to ascending; **Ped** stout, 1.5–3.5 mm; **Sep** light brown, ovate, 1.3–1.9 × 1.3–2.2 mm, glabrous, margin hyaline, acuminate, acute; **Pet** rose, triangular, 3–4 × 2–2.5 mm; **Ov** purple, ovoid, ±3.5 mm; **Fr** purple, drying light brown, triquetrous, 5.5–10 × 5–6 mm, glabrous, smooth; **Se** yellowish-brown, 3.5–4 mm.

**H. malvernii** Gilmartin (Ceiba 11(2): 9, fig. 4, 1965). **Type:** Honduras, El Paraíso (Gilmartin 966 [US, US]). — **Distr:** Honduras (El Paraíso); hillsides and bank of road cuts, ±700 m; known only from the type collection.

Growth habit not described, flowering to 2 m tall; **L** numerous, **L** lamina ±50 × 3.5–4.5 cm, pale appressed-lepidote, becoming glabrous

**Fig. 4** *Hechtia lyman-smithii*. (Copyright: A. Espejo-Serna)



adaxially, glabrescent abaxially, margin undulate, **Sp** divaricate to antrorse, 3 mm, 0.9–1.1 cm apart; **Inf** glabrous, 1× branched; peduncular **Bra** to 16 cm, reflexed, lepidote abaxially, nearly glabrous adaxially; **male Inf** unknown; **female Inf** with  $\pm 8$  reflexed weak primary **Br** to 55 cm long; floral **Bra** narrowly ovate, 5–10  $\times$   $\pm 2$  mm, glabrous, acuminate; **Fl** divaricate to reflexed, laxly disposed, subsessile; **Sep** reddish, ovate,  $\pm 3 \times \pm 1.5$  mm, glabrous, mucronate; **Pet** whitish,  $\pm 5 \times \pm 1$  mm; **Ov** inferior, ellipsoid; **Fr**  $\pm 10$  mm, glabrous.

**H. mapimiana** López-Ferrari & Espejo (Acta Bot. Mex. 102: 90–92, ills. (pp. 91, 93–95), 2013). **Type:** Mexico, Durango (*Mercado & al.* 259 [CIIDIR, IEB, UAMIZ]). — **Distr:** Mexico (Durango: Lerdo); thorn scrub, limestone cliffs, on rocks, 1400–1750 m. – Fig. 5.

Caespitose in small groups, flowering to 2.3 m tall; **Ros** 40–70 cm  $\varnothing$ ; **L** numerous, sheaths light brown adaxially, dark brown abaxially, broadly ovate to subquadrate, 6–15  $\times$  5.5–10 cm, lustrous, glabrous on both faces, **L** lamina glaucous, cylindrical-conical and slightly curved upwards at the apex, 30–45  $\times$  2.5–4 cm, densely white-lepidote on both faces, **Sp** light brown, reddish at the apex, retrorse, 3–6 mm, 2–5 cm apart; **male**

**Inf** 2–3× branched, with numerous **Br** per node, apparently fasciculate by the reduction of the rachis; peduncular **Bra** foliaceous, sheaths ovate-triangular, papery, brittle, 4.5–5.5  $\times$  2.6–3.2 cm, entire, very sparsely white-lepidote to glabrous, lamina narrowly triangular, 8–10  $\times$  5–7 mm, densely white-lepidote on both faces, pungent, margins spiny; primary **Br** oblong-cylindrical, 5.4–6.8 cm, with 2 secondary basal branches 2.8–4.5 cm long; floral **Bra** white, filiform, 3–5 mm, shorter than the pedicels, entire, glabrous; **Fl** polystichous, ascending; **Ped** filiform, 5.5–11 mm; **Sep** white tinged with pink to purple, triangular, 3.6–4  $\times$  1.5–1.7 mm, acute; **Pet** light green, elliptic, 6.5–7.5  $\times$  4–4.2 mm, rounded; **St** subequal; **Fil** 3.2–3.5 mm; **Anth** green, 4.2–4.5 mm; **female Inf** 2× branched, with numerous **Br** grouped apparently in fascicles by the reduction of the rachis; peduncular **Bra** foliaceous, sheaths ovate-triangular, 5–6  $\times$  2.8–3 cm, papery, brittle, entire, very sparsely white-lepidote to glabrous, lamina 7–16.5  $\times$  0.5–0.7 cm wide, pungent, densely white-lepidote on both faces, margins spiny; primary **Br** oblong-cylindrical, 6–9 cm, with 2 solitary flowers at the base; floral **Bra** white, filiform, 3–5 mm, entire, glabrous, shorter than the pedicels; **Ped** filiform, 7–8 mm; **Fl** polystichous, ascending; **Sep** white tinged with pink to

**Fig. 5** *Hechtia mapimiana*. (Copyright: A. Espejo-Serna)



purple, triangular,  $\pm 3.5 \times 2.5$  mm, acute; **Pet** light green, ovate-triangular,  $5\text{--}5.2 \times 2.5\text{--}2.7$  mm, acute; **Ov** green, ovoid; **Fr** light brown, triquetrous,  $\pm 10 \times 8\text{--}9$  mm, with thin papery walls when mature.

**H. marnier-lapostollei** L. B. Smith (Bromeliad Soc. Bull. 11: 58, ills., 1961). **Type:** Mexico, Oaxaca (*Schwartz* s.n. in *Marnier-Lapostolle* s.n. [US]). — **Distr:** Mexico (Oaxaca: San Carlos Yautepec, San Juan Lajarcia); thorn scrub and tropical deciduous forest, on the ground or on limestone rocks, 750–1500 m.

Caespitose, flowering to 1 m tall; **L** 15–20, sheaths yellowish, suborbicular,  $\pm 2$  cm  $\varnothing$ , glabrous and lustrous, densely lepidote distally, **L** lamina  $15\text{--}28 \times \pm 2$  cm, pungent, densely and closely pale-lepidote on both faces, **Sp** antrorse, slender, 2.5–4 mm, 0.12–1.3 cm apart; **Inf** 1  $\times$  branched, glabrous; peduncle 2–4 mm  $\varnothing$ ; peduncular **Bra** exceeding the internodes, stramineous, broadly ovate with a long linear lamina, 1–4 cm, pungent; **male Inf** with 8–24 ascending primary **Br** 1.5–5.5 cm long; floral **Bra** stramineous, broadly ovate,  $\pm 2$  mm, erose apically, acuminate, longer than the pedicel; **Fl** divaricate; **Ped**  $\pm 1$  mm; **Sep** white-purpureous, triangular-ovate,  $\pm 2$  mm; **Pet** white tinged with purple, elliptic,

3–4 mm, rounded; **St** as long as the petals; **Fil**  $\pm 3.5$  mm; **Anth** green,  $\pm 1.5$  mm, mucronate; **female Inf** with  $\pm 22$  divaricate to ascending primary **Br** 2–5 cm long; floral **Bra** broadly ovate, erose, 2–2.5 mm; **Fl** divaricate; **Ped**  $\pm 2$  mm; **Sep** ovate-triangular,  $\pm 2$  mm, acute; **Pet** triangular to narrowly triangular, with a large callus at the base,  $\pm 3.8$  mm; **Ov** ovoid, trigonous, glabrous; **Fr** dark brown, 5.5–9 mm, shiny.

**H. matudae** L. B. Smith (Phytologia 5: 395–396, t. 1, figs. 1–2, 1956). **Type:** Mexico, Morelos (*Matuda* 26351 [US]). — **Lit:** López-Ferrari & al. (2008: with ills.). **Distr:** Mexico (México: Ocuilan; Morelos: Tepoztlán); oak and tropical deciduous forests, on the ground or on cliffs and crags of volcanic rocks, 1700–1900 m. — Fig. 6.

Caespitose, forming large colonies, flowering 0.8–1.6 m tall; **Ros** symmetrical to slightly asymmetrical in mature plants, 40–80 cm  $\varnothing$ ; **L** numerous, sheaths white to yellowish, broadly oblong to square,  $6\text{--}12.5 \times 5\text{--}10$  cm, lustrous basally and white-lepidote apically on both faces, **L** lamina extended, pendent in mature plants, glaucous-green,  $19\text{--}80 \times 1.7\text{--}6.5$  cm, densely white-lepidote on both faces, glabrescent adaxially, **Sp** yellowish, antrorse, 1.6–2 mm, 0.6–1.2 cm apart;





**Fig. 6** *Hechtia matudae*. (Copyright: A. Espejo-Serna)

**Inf** 2× branched; peduncle cylindrical, 2.5–3 cm Ø; peduncular **Bra** straw-coloured, foliaceous, densely lepidote on both faces, becoming progressively reduced distally, densely imbricate; **male Inf** with up to 40 ascending to divaricate primary **Br** 6–11.5 cm long, each with 2 basal secondary branches; floral **Bra** white, linear, 4–8 × ±1 mm, acuminate, entire; **Fl** ascending to divaricate, densely disposed; **Ped** 2.2–2.7 mm; **Sep** rose, triangular to triangular-oblong, 4.6–5.2 × 1.9–2.7 mm, acute, entire; **Pet** rose, widely elliptic to oblong-elliptic, 6.5–8.5 × 4–4.7 mm, rounded, entire; **St** subequal, shorter than the petals; **Fil** 2.8–4 mm; **Anth** purple to dark purple, 1.5–1.8 mm; **female Inf** with 30–35 primary **Br** 7.8–8 cm long, each with 2 basal secondary branches; floral **Bra** white, linear, 4.5–8 × ±1.5 mm, acuminate, entire; **Fl** ascending to appressed, densely disposed; **Ped** ±4.5 mm; **Sep** rose, linear triangular, 4–4.2 × ±1 mm, acuminate, entire; **Pet** rose to dark rose,

triangular to ovate-triangular, 7–7.5 × 3–3.5 mm, acute, entire; **Ov** purple, ovoid to elongate-ovoid, 5–5.1 × 2.5 mm, glabrous; **Fr** brown, 12–15 × 7–8 mm.

**H. melanocarpa** L. B. Smith (Contr. Gray Herb. 161: 32, t. 4, figs. 8–9, 1946). **Type:** Mexico, Guerrero (*Foster* 1258 [GH]). — **Distr:** Mexico (Guerrero: widespread); tropical deciduous forest, on steep limestone slopes and riversides, 550–1350 m.

Solitary or with few rosettes, flowering 2–3 m tall; **L** numerous, sheaths widely ovate, ±7 × 5–8 cm, serrate, white-lepidote distally, **L** lamina green, 80–120 × 3.4–5 cm, glabrous adaxially, appressedly white-lepidote abaxially, **Sp** reddish, antrorse, 5–7 mm, 2.2–3 cm apart; **Inf** erect to ascending, 2× branched, sometimes the lower branches appearing verticillate, white-lepidote; peduncle cylindrical, 1.8–2 cm Ø; peduncular **Bra** foliaceous, pungent, margins spiny, becoming smaller distally; **male Inf** with >35 divaricate to ascending primary **Br** 15–37 cm long, with 2–4 (–8) basal secondary branches; floral **Bra** light brown, ovate, acuminate, erose, ±3 mm; **Fl** divaricate, laxly disposed, sessile; **Sep** green tinged with purple dots, triangular-ovate, 2.7–3.2 × 1.7–2.2 mm, glabrous, acute; **Pet** white, elliptic to oblong, 4.5–5 × 2.5–3 mm, rounded; **St** longer than the petals; **Fil** 4.3–5.3 mm; **Anth** green to yellowish, ±2 mm; **female Inf** with >25 divaricate to ascending primary **Br** 8–35 cm long, with 2 basal secondary branches; floral **Bra** light brown, ovate, 4.7–5.2 mm, lepidote, erose, acute, long mucronate; **Fl** ascending; **Ped** stout, ±1 mm; **Sep** green with purple dots, triangular to ovate, 3.7–4 × 2.5–3 mm, glabrous, acute; **Pet** white, ovate-triangular, 5.5–6 × 3.7–4 mm; **Ov** rose, ovoid, 4.5–5 × 2.6–3 mm, glabrous; **Fr** black, 9–14 × ±4.5 mm, glabrous; **Se** reddish-brown, ±5 mm.

**H. mexicana** L. B. Smith (Contr. Gray Herb. 117: 19–20, t. 1, fig. 60, 1937). **Type:** Mexico, San Luis Potosí (*Mauray* 6593 [F, GH]). — **Distr:** Mexico (Tamaulipas, San Luis Potosí); tropical deciduous and semi-deciduous forests, on rocks, 200–300 m.

Usually forming clumps of 3 or more rosettes, flowering to 2 m tall; **L** numerous in spreading rosettes, sheaths yellowish to light brown, with a dark brown central spot, suborbicular, 6–9 × 5–9 cm, glabrous, lustrous, **L** lamina 80–100 × 2.5–4 cm, glabrous and shiny adaxially, white-lepidote abaxially, **Sp** light brown, divaricate to antrorse, 3–5.5 mm, 1.3–2.3 cm apart; **Inf** seemingly lateral, erect to ascending, densely lepidote, 2× branched; peduncle 12–15 mm Ø; peduncular **Bra** triangular to narrowly triangular, acuminate, densely white-lepidote; **male Inf** unknown; **female Inf** with 16–30 divaricate to ascending primary **Br** 2–18 cm long, with 2 basal secondary branches; floral **Bra** brown, broadly ovate, 3.5–4 × ±2.5 mm, margins hyaline, densely white-lepidote, acute to acuminate; **Fl** divaricate, subsessile; **Sep** brown, broadly ovate, ±3.5 mm, lepidote, rounded, mucronate; **Pet** white, ovate, ±6 mm; **Fr** dark brown, ±10 mm, sparsely lepidote, acute.

**H. montana** Brandege (Erythea 7: 9, 1899). **Type:** Mexico, Baja California Sur (*Brandegee* s.n. [US, NY]). — **Lit:** Felger & Yetman (2000). **Distr:** NW Mexico (Sonora, Baja California Sur); thorn scrub, steep ledges, on the ground or on rocks.

**Incl.** *Hechtia montana* ‘Burgundy’ Kimmach & Trager (1993); **incl.** *Hechtia gayorum* L. W. Lenz (1995); **incl.** *Hechtia gayii* L. W. Lenz (1995) (*nom. inval.*, Art. 61.1).

Caespitose, forming dense colonies, flowering to 1 m tall; **Ros** compact, small, ±30 cm Ø, rhizomatous; **L** numerous, sheaths light brown to stramineous, ovate to suborbicular, ±3.5 × 3–3.5 cm, margins finely ciliate and spiny-denticulate, glabrous or sparingly lepidote, **L** lamina grey-green, 15–45 × 2–3 cm, lepidote but glabrescent adaxially, white-lepidote abaxially, margins sinuate, **Sp** reddish-brown, retrorse, 2–5 mm, 1.7–2 cm apart; **Inf** 1× branched, white-lepidote, glabrescent with age; peduncle cylindrical, ±7 mm Ø; peduncular **Bra** narrowly triangular, 10–10.5 × ±0.5 cm, margins spiny, becoming smaller distally; **male Inf** with 17–25 divaricate to ascending primary **Br** 3–8 cm long; floral **Bra** hyaline, linear to linear-triangular, 2–2.5 mm; **Fl** laxly disposed, divaricate to reflexed;

**Ped** 4–7 mm; **Sep** whitish, triangular, 3 mm, lepidote, acute; **Pet** yellowish-white, obovate, 5–6 mm, acute; **female Inf** with 8–9 ascending primary **Br** 4.5–12 cm long; floral **Bra** narrowly triangular, shorter than the pedicels; **Fl** laxly disposed, ascending; **Ped** 6–8 mm; **Sep** whitish, purplish basally, narrowly triangular, 3–3.5 × 1.2–1.3 mm, sparsely lepidote, acuminate to acute; **Pet** yellowish-white, oblong, 4–6 × ±1.6 mm, rounded to acute; **Ov** green, glabrous, smooth, ±3.3 × ±1.5 mm Ø; **Fr** light to reddish-brown, 10–12 × 7–8 mm, rostrate; **Se** brownish, 5–5.5 mm.

As in other species (*H. iltisii*, *H. tillandsioides*, *H. glomerata*), abnormal flowers are sometimes produced. This is the case of the cultivated *H. gayorum* (here treated as synonym) that comes from the same region.

Felger & Yetman (2000) mention that the Guajirío, an ethnic group native to the lower Sierra Madre of SE Sonora and adjacent SW Chihuahua, have for many years used plants (which they call “hichiconi”) of *H. montana* as a supplemental food.

**H. montis-frigidi** González-Rocha & al. (Acta Bot. Mex. 109: 44–47, ills., 2014). **Type:** Mexico, Morelos (*López-Ferrari & al.* 2206 [UAMIZ]). — **Distr:** Mexico (Morelos: Puente de Ixtla); oak forests, on the ground or on rocks, 1750–2120 m.

Caespitose in small groups, flowering to 2 m tall; **Ros** 60–70 cm Ø; **L** numerous, sheaths straw-coloured adaxially, light brown and lustrous abaxially, depressed-ovate, 5.5–6 × 5–7.5 cm, glabrous at the base, densely white-lepidote at the apex on both faces, **L** lamina dark green, narrowly triangular, 32–48.5 × 2.8–4.8 cm, lepidote on both faces, **Sp** yellowish to brownish, antrorse, 1.5–5 mm, 1–2 cm apart; **male Inf** 3× branched with up to 97 primary branches; peduncular **Bra** foliaceous, sheaths ovate triangular, 3–3.4 × 2.4–2.5 cm, lamina narrowly triangular, 10–13.2 × 0.3–0.5 cm, glabrescent adaxially, sparsely white-lepidote abaxially, acuminate, margins entire to slightly erose; primary **Br** ascending, 9–18 cm, sessile to shortly stalked; secondary **Br** longer than primary branches, 3–10 cm; tertiary **Br** when present 2 cm long; floral **Bra** light brown, triangular, 1.7–3.8 mm,



equal to slightly longer than the pedicels, entire to slightly erose, lepidote; **Fl** polystichous, ascending; **Ped** 1.5–3 mm; **Sep** light brown, triangular, 1.5–3 × 1.1–2 mm, acute and shortly apiculate; **Pet** white-greenish, ovate-elliptic, 3.1–5 × 2–3 mm, rounded to slightly emarginate; **St** subequal; **Fil** 3–5.5 mm; **Anth** green, 1–2 mm; **female Inf** 2× branched with 30–60 primary branches; peduncular **Bra** ovate-triangular, 3–14 × 0.6–2.5 cm, glabrescent adaxially, densely white-lepidote abaxially, acuminate, margins entire to slightly erose; primary **Br** ascending, 6–23 cm, sessile; secondary **Br** 4–10.5 cm; floral **Bra** brownish, narrowly triangular to ovate, 2.8–5.6 × 0.6–1.6 mm, entire to slightly erose, lepidote, longer than the pedicels; **Ped** 1–2 mm; **Fl** polystichous, ascending; **Sep** green-brownish, triangular, 2–3 × 1.7–2.5 mm, densely lepidote, acute and shortly apiculate; **Pet** green-brownish, triangular, 3.5–4.6 × 2–3 mm, acute; **Ov** green, ellipsoid; **Fr** brownish, ovoid, 10–13 × 3–7 mm; **Se** brownish, 3.5–6 mm.

**H. mooreana** L. B. Smith (Contr. US Nation. Herb. 29: 522–523, fig. 78, 1954). **Type:** Mexico, Guerrero (*Moore* 5196 [US, BM, G, UC]). — **Distr:** Mexico (Guerrero: Chilapa, Copalillo, Eduardo Neri, Mártir de Cuilapan, Tepecoacuilco); tropical deciduous forest, on the ground or more rarely on rocks on steep limestone slopes, 500–1300 m.

Solitary or in clumps of few caulescent elongated rosettes, flowering to 1.5 m tall; stems conspicuous, 25–50 × 1.3–2 cm Ø; **L** numerous, sheaths stramineous, suborbicular to ovate, 3.8–4 × 3.6–4 cm, glabrous, densely white-lepidote and spiny at the margins distally, **L** lamina light green, squarrose, 15–35 × 0.85–1.5 cm, glabrous adaxially, densely white-lepidote abaxially, **Sp** light brown, antrorse, 2.4–3.3 mm, 1.1–2 cm apart; **Inf** 1× branched, glabrous; peduncle ±1 cm Ø; **male Inf** with ±15 divaricate primary **Br** ±10 cm long; floral **Bra** hyaline with purple dots, narrowly triangular, ±1 mm, erose, acuminate; **Fl** divaricate, subverticillate; **Ped** slender, ribbed, 2–2.5 mm; **Sep** white with purple dots, ovate-triangular, 1.5–1.7 × ±0.7 mm, glabrous, rounded; **Pet** white, elliptic, 2.9–3.1 × ±1.7 mm, rounded; **St** ± equalling the petals; **Fil** ±1.5 mm;

**Anth** yellow, ±1.3 mm; **female Inf** with 25–32 divaricate to ascending primary **Br** 3–10 cm long; primary **Bra** ±1.2 mm; **Fl** divaricate to ascending, laxly disposed; **Ped** 1.9–2.1 mm; **Sep** white, ovate, 1.9–2.2 × 1–1.2 mm, margin hyaline, rounded; **Pet** white, triangular, 3.2–3.4 × 1–1.1 mm, acuminate; **Ov** green, ovoid, ±3 mm; **Fr** brown to dark brown, 7–8 × 2–4 mm, glabrous, smooth; **Se** light brown, ±2.2 mm.

**H. myriantha** Mez (Bot. Jahrb. Syst. 30 (Beiblatt 67): 6, 1901). **Type:** Mexico, Veracruz (*Liebmann* s.n. [C, B]). — **Distr:** Mexico (Veracruz: Actopan, Coatepec, Emiliano Zapata, Jalcomulco); tropical deciduous forest and arid scrub, on the ground or on rocks on rocky slopes, 0–800 m. **I:** Espejo-Serna & al. (2005: 91).

**Incl.** *Hechtia macrophylla* Greenman (1907).

Solitary, caulescent, flowering to 3–4 m tall; **Ros** globose to elongated, to 1.5 m high, ±1 m Ø, stems conspicuous, to 20 cm Ø; **L** very numerous, sheaths white, with a dark brown spot to the apex, lustrous, broadly ovate to depressed-elliptic, 5.5–6 (–9) × 9.5–11.5 cm, spiny towards the apex, **L** lamina green, sometimes reddish at the margins, (0.4–) 1–1.7 m × 2.5–6.5 cm, glabrous adaxially, white-tomentose and conspicuously veined abaxially, **Sp** antrorse to retrorse or divaricate, 3–7 mm, with an ample triangular base, 1–2 cm apart; **Inf** seemingly lateral, white-lepidote, 3× branched; **male Inf** with very numerous primary **Br** 8–40 cm long; peduncle cylindrical, 0.6–2 cm Ø; peduncular **Bra** brown, triangular, 6.5–12 × 1.5–2.5 cm, lepidote, acute to acuminate, longer than the internodes; primary **Bra** brown, triangular to lanceolate, 1.5–9 cm; floral **Bra** broadly triangular to ovate, 3–4 × ±3 mm, lepidote, erose, acute and apiculate; **Fl** ascending to divaricate, loosely arranged, very numerous on each branch, subsessile; **Sep** connate at the base, obovate, ±3 × ±2 mm, rounded, apiculate; **Pet** white, oblong or obovate, 4–4.5 × 2–3 mm; **St** shorter than the petals; **Fil** ±3 mm; **Anth** yellow, ±1.5 mm; **female Inf** with very numerous primary **Br** 10–36 cm long; primary **Bra** brown, triangular, 1–4 cm, ovate to triangular; floral **Bra** brown to white, ovate, 3.8–5 × ±3 mm, margins slightly fimbriate at the base,

attenuate, pungent; **Fl** ascending to divaricate, loosely arranged, very numerous on each branch; **Ped** 1–5 mm; **Sep** brown to white, ovate to triangular,  $3\text{--}3.5 \times \pm 2.5$  mm, entire, acute; **Pet** white, oblong to oblong triangular,  $3.6\text{--}4.1 \times 2.2\text{--}2.5$  mm, acute; **Ov** greyish to blackish, ovoid to long-ovoid,  $4\text{--}5 \times \pm 2.5$  mm, densely white-lepidote; **Fr** dark brown,  $10\text{--}12 \times 4\text{--}5$  mm, white-lepidote to glabrescent; **Se** reddish-brown, 4–7 mm.

**H. nivea** I. Ramírez & C. F. Jiménez (Phytotaxa 178(2): 122–124, ill., 2014). **Type:** Mexico, Oaxaca (Ramírez & al. 1826b [CICY, MEXU]). — **Distr:** Mexico (Oaxaca: San Juan Bautista Cuicatlán); xerophytic scrub, 700–800 m.

Solitary, flowering to 1.4 m tall; **Ros** 35–45 cm Ø; **L** 60–70, sheaths white-yellowish adaxially, brownish abaxially, oblong,  $2.5\text{--}3 \times 3\text{--}5$  cm, glabrous on both faces, **L** lamina green, narrowly triangular,  $21\text{--}39 \times 1.3\text{--}2.9$  cm, glabrous to sparsely white-lepidote adaxially, white-lepidote abaxially, **Sp** reddish, retrorse, 4–7 mm,  $1.6\text{--}4.5$  cm apart; **Inf** 1 × branched; **male Inf** with 65–75 branches; peduncular **Bra** foliaceous, sheaths triangular, lamina narrowly triangular,  $4\text{--}11 \times 0.8\text{--}1$  cm, margins entire, glabrous; **Br** ascending, 1.2–3 cm; floral **Bra** light brown, elliptic,  $6.3\text{--}8 \times 3.5\text{--}5.5$  mm, erose, acute, glabrous; **Fl** polystichous; **Ped** 1–2 mm; **Sep** straw-coloured, oblong,  $3.5\text{--}4 \times 2.2\text{--}3$  mm, erose, acute, glabrous; **Pet** white, elliptic,  $4\text{--}4.4 \times 2.2\text{--}2.5$  mm, rounded; **St** subequal; **Fil** 4–4.6 mm; **Anth** green, 1.7–2 mm; **female Inf** with 40–45 branches; peduncular **Bra**  $2.5\text{--}9 \times 0.8\text{--}0.9$  cm, triangular, acuminate, entire, glabrous; **Br** ascending, 0.8–2.4 cm; floral **Bra** brown, triangular-ovate,  $5\text{--}7 \times 3\text{--}4$  mm, erose, glabrous; **Fl** polystichous, sessile; **Sep** brown, triangular,  $3\text{--}3.5 \times 2.5\text{--}3.5$  mm, apically erose, glabrous; **Pet** green, triangular to ovate,  $3\text{--}4 \times 2\text{--}2.8$  mm, acute; **Ov** oblong, 2.5–3 mm; **Fr** brown, ellipsoid,  $6.3\text{--}9$  mm; **Se** brown, 3.4–4 mm.

**H. nuusaviorum** Espejo & López-Ferrari (Acta Bot. Mex. 78: 98–102, ill., 2007). **Type:** Mexico, Oaxaca (Ceja & al. 1751 [UAMIZ, IEB]). — **Distr:** Mexico (Oaxaca: Santiago Yosondúa); oak-pine forest, on vertical limestone cliffs, 1700–1900 m.

Solitary or in clumps of few rosettes, flowering to 2 m tall; **Ros** caulescent,  $\pm 50$  cm Ø, stems conspicuous, succulent, woody, to  $1.2 \text{ m} \times 15\text{--}30$  cm Ø; **L** numerous, very succulent, soft, sheaths light brown, widely ovate to square,  $3.5\text{--}8.5 \times 3.5\text{--}7.5$  cm, lustrous, white-lepidote on both faces, **L** lamina lime-green,  $30\text{--}75 \times 1.5\text{--}4.5$  cm, glabrous adaxially, lepidote abaxially, **Sp** divaricate to antrorse, green to brown, 4–9 mm, 1–2 cm apart; **Inf** seemingly lateral, flocculose, 1 × branched; peduncle  $1\text{--}2.5$  cm Ø; peduncular **Bra** brown, triangular,  $2.2\text{--}20 \times 1.5\text{--}3.5$  cm, acute, acuminate, lamina erose to spiny, densely lepidote, becoming progressively reduced distally; **male Inf** with 8–38 ascending, short to capitate primary **Br** 2.5–3.2 cm long; floral **Bra** light brown, ovate to triangular-ovate,  $5\text{--}6 \times 4\text{--}5$  mm, acuminate; **Fl** divaricate, very densely disposed, sessile; **Sep** light brown, ovate,  $4\text{--}4.7 \times 2.3\text{--}2.4$  mm, acute; **Pet** white, elliptic to oblong,  $6\text{--}6.3 \times 2.2\text{--}2.4$  mm, acute; **St** subequal, as long as petals; **Fil** 5.5–6.1 mm; **Anth** yellow,  $\pm 1.4$  mm; **female Inf** with 20–25 divaricate, capitate and globose primary **Br** of  $1.2\text{--}3$  cm Ø; floral **Bra** brown, widely ovate,  $5\text{--}7 \times \pm 5$  mm, glabrous, entire; **Fl** densely disposed, sessile; **Sep** brown with margins white with rose dots, ovate,  $4.7\text{--}5 \times 4.3$  mm, entire, acute-apiculate; **Pet** white with rose dots on the median nerve, elliptic,  $6\text{--}7 \times 3.5\text{--}3.8$  mm, entire, acute; **Ov** ovoid, rose,  $7\text{--}7.7 \times \pm 2.6$  mm; **Fr** brown,  $\pm 10 \times \pm 5$  mm, lustrous; **Se** dark brown, falcate,  $\pm 6$  mm.

**H. oaxacana** Burt-Utley & al. (Phytoneuron 2011(59): 3, 2011). **Type:** Mexico, Oaxaca (Utley & Burt-Utley 7960 [MEXU, CAS, GH, M, NY, US, USF]). — **Distr:** Mexico (N Oaxaca); oak and pine forest, steep hillsides and karstic rock outcrops, 1650–2400 m.

Usually in large colonies, flowering to (0.72–) 1.16–1.77 m tall; **Ros** 30–50 cm Ø, occasionally with stout stolons; **L** very numerous, sheaths reniform to transversely elliptic,  $2.3\text{--}5.6 \times (3.5\text{--}) 5\text{--}8.3$  cm, lepidote distally on both faces, marginally spiny and floccose, **L** lamina (11–)  $22\text{--}40.5 \times (1\text{--}) 1.5\text{--}2$  (–2.5) cm, lepidote to glabrescent adaxially, lepidote abaxially, **Sp**

reddish-brown, antrorse, occasionally retrorse, (1.5–) 2.5–3.5 (–4.5) mm, (0.4–) 1.4–2 (–2.5) cm apart; **Inf** glabrous to lepidote, rachis often weakly geniculate; peduncle (6–) 8–14 (–18) mm  $\emptyset$ ; peduncular **Bra** ascending, (2.2–) 3.4–22 cm, with narrowly linear-triangular spiny lamina; **male Inf** 1 $\times$  branched with numerous ascending to subascending primary **Br** (1–) 2–11 (–17.5) cm long, or rarely 2 $\times$  branched with very short basal secondary branches; floral **Bra** shorter to longer than the sepals, narrowly to broadly ovate or ovate-triangular to suborbicular, (2.2–) 3–7 (–9)  $\times$  (1.7–) 2.5–5 (–6) mm, glabrous to finely lepidote, margin finely spinulose to erose, spinulose to apiculate, acute, rounded or praemorse at the apex; **Fl** divaricate to ascending; **Ped** articulated, stout, (0.5–) 1.5–2 (–3) mm; **Sep** ovate to ovate-triangular, 1.2–2.5 (–3.5)  $\times$  1.3–2.5 mm, glabrous, entire to erose, rounded to acute or praemorse; **Pet** greenish-white, oblong-elliptic to ovate-elliptic, 2.5–4.8  $\times$  1.5–3 mm, glabrous, entire, rounded; **Fil** basally briefly adnate to the petals; **female Inf** 1 $\times$  branched, with numerous ascending to subascending primary **Br** (1–) 2–11 (–17.5) cm long; floral **Bra** shorter or longer than the sepals, narrowly ovate to broadly ovate or oblong-ovate, 3–6  $\times$  3–5.5 mm, marginally hyaline, entire to finely spinulose or erose, apiculate to spinulose; **Fl** divaricate to ascending; **Ped** articulated, stout, triquetrous, 1–2 mm; **Sep** triangular to ovate-triangular, 2–3 (–4)  $\times$  1.2–2.5 (–3.5) mm, glabrous or rarely weakly lepidote, entire, rounded to acute, apiculate or praemorse; **Pet** narrowly ovate to triangular, 3–4.5 (–5.5)  $\times$  1.5–2.8 mm, rounded to spinulose; **Ov** glabrous; **Fr** 7–9 (–11.5)  $\times$  (3–) 4–5 (–6) mm, glabrous, smooth or somewhat reticulate.

**H. pedicellata** S. Watson (Proc. Amer. Acad. Arts 26: 155, 1891). **Type:** Mexico, Jalisco (*Pringle* 2970 [GH, VT]). — **Distr:** Mexico (Jalisco: Guadalajara); tropical deciduous forest, on rocks on dry rocky bluffs and ledges,  $\pm$ 1000 m; known from the type only.

Habit unknown, flowering to 1.2 m tall; **L** numerous, sheaths stramineous, suborbicular, 4.5–5  $\times$  3.5–4 cm, margin spiny, **L** lamina 25–65

$\times$  2–3 cm, glabrous adaxially, white-lepidote abaxially, **Sp** yellow to light brown, divaricate to antrorse, 1.5–2 mm, 0.9–1.2 cm apart; **Inf** glabrous; peduncle cylindrical, 6–7 mm  $\emptyset$ ; peduncular **Bra** brown, narrowly triangular, 3–9.5  $\times$  0.7–1 cm, attenuate, pungent, margins serrulate; **male Inf** unknown; **female Inf** 1 $\times$  branched, with 15–18 ascending to divaricate primary **Br** 2–6 cm long; primary **Bra** brown, triangular, 10–14  $\times$  4–5 mm, acuminate; **Fl** laxly disposed, ascending; **Ped** stout, 5–6 mm; **Sep** ovate-triangular, 1.5–2  $\times$   $\pm$ 1 mm, acute; **Pet** triangular, 3–3.3  $\times$   $\pm$ 2 mm, acute; **Fr** brown, 9–12  $\times$   $\pm$ 5 mm; **Se** brown,  $\pm$ 5 mm.

**H. podantha** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 549–550, 1896). **Type** [neo]: Mexico, Hidalgo (*Pringle* 6932 [ENCB, B, BR, CHAPA, GH, LY, MEXU, MICH, P, UC, US, WU, Z]). — **Lit:** Martínez-Correa (2008); Espejo-Serna & al. (2010c). **Distr:** C Mexico (Aguascalientes, Guanajuato, Querétaro, Hidalgo); xerophilous scrub, on limestone hills or volcanic rocks, 1100–2650 m.

Solitary or in small clumps, flowering  $\pm$ 1.5 m tall; **L** numerous, sheaths light yellow to brown, ovate to suborbicular, 2.1–8.8  $\times$  2.3–6.1 cm, glabrous adaxially, glabrous at the base and sparsely lepidote at the apex abaxially, serrate, **L** lamina green, 19–53.7  $\times$  0.5–1.5 cm, sparsely lepidote on both faces, **Sp** antrorse, 3.1–8 mm, 0.65–3.2 cm apart; **Inf** 2 $\times$  branched, glabrous or glabrescent; peduncle cylindrical, 0.46–1.8 cm  $\emptyset$ ; peduncular **Bra** foliaceous, sparsely lepidote, serrate, 6.3–17.8 cm, the upper ones sheathing, sparsely lepidote, entire; primary **Bra** stramineous, widely ovate, glabrous, serrulate, 2.2–4.8 cm; **male Inf** with up to 46 ascending primary **Br** 1.6–6.6 cm long; secondary **Br** ascending, 1.35–5.25 cm; floral **Bra** brown, linear to triangular, 1.2–3.1  $\times$  0.2–1 mm, glabrous, entire, acute; **Fl** divaricate; **Ped** 1.4–2.7 mm; **Sep** brownish, triangular to ovate, 1.7–4.3  $\times$  1–2.1 mm, glabrous, entire, acute; **Pet** green, brownish apically, elliptic to ovate, 2.5–5.4  $\times$  1.4–2.8 mm, glabrous, entire, rounded; **St** equal, longer than the petals; **Fil** 1.3–4.2 mm; **Anth** yellow, 0.7–2 mm; **female Inf** with up to 47 ascending primary **Br** 2.5–9 cm

long; secondary **Br** ascending, 1.4–5.3 cm; floral **Bra** brown, triangular, 1.1–5.3 × 0.1–0.6 mm, entire, acute; **Fl** numerous, divaricate; **Ped** 1.6–5.1 mm; **Sep** brownish, triangular to ovate, 1.5–4 × 0.7–2.2 mm, glabrous, entire, acute; **Pet** green, triangular, 1.9–4.7 × 1.4–2.7 mm, glabrous, entire, acute; **Ov** green, ovoid, 3.8–7 × 1.2–2.4 mm; **Fr** brownish, 7–15 × 4–6.5 mm; **Se** reddish-brown, 6–7 mm.

**H. pretiosa** Espejo & López-Ferrari (Acta Bot. Mex. 83: 50–53, ill., 2008). **Type:** Mexico, Guanajuato (*López-Ferrari & al.* 3268 [UAMIZ, IEB]). — **Distr:** Mexico (Guanajuato: Xichú); cactus scrub, slopes and cliffs, on igneous rocks, 800–1400 m.

Caespitose, flowering to 1.7 m tall; **Ros** with 2 or more conspicuous narrowly cylindrical stolons; **L** numerous, sheaths yellowish to light brown, widely ovate to square, 4–5.5 × 5 cm, glabrous, lustrous, **L** lamina 30–50 × 2.2–3.5 cm, glabrous adaxially, densely brown-lepidote abaxially, **Sp** green to brown, antrorse, 2.5–5 mm, 0.5–1.5 cm apart; **Inf** seemingly lateral, simple to 1 × branched, procumbent; **male Inf** with 4–9 divaricate primary **Br** 5–22 cm long; floral **Bra** rose to rose-brownish, ovate to triangular-ovate, 6–8 × 3–4.5 mm, with capitate gland-hairs, acuminate, margin slightly erose; **Fl** divaricate to reclinate, sessile to subsessile; **Sep** rose to rose-brownish, oblong to lanceolate-oblong, connate at the base forming a tube, 5.5–7 mm, limb 6–8.5 × 2.5–3.5 mm, with capitate gland-hairs, acute and shortly apiculate; **Pet** rose, elliptic, 6–8 × 3.5–4 mm, with capitate gland hairs, rounded; **St** unequal, united at the base with the perigone tube; **Fil** 2–5 mm; **Anth** dark purple, 1–1.5 mm; **female Inf** simple or with 2–7 divaricate primary **Br** 8–19 cm long; floral **Bra** rose to rose-brownish, triangular to triangular-ovate, 8–13 × 4–4.5 mm, with capitate gland-hairs, acuminate, margin slightly and irregularly erose; **Fl** sessile to subsessile; **Sep** rose to rose-brownish, narrowly triangular, 7–11 × 4–5 mm, with capitate gland-hairs, acute and shortly apiculate, margin lightly erose; **Pet** rose, elliptic, 8–9 × 3–5 mm, with capitate gland-hairs, entire, rounded and shortly apiculate; **Ov** ovoid to

narrowly ovoid, 6–10 × 3–4 mm, with capitate gland hairs and scarcely pedate scales; **Fr** light brown, 9–13 × 8–9 mm, lustrous, sparsely lepidote; **Se** light brown, 5–6 × 0.5 mm.

**H. pringlei** B. L. Robinson & Greenman (Amer. J. Sci. (New York) ser. 3, 50: 167, 1895). **Type:** Mexico, Oaxaca (*Pringle* 4637 [GH, AC, B, BHUPM, BKL, BM, BR, ENCB, G, GOET, HAL, ISC, K, MANCH, MEXU, MIN, MO, MSC, NY, P, PH, S, UC, US, VT, WU, Z]). — **Distr:** S Mexico (C Oaxaca); shrublands, oak forest and/or tropical deciduous forest, on calcareous soils or rarely on limestone cliffs.

Solitary or in small clumps, flowering to 1–2 m tall; **L** 15–30, fleshy, sheaths stramineous to light brown, ovate to depressed-ovate, 3.1–4.5 × 4–7 cm, **L** lamina green, 13–55 × 1–4 cm, white-lepidote on both faces, **Sp** reddish to dark brown, retrorse to antrorse or divaricate, 3–5 mm, 0.23–3.9 cm apart; **Inf** 1 × branched, farinose-lepidote to glabrescent with age; peduncle ±1.5 cm Ø; peduncular **Bra** linear to narrowly triangular, attenuate, entire, pungent, becoming gradually shorter further up; **male Inf** with 24–35 ascending to divaricate primary **Br** 3–6 cm long; primary **Bra** linear to lanceolate from a triangular base, 1.5–2 cm; floral **Bra** white, ovate, ±2.5 × ±1.6 mm, erose, longer than the sepals; **Fl** polystichous, divaricate, subsessile; **Ped** inconspicuous, lepidote; **Sep** whitish to light brown, ovate-triangular, 1.7–2 × 1.2–1.3 mm, margin scarious, erose, somewhat farinose-lepidote, rounded; **Pet** white, oblong to elliptic-oblong, 2.9–3 × 1–2 mm, obtuse; **St** equal, shorter than the petals; **Fil** ±2.5 mm; **Anth** yellow, 0.8–1 mm, apiculate; **female Inf** with 20–30 ascending to divaricate primary **Br** 3–17 cm long; primary **Bra** light brown, triangular, 1–3 cm, erose, attenuate; floral **Bra** brown, ovate to elliptic, 2–3 mm, farinose-lepidote, erose-spiny, acute to acuminate; **Fl** 3–3.5 × 1–1.7 mm; **Ped** stout, to 2 mm, sulcate; **Sep** brown, ovate, ±2.4 × ±1.3 mm, acuminate; **Pet** green, triangular, 3.2 × 1.2 mm; **Ov** light brown to rose, ellipsoid, ±2.7–3.5 × ±1.2 mm; **Fr** brown to light brown, 6–7 × 3–4.5 mm; **Se** brown, 4–4.5 mm.

**H. pumila** Burt-Utley & Utley (Syst. Bot. 13 (2): 279–281, ills., 1988). **Type:** Mexico, Guerrero (*Burt-Utley & Utley* 7908 [MEXU, B, BH, BM, CAS, DUKE, F, GH, K, MEXU, MICH, MO, NY, TEX, UC, US, WIS]). — **Distr:** Mexico (Guerrero: Chilpancingo, Tepecoacuilco); thorn scrub with palms and tropical deciduous forest, rocky places on steep limestone hills, 600–1650 m.

Usually forming small clumps of 2 or more rosettes, flowering 58–151 cm tall; **Ros** 11–34 cm  $\varnothing$ ; **L** few, spreading, sheaths stramineous, broadly ovate to reniform, 1.3–2.2  $\times$  2.3–4.6 cm, margins finely spiny, glabrous and lustrous on both faces, becoming densely lepidote distally, **L** lamina 9–25  $\times$  1.3–2 cm, appressedly cinereous-lepidote on both faces, **Sp** red-brown or rarely stramineous, antrorse or occasionally retrorse, 1–2 mm, 0.45–1 cm apart; **Inf** 1  $\times$  branched, glabrous; peduncle cylindrical, 3.5–8 mm  $\varnothing$ ; peduncular **Bra** 0.7–7.5 cm, with ovate or broadly ovate glabrous sheaths and linear lepidote lamina, entire; **male Inf** with  $\pm$ 12 subascending primary **Br** (1.5–) 2–4 cm long, appearing somewhat winged when dry; floral **Bra** ovate or ovate-triangular, 1–2.5  $\times$  0.8–2 mm, glabrescent, attenuate-acuminate, erose, esp. at the apex, exceeding the pedicels; **Fl** sessile to subsessile; **Ped** articulated, stout, to 1 mm; **Sep** ovate or ovate-triangular, 1.1–1.8  $\times$  0.7–1.3 mm, praemorse or occasionally acuminate, entire and occasionally hyaline, glabrous; **Pet** elliptic, 2–3.5  $\times$  (1–) 1.6–2 mm, rounded, glabrous; **St** subequal, shorter than the petals; **Fil** 2.9–3 mm; **Anth** yellow,  $\pm$ 1 mm; **female Inf** with 12–17 subcapitate primary **Br** 0.3–2.5 cm long; floral **Bra** exceeding the pedicels, triangular to ovate-triangular, 1.1–2.5  $\times$  0.6–2.6 mm, glabrous, attenuate-acuminate, erose distally, occasionally hyaline; **Fl** sessile to subsessile; **Sep** dark red-brown, ovate to ovate-triangular, 1.3–2.5  $\times$  1.3–2 mm, glabrous, acute or praemorse, margins often hyaline; **Pet** triangular to narrowly ovate-triangular, 2.6–4.3  $\times$  1.3–2.3 mm, rounded to acute; **Fr** dark red-brown, 5.5–11  $\times$  3.1–5.5 mm, glabrous.

**H. purhepecha** I. García & al. (Acta Bot. Mex. 107: 10–14, ills., 2014). **Type:** Mexico, Michoacán (*Espejo & al.* 7547 [UAMIZ, CIMI, IEB]). — **Distr:** Mexico (Michoacán: Los Reyes, Peribán);

(sub-) deciduous tropical forest, slopes and cliffs, on rocks, 900–1000 m.

Caespitose, stoloniferous, flowering to 1.7 m tall; **Ros** 30–50 cm  $\varnothing$ , at the tip of narrowly cylindrical stolons; **L** 15–25, sheaths white on both faces, depressed-ovate, 3–4  $\times$  5–6.5 cm, glabrous, lustrous, **L** lamina 11–50  $\times$  2.6–4.5 cm, light green with a purple stripe along the margins, glabrous adaxially, densely white-lepidote abaxially, **Sp** yellow to light brown, 2–4.5 mm, 0.8–1.3 cm apart; **Inf** seemingly lateral, 1–2  $\times$  branched, erect, glabrous; **male Inf** 2  $\times$  branched with 25–30 divaricate to ascending primary **Br** 4–28 cm long; secondary **Br**, when present, 2–4 cm; floral **Bra** brown-purplish to dark brown with purplish dots, triangular-ovate, 1.5–1.9  $\times$  0.9–1.2 mm, erose, glabrous, apiculate; **Fl** divaricate, sessile; **Sep** brown-purplish to dark brown with purplish dots, triangular-ovate, 3.1–3.4  $\times$  3–3.5 mm, entire, glabrous, rounded; **Pet** white, elliptic, 4.8–5  $\times$  3.3–3.5 mm, rounded; **St** subequal; **Fil** 3.9–4.2 mm; **Anth** yellow, 2–2.5 mm, apiculate; **female Inf** 1  $\times$  branched with 13–20 ascending primary **Br** 10–21 cm long; floral **Bra** green with rose apex and purplish dots, ovate-triangular, 1.4–2  $\times$  0.5–0.7 mm, glabrous, minutely crenate, acute; **Fl** sessile; **Sep** green with rose apex and purplish dots, ovate-triangular, 3.5–4.5  $\times$  2.6–3.6 mm, entire, glabrous, rounded; **Pet** white-greenish, narrowly triangular-elliptic, 5.8–6  $\times$  3.2–3.8 mm, rounded; **Ov** narrowly ovoid, 5–6  $\times$  2.6–3 mm; **Fr** brown-reddish to dark brown, 10–12  $\times$  4–6 mm, lustrous; **Se** reddish, 8–9 mm.

**H. purpusii** Brandegee (Univ. Calif. Publ. Bot. 7: 325, 1920). **Type:** Mexico, Vera Cruz (*Purpus* 8420 [UC, NY, US]). — **Distr:** Mexico (Veracruz: Coatepec, Jalcomulco, Totutla, Puente Nacional, Tenampa); tropical deciduous forest, on limestone cliffs, 30–1200 m. — Fig. 7.

**Incl.** *Hechtia lindmanioides* B. L. Robinson (1937).

Caespitose, pendulous, flowering to 1 m tall; **Ros** short to long caulescent, stems rhizomatous, cylindrical, 20–80  $\times$  2–3 cm  $\varnothing$ , covered by the persistent leaf sheaths; **Ros** somewhat asymmetrical, 20–50 cm  $\varnothing$ ; **L** 10–15, recurved and pendent, brittle, sheaths yellowish, oblong to ovate,



5–7.5 × 3.5–5 cm, lustrous, white-lepidote distally on both faces, minutely serrate, **L** lamina yellowish-green, 20–50 × 1–1.5 cm, densely white-lepidote abaxially, long-attenuate, minutely serrate; **Inf** erect to pendent; **male Inf** 3× branched, with numerous primary **Br** 10–28 cm long; peduncle cylindrical, 20–32 cm, 4–5 mm Ø; peduncular **Bra** yellowish, narrowly triangular to linear, 2–10 cm × 2–5 mm, densely white-lepidote, much longer than the internodes, decreasing in size further up, deciduous; floral **Bra** filiform, 1–1.5 mm, glabrous, deciduous, shorter than the pedicel; **Fl** polystichous, divaricate to descending; **Ped** filiform, 3–5 mm; **Sep** brownish, triangular, 1.5–2 × ±1 mm, acute; **Pet** white, broadly elliptic, 4–5 × 1.5–2 mm, rounded; **St** shorter than the petals; **Fil** 2.5–3 mm; **Anth** yellow, ±1 mm; **female Inf** 3× branched, with numerous primary **Br** 10–16 cm long; peduncle cylindrical, 25–50 cm, ±3 mm Ø; peduncular **Bra** yellowish, narrowly triangular to linear, 5–13 × 0.2–0.5 cm, densely white-lepidote, much longer than the internodes, decreasing in size upwards; floral **Bra** filiform, inconspicuous, to 2.5 mm; **Fl** polystichous, divaricate to descending; **Ped** filiform, 1.5–2.5 mm; **Sep** brown-greenish, triangular to narrowly triangular, ±0.9 × ±0.8 mm, acute; **Pet** white to rose-whitish, elliptic to oblong,

4–6 × ±3 mm, rounded; **Ov** dark brown, ovoid, 4–5 × 2–3 mm; **Fr** light brown, 5–10 × 2.6–3 mm, divaricate to reflexed; **Se** brown, 2.5–3 mm.

**H. reflexa** L. B. Smith (Contr. Gray Herb. 117: 18–19, t. 1, figs. 54–55, 1937). **Type:** Mexico, Michoacán (*Langlassé* 238 [US, GH, K, P]). — **Distr:** S Mexico (Michoacán: Aquila, Arteaga; Guerrero: José Azueta); tropical deciduous and semideciduous forest, on karstic limestone rocks, 50–650 m.

**Incl.** *Hechtia michoacana* Burt-Utley & al. (2011).

Usually caespitose, flowering (0.55–) 1–1.4 m tall; **Ros** 30–90 cm Ø; **L** numerous, sheaths reniform to transversally elliptic, 2.5–4.5 × (3.5–) 4.4–5.7 (–8.5) cm, marginally spiny and floccose, both faces glabrous and lustrous becoming lepidote distally, **L** lamina green to maroon, straight to falcate, 24–57 × 1.2–2.4 (–2.9) cm, densely lepidote adaxially and lepidote abaxially, **Sp** red-brown, antrorse or occasionally divaricate or retrorse, (2–) 2.5–4.5 (–5) mm, 0.7–2.5 cm apart; **Inf** glabrous; peduncle 3.5–7 mm Ø; peduncular **Bra** foliaceous, ascending, 1.1–26 cm, lepidote, becoming progressively reduced upwards, ovate-triangular with linear lamina; **male Inf** 2× branched, with numerous ascending to

**Fig. 7** *Hechtia purpusii*.  
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subascending reflexed primary **Br** 6–22.5 cm long; floral **Bra** adnate to and often exceeding the pedicels, ovate, 1.2–2.5 × 0.7–1.2 mm, finely serrulate distally, apiculate to attenuate-acuminate, glabrous; **Fl** divaricate to subascending; **Ped** slender, 0.5–2.2 mm; **Sep** deep to light pink or green with brownish maculation, ovate, 0.9–1.5 × 0.5–1.1 mm, entire to serrulate distally, incised to praemorse or apiculate distally; **Pet** white, cream or light to dark pink, elliptic, (1.6–) 3–3.5 × 1–1.7 mm, rounded; **St** longer than the sepals; **female Inf** 1 × branched, with 20–22 arcuate to ascending or subascending primary **Br** 6.5–22.5 cm long, rarely with 1–2 short basal secondary branches; floral **Bra** adnate to the pedicels, shorter than the sepals, narrowly ovate to ovate, 1.5–2.5 × 0.8–1.8 mm, glabrous, entire to finely erose, apiculate to attenuate-acuminate or praemorse; **Fl** ascending to subascending; **Ped** slender, 1.5–3.5 (–4.5) mm; **Sep** deep to light pink or green with maroon maculation, triangular to ovate-triangular, 1.2–2 × 0.7–1.1 mm, glabrous, entire to serrulate distally, acute-praemorse to apiculate; **Pet** white, cream or light to dark pink, narrowly triangular, (2.3–) 3–4.5 × 1–1.2 mm, glabrous, rounded; **Ov** ovoid, 2.8–3 × ±1 mm; **Fr** green suffused with red when immature but becoming yellow-brown and reticulate at maturity, (5–) 6–9 × 2.5–4.5 mm, glabrous, smooth.

**H. reticulata** L. B. Smith (Contr. Gray Herb. 117: 17–18, t. 1, fig. 46, 1937). **Type:** Mexico, Colima (*Palmer* 1352 [GH, F, UC, US]). — **Distr:** Mexico (Jalisco: La Huerta; Colima: Colima, Manzanillo; Michoacán: Arteaga, La Huacana); tropical deciduous forest, 40–750 m.

Caespitose, flowering to 1.2 m tall; **Ros** 60–140 cm Ø; **L** numerous, densely rosulate, spreading, sheaths stramineous to light brown, orbicular to depressed-ovate, 5.2–6.8 × 6–7.6 cm, glabrous, lustrous, margins irregularly spiny, **L** lamina green to reddish adaxially, 30–70 × 3–4 cm, **Sp** brown to yellowish, antrorse, 3–4.5 mm, 0.7–1.5 cm apart; **Inf** barely 2 × branched, glabrous; peduncle ±1 cm Ø; peduncular **Bra** erect, the lower exceeding the internodes, progressively smaller distally, pungent;

**male Inf** unknown; **female Inf** with 15–20 ascending primary **Br** 10–15.5 cm long; primary **Bra** brown, triangular, 5–15 mm, filiform-acuminate; floral **Bra** ovate, ±3.5 × ±1 mm, acuminate, equal or barely longer or shorter than the pedicels; **Fl** divaricate, laxly disposed; **Ped** stout, conical, 2–4 mm, glabrous, sulcate; **Sep** green, ovate, 2.5–4 × ±1.5 mm, margins hyaline, erose, rounded; **Pet** white, narrowly triangular, 3.5–4 × 1.5–2 mm, acute; **Ov** superior, green, ovoid, ±3 × ±1 mm; **Fr** brown, 7.5–10 × 3–5 mm, irregularly reticulate; **Se** brown, 4.8–5.4 mm.

**H. rosea** E. Morren ex Baker (Handb. Bromel., 140, 1889). **Type:** Mexico (*Anonymus* s.n. in *Hort.* Liège s.n. [LG [Morren drawing], GH [photo]]). — **Distr:** Mexico (Oaxaca, Chiapas); tropical deciduous and semideciduous forests and thorn scrub, on the ground or on rocks, 10–600 m. **I:** Roguenant & al. (2016: 150–151).

**Incl.** *Hechtia roezlii* hort. ex Baker (1889) (*nom. inval.*, Art. 34.1c); **incl.** *Dyckia desmetiana* Baker (1894) ≡ *Hechtia desmetiana* (Baker) Mez (1896); **incl.** *Bromelia desmetiana* hort. ex Baker (1894) (*nom. inval.*, Art. 34.1c); **incl.** *Hechtia meziana* L. B. Smith (1935); **incl.** *Hechtia macdougallii* L. B. Smith (1969).

Caespitose, flowering to 1.5 m tall; **L** rather few, rosulate, sheaths stramineous to light brown, suborbicular to transversally oblong, 4.5–6 × 5.5–7 cm, densely brown-lepidote on both faces, glabrous to the base, lustrous, margins spiny to the apex, **L** lamina dark green to purple, 15–90 × 3.6–4.2 cm, fleshy, densely lepidote on both faces, **Sp** divaricate to antrorse, coarse, 5–7 mm, 0.7–2.7 cm apart; **Inf** reddish, 1 × branched, glabrescent; peduncle ±1 cm Ø; peduncular **Bra** broadly ovate, the lower ones with a long linear lamina exceeding the internodes, the upper ones merely acuminate; **male Inf** with (5–) 13–25 ascending primary **Br** 5.5–22 cm long; **Fl** divaricate to ascending, laxly disposed, subsessile; floral **Bra** rose, ovate to oblong-ovate, 3.8–4.7 × 1.8–2 mm, acuminate, shorter than the sepals; **Sep** rose, broadly ovate, 5–5.6 × 3.3–3.8 mm, entire, acuminate to apiculate, glabrous; **Pet** rose, basally very shortly connate, elliptic, 9.5–10 × 3.7–5 mm, glabrous, obtuse; **St** subequal,

shorter than the petals; **Fil** 7.6–8.4 mm; **Anth** yellow,  $\pm 3$  mm, shortly apiculate; **female Inf** with 10–25 ascending primary **Br** 5.8–15 cm long; floral **Bra** triangular,  $3.5\text{--}4.5 \times \pm 3.3$  mm, acute to acuminate, longer than the sepals; **Fl** divaricate, pedicellate; **Ped**  $\pm 1$  mm; **Sep** rose, triangular,  $2.4\text{--}4.6 \times 2.65\text{--}3.4$  mm, glabrous, acuminate; **Pet** rose, narrowly triangular,  $8\text{--}10 \times 3.7\text{--}4.2$  mm, glabrous, acute; **Ov** reddish, ellipsoid,  $5\text{--}5.7 \times 1.7\text{--}2.7$  mm; **Sty**  $\pm 0.9$  mm; **Fr** green to light brown,  $12\text{--}23 \times 5.6\text{--}9$  mm, smooth; **Se** reddish to brown, 5.5–10 mm.

**H. roseana** L. B. Smith (Contr. Gray Herb. 117: 17, t. 1, figs. 41–42, 1937). **Type:** Mexico, Puebla (*Rose & al.* 9970 [US]). — **Distr:** Mexico (Puebla, Oaxaca); arid thorn scrub and cactus scrub, on limestone soils, 1500–1700 m. — Fig. 8.

Caespitose, flowering to 2.9 m tall; **Ros** to 60 cm  $\varnothing$  with 1 to several conspicuous, stout stolons to 1 m long; **L** 40–50, sheaths yellow adaxially, light brown abaxially, transversally elliptic,  $3.5\text{--}4.5 \times \pm 6$  cm, glabrous and lustrous on both faces, lepidote abaxially at the distal end, **L** lamina yellow-green to light green with red spots at the spine bases,  $29\text{--}43 \times 2.5\text{--}4$  cm, glabrous adaxially, finely appressedly white-lepidote abaxially, **Sp** reddish-brown, divaricate, some

antrorse or retrorse, 4–6 mm, 1.3–3.8 cm apart; **Inf**  $2 \times$  (rarely  $1 \times$ ) branched, glabrous; peduncle  $\pm 1.5$  cm  $\varnothing$ ; peduncular **Bra** light brown, linear to narrowly triangular, the lower spiny, the upper entire, gradually becoming shorter upwards; **male Inf** with  $>60$  primary branches 7.5–23 cm long, the basal primary **Br** with 2 basal lateral secondary branches; floral **Bra** stramineous to light brown, ovate,  $5.5\text{--}7.5 \times 3.5\text{--}4.2$  mm, erose and hyaline at the margins, much longer than the sepals; **Fl** divaricate to ascending, laxly disposed; **Ped** stout, 1–1.6 mm; **Sep** stramineous to light brown, widely ovate,  $3.2\text{--}3.4 \times 3.1\text{--}3.4$  mm, entire, glabrous, obtuse; **Pet** white, elliptic,  $5.3\text{--}5.8 \times 2.5\text{--}2.6$  mm, entire, glabrous, obtuse; **St** subequal, barely longer than the petals; **Fil** 2.8–4.2 mm; **Anth** greenish, 1.5–2 mm; **female Inf** with  $>50$  primary **Br** 9–25 cm long, basal primary branches with 2 basal lateral secondary branches; primary **Bra** triangular-ovate, long acuminate, 1.5–3 cm; floral **Bra** triangular-ovate, 4.5–6.2 mm, acute, longer than the sepals; **Fl** ascending, very laxly disposed, sometimes appearing subverticillate, sessile to subsessile; **Sep** greenish to light brown, triangular-ovate,  $3.2\text{--}3.7 \times 2\text{--}2.2$  mm, entire, glabrous, margin hyaline, acuminate; **Pet** white, triangular to ovate-triangular,  $5\text{--}5.2 \times 2.5\text{--}2.9$  mm, glabrous,

**Fig. 8** *Hechtia roseana*. (Copyright: A. Espejo-Serna)



entire, acute to acuminate; **Ov** wholly superior, greenish to rose, ellipsoid,  $4.9\text{--}5.1 \times \pm 2.4$  mm; **Fr** brown,  $10\text{--}12 \times 5\text{--}5.5$  mm, slightly lustrous, very faintly rugose; **Se** reddish-brown,  $5.5\text{--}6 \times \pm 1$  mm.

**H. rubicunda** López-Ferrari & Espejo (Acta Bot. Mex. 107: 154–158, ills., 2014). **Type:** Mexico, Oaxaca (*Martínez-Correa & al.* 116 [UAMIZ, IEB]). — **Distr:** Mexico (Oaxaca: Yautepec); tropical deciduous forest, on rocks on igneous cliffs, 500–850 m.

Solitary, flowering to 1.5 m tall; **Ros** 50–75 cm Ø; **L** 15–30, sheaths dark brown, glabrous and lustrous on both faces, depressed ovate,  $2.7\text{--}3.7 \times 5\text{--}6.5$  cm, margins minutely spinose, **L** lamina red-yellowish, narrowly triangular,  $28\text{--}60 \times 3.5\text{--}6.5$  cm, glabrous adaxially, densely appressed-lepidote abaxially, **Sp** yellowish to light brown, divaricate to antrorse except in the basal portion where they are retrorse,  $2\text{--}4.5$  mm,  $0.9\text{--}1.2$  cm apart; **Inf** erect to arcuate; **male Inf** 2× branched with 45–50 primary branches; peduncular **Bra** foliaceous, straw-coloured, sheaths triangular,  $0.8\text{--}1.2$  cm, lamina linear,  $1.7\text{--}15.5 \times 0.15\text{--}0.4$  cm, lepidote on both faces, margins entire, pungent; primary **Br** 6.6–30 cm, stalked; secondary **Br** ascending, 2–4.5 cm; floral **Bra** straw-coloured, ovate-triangular,  $1\text{--}1.5 \times 0.5\text{--}0.7$  mm, erose, glabrous, attenuate; **Fl** polystichous, divaricate; **Ped** 2 mm; **Sep** light brown, triangular,  $1.3\text{--}1.7 \times 1\text{--}1.3$  mm, acute; **Pet** white, elliptic,  $2.7\text{--}4 \times 2\text{--}2.3$  mm, acute; **St** subequal; **Fil** 3–3.2 mm; **Anth** yellow, 1.5 mm; **female Inf** 1× branched with 35–40 branches, occasionally the lower branches with a pair of secondary basal branches; peduncular **Bra** foliaceous, straw-coloured, sheaths triangular,  $0.8\text{--}1.2$  cm, lamina linear,  $1.7\text{--}15.5 \times 0.15\text{--}0.4$  cm, lepidote on both faces, margins entire, pungent; **Br** divaricate to ascending, 4.5–40 cm; floral **Bra** straw-coloured, ovate-triangular,  $1\text{--}1.5 \times 0.5\text{--}0.7$  mm, erose, acuminate, glabrous, longer than the pedicels; **Ped** 1 mm; **Fl** polystichous, reflexed at anthesis; **Sep** green with rose apex, triangular,  $1.5\text{--}1.7 \times 1.2\text{--}1.4$  mm, acute; **Pet** white, triangular,  $3.8\text{--}4 \times 1.8\text{--}2$  mm, attenuate and acuminate; **Ov** rose-coloured, ovoid, 3.8–4 mm; **Fr** light green, ovoid,  $10\text{--}12 \times 4\text{--}4.5$  mm, lustrous; **Se** reddish.

**H. santanae** I. Ramírez & P. Carrillo (Phytotaxa 266(4): 262–266, ills., 2016). **Type:** Mexico, Jalisco (*Ramírez & al.* 1940 [CICY, IBUG, MEXU, US, ZEA]). — **Distr:** Mexico (S Jalisco); tropical deciduous forest, 780–920 m.

Caespitose, flowering 1.1–1.4 m tall; **Ros** globose, to  $30 \times 20\text{--}40$  cm Ø; **L** 30–40 per rosette, sheaths pale yellow with light brown spots when dry, broadly ovate to broadly oblong,  $3\text{--}4 \times 3.5\text{--}4.8$  cm, finely spiny, glabrous in the middle area but with white-lepidote margins, **L** lamina narrowly triangular, attenuate,  $12\text{--}34 \times 1.7\text{--}2.8$  cm, succulent, green, densely to sparsely silvery-lepidote adaxially, densely white-lepidote abaxially, **Sp** brownish, antrorse, 1–3 mm,  $0.4\text{--}1.7$  cm apart; **Inf** 1× branched; **male Inf** with 40–45 **Br** 5.5–13.5 cm long; floral **Bra** purple with a brown apex, oblong-triangular,  $3.4\text{--}3.9 \times 2.2\text{--}2.4$  mm, acuminate, erose and hyaline, glabrous, shorter than the sepals; **Fl** erect,  $5\text{--}5.5 \times 3.8\text{--}4.2$  mm, subsessile; **Sep** purple with a brown apex, ovate,  $2.3\text{--}2.7 \times 1.8\text{--}2.3$  mm, entire, glabrous, acute; **Pet** white, elliptic,  $4.3\text{--}4.8 \times 3\text{--}3.2$  mm, entire, rounded; **St** unequal, shorter than the petals; **Fil** 3.8–4.4 mm; **Anth** reddish, 2–2.2 mm; **female Inf** with 30–70 **Br** 4–9.5 cm long; floral **Bra** purple with a brown apex, oblong,  $4\text{--}4.2 \times 3\text{--}3.2$  mm, acuminate, erose and hyaline, glabrous, longer than the sepals; **Fl** erect,  $5.7\text{--}6 \times 3\text{--}4$  mm, pedicellate; **Ped** 2.8–3.2 mm; **Sep** purple with a brown apex, triangular,  $2.4\text{--}2.9 \times 2\text{--}2.2$  mm, entire, glabrous, acute; **Pet** white-purplish, oblong,  $4.7\text{--}5 \times 2\text{--}2.2$  mm, entire, acute; **Ov** purple to reddish, oblong to ellipsoid,  $3\text{--}3.2 \times 1.7\text{--}2$  mm Ø; **Fr** brown,  $6\text{--}11 \times 3\text{--}4$  mm Ø; **Se** 5–6.8 mm.

Material of this species was previously identified as *H. laevis*.

**H. schottii** Baker *ex* Hemsley (Biol. Centr.-Amer., Bot. 3: 318, 1884). **Type:** Mexico, Yucatán (*Schott* 645 [BM, F]). — **Distr:** Mexico (Yucatán: Opichén; Campeche: Calakmul); tropical deciduous forest, on the ground or on limestone rocks, 30–260 m.

Forming extensive colonies, flowering 2–2.5 m tall, rhizomatous; **L** numerous, sheaths stramineous to light brown, suborbicular,  $4\text{--}5 \times 4\text{--}5$  cm,



glabrous, lustrous, margins spiny, **L** lamina green, 50–100 × 3.5–4.5 cm, glabrous adaxially, finely cinereous-lepidote abaxially, **Sp** mostly divaricate, some retrorse or antrorse, 5–6 mm, 1.4–3 cm apart; **Inf** seemingly lateral, 2–3× branched, densely and finely white-flocculose throughout; peduncle ±1 cm Ø; peduncular **Bra** light brown, triangular, 4.5–5 cm, acuminate; **male Inf** with numerous ascending to erect primary **Br** 4–20 cm long; secondary **Br** 1.5–8 cm; primary **Bra** light to dark brown, ovate, 1–6 × 0.6–1.5 cm, entire, acuminate; floral **Bra** brown, ovate to broadly ovate, 4–5 mm, acute, apiculate, about equalling the sepals; **Fl** ascending, subverticillate and densely to laxly disposed, subsessile; **Sep** brown, ovate, 2.8–3 × 2.2–2.4 mm, floccose-lepidote, margins hyaline, erose, obtuse; **Pet** basally shortly connate, white, elliptic, 4.4–4.8 × 2.7–2.8 mm, glabrous, entire, obtuse; **St** unequal, barely shorter than the petals; **Fil** 2.3–3.9 mm; **Anth** greenish, ±1.7 mm, apiculate; **female Inf** with numerous ascending to erect primary **Br** 10–20 cm long; secondary **Br** 2–8 cm; primary **Bra** light to dark brown, ovate, 1–6 × 0.6–1.5 cm, entire, acuminate; floral **Bra** brown, ovate to broadly ovate, 4–5 mm, acute, apiculate, about equalling the sepals; **Fl** ascending, subverticillate and densely to laxly disposed, subsessile; **Sep** brown, ovate, 4–4.4 × 3–3.3 mm, floccose-lepidote, margin hyaline, erose, obtuse to acute; **Pet** basally shortly connate, white, triangular to ovate, 5–5.2 × 3–3.3 mm, glabrous, entire, acute; **Ov** rose, ellipsoid, ±4.5 × ±2.3 mm, white-lepidote; **Fr** light brown, 8–9 × 4.5–4.7 mm, white-lepidote to glabrescent, acute; **Se** reddish-brown, 3.5–6 mm.

**H. sphaeroblata** B. L. Robinson (Proc. Amer. Acad. Arts 35: 323, 1900). **Type:** Mexico, Guerrero (*Nelson* 2044 [GH, US]). — **Distr:** Mexico (Puebla, Guerrero, Oaxaca); tropical deciduous forest, on the ground or rarely on rocks, 800–1900 m.

Caespitose, flowering 2.5–3.5 m tall; **L** numerous, sheaths stramineous, orbicular to ovate, 5.6–8 × 5.8–11 cm, lepidote adaxially, glabrous and lustrous abaxially, margins spiny, **L** lamina green, 25–110 × 3–5.5 cm, inconspicuously

finely white-lepidote on both faces, **Sp** brownish to reddish, antrorse, 2.5–5 mm, 1.5–3.2 cm apart; **Inf** seemingly lateral, 2× branched, glabrous; peduncle 2.5–2.8 cm Ø; peduncular **Bra** green to light brown, foliaceous, linear, 24–50 × 0.5–0.7 cm, margin spiny, pungent; **male Inf** with numerous ascending flattened primary **Br** 28–40 cm long and with 2–15 divaricate secondary **Br** 3–12 cm long; primary **Bra** stramineous, ovate-triangular, 1.5–2 cm, attenuate; floral **Bra** scarious, triangular, 1–1.5 mm; **Fl** divaricate, single to subverticillate, subsessile; **Sep** light brown, ovate, 2–2.3 × ±1.6 mm, glabrous, entire, obtuse; **Pet** white, suborbicular to elliptic, 3–3.4 × 2–2.2 mm, glabrous, entire, obtuse; **St** subequal, barely shorter than the petals; **Fil** 2.5–2.7 mm; **Anth** yellowish, ±1 mm; **female Inf** with numerous ascending flattened primary **Br** 22–42 cm long, with 8–15 ascending secondary **Br** 2.5–10 cm long; primary **Bra** stramineous, ovate-triangular, 1.2–2.5 cm, attenuate; floral **Bra** white, ovate-triangular, 1.5–1.8 mm, erose, apiculate, shorter than the sepals; **Fl** ascending to divaricate, subverticillate, subsessile to shortly pedicellate; **Ped** stout, 0.8–1.2 mm; **Sep** white, ovate, 1.9–2.3 × ±1.6 mm, glabrous, entire, obtuse; **Pet** white, triangular, 2.5–3 × ±1.5 mm, glabrous, entire, acute; **Ov** green, ellipsoid, 2–2.5 × ±1.2 mm, glabrous; **Fr** light brown, 5.8–6.8 × 2.5–4 mm; **Se** dark brown, 4.7–5 mm.

**H. stenopetala** Klotzsch (Allg. Gartenzeitung 3: 402, 1835). **Type:** Mexico, Veracruz (*Schiede & Deppe* s.n. [B, HAL]). — **Distr:** Mexico (C Veracruz); tropical deciduous forest, on the ground and on rocks of lava flows, 100–700 m.

**Incl.** *Hechtia besseriana* J. Verschaffelt (1874); **incl.** *Hechtia glabra* Brandege (1920).

Caespitose, flowering 0.5–2 m tall; **Ros** ± elongated, short- to long-caulescent, stems rhizomatous, ±1.6 cm Ø; **L** numerous, sheaths yellowish-brown, ovate to widely ovate to oblong, 3.5–6 × 2–4.6 cm, lustrous towards the base, brown-lepidote toward the apex, margins finely serrate and densely lepidote, **L** lamina green, sometimes tinged with red, 28–56 (–70) × 1.3–3.5 cm, densely lepidote on both faces, **Sp** divaricate to antrorse, light brown, 1.5–2.3 mm,



1.4–2.2 cm apart; **Inf** 2× branched; **male Inf** with numerous primary **Br** 10–15 cm long; peduncle 9–11 mm Ø, glabrous; peduncular **Bra** yellowish, narrowly triangular to linear, 6–12 × 0.2–1 cm, white-lepidote, entire, decreasing in size upwards; floral **Bra** whitish-brown, oblong to elliptic, 0.7–1.2 mm, erose, acute, equal or shorter than the pedicels; **Fl** polystichous, divaricate; **Ped** 0.8–1 mm; **Sep** elliptic to broadly triangular, 1.6–2.1 × 1–1.7 mm, rounded; **Pet** white, broadly elliptic to broadly oblong, 2.5–3 × 1.6–2 mm, rounded; **St** longer than the petals; **Fil** 2.5–3 mm; **Anth** green, 1.1–1.4 mm; **female Inf** with numerous primary **Br** 10–15 cm long; peduncle cylindrical, 8–13 mm Ø; peduncular **Bra** yellowish, narrowly triangular to linear, (2–) 11–12 (–18) × (0.5–) 0.8–1 cm, deciduous; floral **Bra** oblong to triangular, 0.9–1.1 × ±0.5 mm, rounded, equal or longer than the pedicels; **Fl** polystichous, divaricate; **Ped** obconical, 0.7–1 mm; **Sep** green, triangular to ovate, 1.4–2.3 × 1–2 mm, rounded or acute; **Pet** white, triangular, 2.5–3 × 1.3–1.6 mm, acute; **Ov** green, ellipsoid, 3–4 × 1.3–2 mm; **Fr** dark brown, 6–8 × 3–4 mm; **Se** brown, 2.5–2.9 mm.

**H. subalata** L. B. Smith (Contr. Gray Herb. 117: 15–16, t. 1, fig. 29, 1937). **Type:** Mexico, Durango (*Rose* 3467 [US]). — **Distr:** Mexico (Durango, Zacatecas, Nayarit, Jalisco); tropical shrubland, on the ground or on rocks, 900–1750 m.

Caespitose, flowering to 1.5 m tall; **L** numerous, sheaths stramineous, square to transversely oblong, 4–4.5 × 4.5–4.7 cm, glabrous, lustrous, erose to spiny at the margins, **L** lamina green to glaucous, 20–36 × 1.5–3 cm, densely appressedly white-lepidote on both faces, long attenuate and coiled in the apical portion, margins repand, **Sp** light brown, divaricate to retrorse or some antrorse, 2.2–4.5 mm, 0.65–1.3 cm apart; **Inf** 1× branched, white-lepidote, glabrescent with age; peduncle 1.3–1.5 cm Ø; peduncular **Bra** light brown, amplexicaul, ovate to oblong-ovate, with a short narrowly triangular lamina, 5–5.6 × 1.5–2.3 cm, irregularly dentate, white-lepidote abaxially, margins irregularly dentate; **male Inf** with numerous ascending to erect primary **Br** 4–8 cm long; primary **Bra** stramineous to light brown, ovate to lanceolate, 4–6.6 × 1.6–2 cm,

acuminate, glabrous adaxially, white-lepidote abaxially, margins irregularly dentate; floral **Bra** light brown, linear to very narrowly triangular, 1.6–2.5 mm, shorter than the pedicels; **Fl** polystichous, ascending to divaricate; **Ped** conical, 2.5–3.5 mm, sulcate; **Sep** brownish, triangular, 4.8–5.3 × 2–2.3 mm, entire, glabrous, acute; **Pet** white, elliptic, 5.7–6 × 3–3.3 mm, entire, glabrous, rounded; **St** subequal, shorter than the petals; **Fil** 5.3–5.6 mm; **Anth** yellow, ±2 mm; **female Inf** with numerous ascending primary **Br** 2–10 cm long; primary **Bra** stramineous to light brown, ovate-triangular, 2.5–4.6 × 1.4–1.6 cm, glabrous adaxially, white-lepidote abaxially, margins irregularly spiny-dentate, acuminate; floral **Bra** light brown, narrowly triangular to linear, 2–2.5 mm, shorter than the pedicels; **Fl** densely disposed to agglomerated, ascending; **Ped** stout, conical, 2.5–3.5 mm, sulcate; **Sep** brownish, elliptic to ovate-triangular, ±3.5 mm, erose, hyaline, rounded; **Pet** white, triangular, 4.5–5.2 × 2.3–2.5 mm, entire, glabrous, acute; **Ov** green, ellipsoid, ±4 mm; **Fr** green to light brown, 10–14 × 7–9 mm; **Se** brown-reddish, 4–4.8 mm.

**H. tehuacana** B. L. Robinson (Proc. Boston Soc. Nat. Hist. 31: 265–266, 1904). **Type:** Mexico, Puebla (*Pringle* 8578 [GH, B, BM, ENCB, G, GOET, K, MEXU, NY, P, UC, US, VT, Z]). — **Distr:** Mexico (Puebla, Oaxaca); xerophytic shrubland, calcareous hills, 1650–1750 m.

**Incl.** *Hechtia pueblensis* Burt-Utley & al. (2011).

Solitary or in small groups, flowering to 2.2 m tall; **Ros** ±50 cm Ø; **L** numerous, sheaths yellow adaxially, brownish abaxially, square to ovate, 4.4–7 × 4.3–7.2 cm, glabrous, distally densely lepidote on both faces, serrate, **L** lamina green, 25–46 × 0.8–1.8 cm, sparsely lepidote to lepidote on both faces, **Sp** light brown to reddish, divaricate to antrorse or sometimes retrorse, 3.8–8.9 mm, 0.53–2.5 cm apart; **Inf** 2× branched, glabrescent; peduncle cylindrical, 1–2 cm Ø; basal peduncular **Bra** foliaceous, brown, 7.3–16.5 cm, sparsely lepidote, serrate, upper peduncular **Bra** caudate, entire; **male Inf** with up to 86 ascending primary **Br** 3.6–8 cm long; secondary **Br** basal, ascending, 1.9–4.9 cm; primary **Bra** ovate-triangular, sparsely

lepidote, serrate, 2–7.3 cm; floral **Bra** brownish, triangular, 2–3.5 × 0.2–1.2 mm, entire, glabrous, acuminate; **Fl** divaricate, densely disposed; **Ped** stout, 1–2.7 mm, glabrous; **Sep** brownish, ovate, 1.6–4.3 × 0.6–2.1 mm, glabrous, entire, acute; **Pet** green, oblong, 3.2–4.7 × 1.7–3.2 mm glabrous, entire, rounded; **St** equal, longer than the petals; **Fil** 2.3–4.2 mm; **Anth** yellow, 0.5–1.9 mm; **female Inf** with up to 44 ascending primary **Br** 5.1–6 cm long; secondary **Br** ascending, 1.3–2.4 cm; primary **Bra** brown, ovate-triangular, 3.1–4.6 cm, sparsely lepidote, serrate; floral **Bra** brownish, triangular, 1.5–2.8 × 0.4–1.2 mm, entire, glabrous, acute; **Fl** divaricate, densely disposed; **Ped** stout, 2.8–4.4 mm; **Sep** brownish, ovate, 1.3–2.6 × 0.6–1.2 mm, glabrous, entire, acute; **Pet** green, triangular, 2.1–3.6 × 0.9–1.4 mm, glabrous, entire, acute; **Ov** green, ovoid, ±2 mm; **Fr** brownish, 7–10 × 4.4–7.5 mm Ø; **Se** brownish, 3–3.8 mm.

**H. texensis** S. Watson (Proc. Amer. Acad. Arts 20: 374–375, 1885). **Type:** USA, Texas (*Havard* 85 [GH, GH]). — **Distr:** USA (Texas), Mexico (Coahuila, Nuevo León, Durango, Zacatecas); xerophytic scrub and rosette-rich shrubland, limestone hills and ledges, on the ground or on rocks, 900–1850 m.

**Incl.** *Hechtia scariosa* L. B. Smith (1937);

**incl.** *Hechtia zacatecae* L. B. Smith (1937).

Caespitose, flowering 0.55–2 m tall; **L** numerous, sheaths light brown, broadly ovate to suborbicular, 2.5–5.5 × 3–5.5 cm, glabrous and lustrous on both faces, densely serrulate to serrulate, **L** lamina green or green with red to bright rose stripes, 20–45 × 1–5 cm, glabrous and lustrous adaxially, densely appressedly white-lepidote abaxially, **Sp** yellow to dark castaneous, antrorse to divaricate or some retrorse, 4–6 mm, 1–2.7 cm apart; **Inf** seemingly lateral, lepidote, 1× to rarely 2× branched; peduncle strongly flattened at the base, 3.5–7.5 mm Ø; peduncular **Bra** stramineous to dark brown, ovate to triangular, 2.7–5 × ±1 cm, acuminate, shorter than the internodes; **male Inf** with 7–18 ascending slender primary **Br** 4–26 cm long; primary **Bra** stramineous, ovate-triangular, 3.7–12 mm, attenuate; secondary **Br** 1.7–4 cm; floral **Bra** rose with a broad hyaline margin, suborbicular, 4.5–7 mm, erose, apiculate, shorter than

or nearly equalling the sepals; **Fl** ascending, subverticillate, sessile; **Sep** green, ovate to elliptic, 4.5–6 × 2.5–4 mm, margin hyaline, densely lepidote, carinate, obtuse; **Pet** white, elliptic, connate basally, 5–8.5 × 2.2–3.5 mm, obtuse, slightly lepidote abaxially; **St** unequal, shorter than the petals; **Fil** 3–6 mm; **Anth** green, sagittiform, 1.5–2 mm; **female Inf** with 11–17 ascending to appressed primary **Br** 3–23 cm long; primary **Bra** 1.2–1.5 cm, attenuate, acute; **Fl** ascending, subverticillate, sessile to subsessile; floral **Bra** brownish, triangular-ovate, 4–6 mm, shorter than the sepals; **Sep** brownish, ovate to broadly ovate, 4.5–7 × ±4 mm; **Pet** white, elliptic, 7.5–10 × 4.5–5 mm, glabrous, entire, rounded; **Ov** green to brownish, ovoid, densely lepidote; **Fr** brown, 8–12 × 5–6 mm, lepidote, glabrescent.

Vernacular names: “Texas False Agave”, “Guapilla de Texas”.

**H. tillandsioides** (André) L. B. Smith (Contr. US Nation. Herb. 29: 431, 1951). **Type:** Mexico (*Anonymus* s.n. [K]). — **Distr:** Mexico (San Luis Potosí, Querétaro, México, Guerrero); tropical deciduous forest and shrublands, on perpendicular limestone cliffs and ledges, 600–1800 m. **I:** Roguenant & al. (2016: 145, as *H. caerulea*).

≡ *Bakeria tillandsioides* André (1889) (*incorrect name*, Art. 11.4) ≡ *Bakerantha tillandsioides* (André) L. B. Smith (1934); **incl.** *Vriesea glaucophylla* hort. ex Mez (1934) (*nom. illeg.*, Art. 53.1); **incl.** *Niveophyllum caeruleum* Matuda (1965) ≡ *Hechtia caerulea* (Matuda) L. B. Smith (1972); **incl.** *Hechtia integerrima* M. B. Foster (1968).

Solitary to caespitose, pendulous, flowering to 1.6 m tall, shortly caulescent; **Ros** asymmetrical, 30–80 cm Ø; **L** numerous, recurved and pendent, sheaths white to light brown, square to transversally oblong, 5–7.5 × 3.5–5 cm, white-lepidote on both faces, glabrescent, entire and sinuate, **L** lamina light green adaxially, white-lepidote abaxially, 30–80 × 1.5–4 cm, long-attenuate, minutely serrate to entire; **Inf** erect to arching or pendent, 1–2× branched, glabrous; peduncle 6–13 mm Ø; peduncular **Bra** light brown to purplish-brown, foliaceous, linear to very narrowly triangular, 5–70 × 0.8–1 cm, entire

to minutely serrate, glabrous adaxially, densely white-lepidote abaxially, involute, long-attenuate, longer than the internodes, becoming gradually shorter upwards; **male Inf** with 20–25 ascending primary **Br** 8–30 cm long; primary **Bra** light brown, linear to triangular, 10–20 × 3–8 mm, acuminate; secondary **Br** when present 2–6, 4–14 cm, divaricate to diffuse; floral **Bra** brown to purplish, linear, 2–3 × ±0.5 mm, shorter than the pedicels; **Fl** polystichous, divaricate; **Ped** filiform, 5–7 mm; **Sep** purplish to rose, triangular to narrowly triangular, 1.5–2.8 × 1–1.7 mm, glabrous, entire, rounded; **Pet** lilac, ovate to elliptic, 5–6 × 3.3–3.8 mm, rounded; **St** subequal, longer than the petals; **Fil** 3–4.5 mm; **Anth** green, ±1 mm; **female Inf** with 14–16 ascending primary **Br** 25–35 cm long; primary **Bra** brown-purplish, triangular, 2–7 × 0.8–1.2 cm, long-attenuate to acuminate; secondary **Br** 7–12, 5–16 cm, ascending; floral **Bra** light brown, linear to triangular, 1.6–1.8 × ±1 mm, acuminate; **Fl** polystichous, divaricate; **Ped** filiform, 2.3–4 mm; **Sep** green to purplish, triangular, 2–2.2 × 1–1.3 mm, acute; **Pet** lilac, elliptic to oblong, 4–5 × 2.3–2.6 mm, rounded; **Ov** green, ±3.5 × ±3 mm; **Fr** green, narrowly ovoid, 7.7–8 × ±3 mm, reflexed and pointing downwards at maturity.

**H. zamudioi** Espejo & al. (Acta Bot. Mex. 83: 55–59, ills., 2008). **Type:** Mexico, Querétaro (*Zamudio & Hernández* 11285 [IEB, MEXU, NY, UAMIZ]). — **Distr:** Mexico (Querétaro: Peñamiller, Pinal de Amoles, San Joaquín); arid and montane shrubland, on vertical calcareous cliffs or rocky bluffs and ledges, 850–1650 m.

Caspirose, forming extensive colonies, flowering to 2 m tall; **Ros** spreading, 60–70 cm Ø; **L** numerous, sheaths straw-yellow, widely ovate to subquadrate, 8.5–9 × 8.8–10.2 cm, lustrous, glabrous on both faces, with a yellow exudate, **L** lamina blue-green, slightly discoloured, 30–48 × 3.5–5 cm, densely white-lepidote on both faces, **Sp** light brown to reddish, antrorse, slender, 1.5–2 mm, 0.6–1.5 cm apart; **Inf** glabrous; peduncle cylindrical, 1.2–2 cm Ø; peduncular **Bra** foliaceous, straw-yellow, narrowly triangular to triangular, 10–30 × 1.8–2.5 cm, attenuate, pungent, the basal ones imbricate and

longer than the internodes, becoming progressively reduced distally, sheaths subquadrate, 2–2.5 cm long, entire, lamina densely white-tomentose on both faces, spiny along the margins; **male Inf** 1–2 × branched, with numerous primary **Br** 15–25 cm long, with 2 basal secondary **Br** 5–9.5 cm long; primary **Bra** light brown, narrowly triangular to lanceolate, 5.5–7 × 1.5–1.7 cm, glabrous, acuminate, hyaline and minutely spiny along the margins; floral **Bra** filiform, white, inconspicuous, to 3 mm, entire, glabrous; **Fl** divaricate to diffuse, laxly disposed; **Ped** filiform, 3–6 mm; **Sep** green, triangular to ovate or oblong, 3.5–4.5 × 2–3.5 mm, hyaline, acute; **Pet** green, elliptic, 6–8 × 3.5–4 mm, rounded; **St** subequal, shorter than the petals; **Fil** 6–7 mm; **Anth** green, ±3 mm; **female Inf** 1 × branched with numerous diffuse to ascending primary **Br** 6–10 cm long; primary **Bra** light brown, lanceolate to narrowly triangular or narrowly ovate, glabrous, 3.5–7 × 0.9–1.5 cm, acuminate, hyaline and minutely spiny along the margins; floral **Bra** white, filiform, inconspicuous, to 3 mm, entire, glabrous; **Fl** divaricate, laxly disposed; **Ped** filiform, 5–9 mm; **Sep** green, triangular to narrowly triangular, 3–4 × 1.2–1.4 mm, apiculate; **Pet** green, narrowly triangular to narrowly ovate, 5–8 × 2.5–3 mm, acute to rounded; **Ov** green, ovoid to ellipsoid, 5–7 × 3–4 mm; **Fr** green, light brown when mature, 8–12 × 5–6 mm; **Se** light brown, 5–6 mm.

## References

- Burt-Utley, K. & Utley, J. F. (2011) Contributions toward a revision of *Hechtia* (Bromeliaceae, Pitcairnioideae) I. New and noteworthy species of *Hechtia* from Mexico. *Phytoneuron* 2011(59): 1–17, ills.
- Espejo-Serna, A. (2012) El endemismo en las *Liliopsida* mexicanas. *Acta Bot. Mex.* 100: 195–257. <http://www.redalyc.org/articulo.oa?id=57424406008>
- Espejo-Serna, A. [& al. 2005], Lopez-Ferrari, A. R. & Ramirez-Morillo, I. (2005) *Bromeliaceae*. In: Sosa, V. (ed.): Flora de Veracruz, 136. Veracruz (MX): Instituto de Ecología A. C.
- Espejo-Serna, A. [& al. 2007], Lopez-Ferrari, A. R., Martinez-Correa, N. & Pulido-Esparza, V. A. (2007) Bromeliad flora of Oaxaca, Mexico: Richness and distribution. *Acta Bot. Mex.* 81: 71–147, maps. <http://www.redalyc.org/articulo.oa?id=57408105>

- Espejo-Serna, A. [& al. 2010a], Lopez-Ferrari, A. R. & Ramirez-Morillo, I. (2010a) *Bromeliaceae*. In: Rzedowski-Rotter, J. & Calderón de Rzedowski, G. (eds.): *Flora del Bajío y de Regiones Adyacentes*, 165. Pátzcuaro (MX): Instituto de Ecología.
- Espejo-Serna, A. [& al. 2010b], López-Ferrari, A. R. & Zamudio, S. (2010b) Reencuentro con *Hechtia epigyna* Harms (*Bromeliaceae*). *Acta Bot. Mex.* 90: 11–18, ills., map. <http://www.redalyc.org/pdf/574/57412073003.pdf>
- Espejo-Serna, A. [& al. 2010c], Martínez-Correa, N. & Lopez-Ferrari, A. R. (2010c) Neotypification of *Hechtia podantha* (*Bromeliaceae*). *J. Bot. Res. Inst. Texas* 4(1): 221–223.
- Espejo-Serna, A. [& al. 2012], López-Ferrari, A. R., Ceja-Romero, J. & Mendoza-Ruiz, A. (2012) Neotipificación de *Hechtia lanata* (*Bromeliaceae*; *Hechtioideae*), especie endémica de Oaxaca, México. *Bot. Sci.* 90(4): 385–388, ills. <http://www.scielo.org.mx/pdf/bs/v90n4/v90n4a3.pdf>
- Espejo-Serna, A. [& al. 2013], López-Ferrari, A. R., Martínez-Correa, N. & Till, W. (2013) A note on the typification of *Hechtia galeottii* (*Hechtioideae*, *Bromeliaceae*). *Phytotaxa* 94(2): 41–48, ills., map. <https://doi.org/10.11646/phytotaxa.94.2.2>.
- Felger, R. S. & Yetman, D. (2000) Roasting the *Hechtia* out of it: The use of *Hechtia montana* (*Bromeliaceae*) as a food plant in Sonora, Mexico. *Econ. Bot.* 54(2): 229–233. <https://doi.org/10.1007/BF02907827>.
- Kemble, B. (2016) *Hechtia lanata*. *Cact. Succ. J. (US)* 88(3): 104–109, ills. <https://doi.org/10.2985/015.088.0302>.
- Kopfstein, R. (2015) An ethnobotanical note: *Hechtia edulis*. *J. Bromeliad Soc.* 64(4): 258–263, ills.
- López-Ferrari, A. R. [& al. 2008], Espejo-Serna, A., Ceja-Romero, J. & Mendoza-Ruiz, A. (2008) *Hechtia matudae*, a spectacular, though neglected Bromeliad from Mexico. *J. Bromeliad Soc.* 58(2): 56–60, ills.
- López-Ferrari, A. R. [& al. 2011], Espejo-Serna, A., Ceja-Romero, J. & Mendoza-Ruiz, A. (2011) *Hechtia lundelliorum*, another spectacular and little known bromeliad from Mexico. *J. Bromeliad Soc.* 60(5): 211–215, ills.
- Martínez-Correa, N. (2008) *Sistematica del complejo de especies de Hechtia podantha Mez (Pitcairnioideae, Bromeliaceae)*. Iztapalapa (MX): Universidad Autónoma Metropolitana; unpubl. M.Sc. thesis.
- McVaugh, R. (1989) *Flora Novo-Galiciana. A descriptive account of the vascular plants of Western Mexico. Vol. 15: Bromeliaceae to Dioscoreaceae*. Ann Arbor (US): University of Michigan Herbarium.
- Mez, C. (1896) *Bromeliaceae*. In: Candolle, C. De (ed.): *Monographiae phanerogamarum*. Vol. 9. Paris (FR): Masson & Cie. <https://doi.org/10.5962/bhl.title.45961>.
- Mez, C. (1935) *Bromeliaceae*. In: Engler, A. & Diels, L. (eds.): *Das Pflanzenreich*; IV(32), Heft 100 [parts 2–4]. Berlin (DE): Wilhelm Engelmann. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=592>
- Pulido-Esparza, V. A. [& al. 2004], Lopez-Ferrari, A. R. & Espejo-Serna, A. (2004) *Flora bromeliológica del estado de Guerrero, Mexico: Riqueza y distribución*. *Bol. Soc. Bot. México* 75: 55–104. <http://www.redalyc.org/articulo.oa?id=57707504>
- Ramírez Morillo, I. M. & Jimenez-Nah, C. F. (2012) A new species of *Hechtia* (*Hechtioideae*, *Bromeliaceae*) from Puebla, Mexico. *Phytotaxa* 42: 1–8. <https://doi.org/10.11646/phytotaxa.42.1.1>.
- Ramírez Morillo, I. [& al. 2014a], Jiménez, C. F., Fernández-Concha, G. C. & Pinzón, J. P. (2014a) Three new species and growth patterns in *Hechtia* (*Bromeliaceae*; *Hechtioideae*). *Phytotaxa* 178(2): 113–127, map, ills. <https://doi.org/10.11646/phytotaxa.178.2.3>.
- Ramírez Morillo, I. [& al. 2014b], Camevali, G., Jiménez Nah, C. & Pinzón, J. P. (2014b) Portraits of *Hechtia* (*Bromeliaceae*; *Hechtioideae* [sic!]): *Hechtia isthmusiana* Burt-Utley. *J. Bromeliad Soc.* 64(1): 26–33, ills.
- Ramírez-Morillo, I. [& al. 2016], Carrillo-Reyes, P., Tapiamunoz, J. L. & Cetzal-Ix, W. (2016) An addition to genus *Hechtia* (*Hechtioideae*; *Bromeliaceae*) from Jalisco, Mexico. *Phytotaxa* 266(4): 261–270, map, ills. <https://doi.org/10.11646/phytotaxa.266.4.3>.
- Roguenant, A. [& al. 2016], Lecouffe, M. & Raynal-Roques, A. (2016) *Les Broméliacées. Approche panoramique d'une grand famille "américaine"*. Paris (FR): Belin.
- Rzedowski, J. (1991) El endemismo en la flora fanerogámica Mexicana: Una apreciación analítica preliminar. *Acta Bot. Mex.* 15: 47–64, ills. <http://www.redalyc.org/articulo.oa?id=57401505>
- Siekkinen, A. (2015) The mystery of *Hechtia argentea* — Part 1 / Part 2. *J. Bromeliad Soc.* 65(1): 48–57, (2): 100–110, ills.
- Smith, L. B. (1938) *Bromeliaceae*. In: *North American Flora* 19(2): 61–228, keys. New York (US): New York Botanical Garden. <http://biodiversitylibrary.org/page/28708822>
- Smith, L. B. & Downs, R. J. (1974) *Flora Neotropica. Monograph No. 14 [Bromeliaceae]. Part 1: Pitcairnioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4393694>
- Utley, J. & Burt-Utley, K. (1994) *Bromeliaceae*. In: Davidse, G., Sousa S., M. & Chater, A. O. (eds.): *Flora Mesoamericana* 6: 89–156. Mexico (MX): Universidad Nacional Autónoma. <http://www.tropicos.org/Name/42000361?projectid=3&langid=66>



## × *Neobergia* BROMELIACEAE

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× **Neobergia** E. L. Smith (J. Bromeliad Soc. 33 (2): 73, 1983). — **Distr:** Cultivated only.

= *Neoregelia* × *Billbergia*. Smith (1983) lists the combination *B. nutans* × *N. spectabilis* (= × *Neobergia* ‘Peneri’), and later, *B. nutans* × *N. carolinae* was mentioned as × *Neobergia* ‘Noddy’. The plants are like a robust *B. nutans* but become red during flowering, and have a

shortened, ± erect (rather than arching or hanging) inflorescence.

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### References

Smith, E. L. (1983) Bigeneric hybrids — A listing. J. Bromeliad Soc. 33(2): 69–75. <http://journal.bsi.org/V33/2/>

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## Neoglaziovia BROMELIACEAE

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**Neoglaziovia** Mez (in Martius, Fl. Bras. 3(3): 426, 1894). **Type:** *Bromelia variegata* Arruda. — **Bromelioideae** — **Lit:** Smith & Downs (1979: 2036–2038, Fl. Neotropica). **Distr:** NE Brazil. **Etym:** Gr. ‘neos’, new (to avoid a homonym); and for Auguste F. M. Glaziou (1828–1906), French botanical traveller collecting 1861–1895 in Brazil.

Perennial terrestrial **Ros** plants, stemless, with underground rhizomes, forming dense to open colonies; **L** 3–10 per rosette, with indistinct entire sheath, lamina very long and narrow, stiff and succulent, margins with laxly arranged short **Sp** 2–4 (–6) mm; **Inf** terminal, shorter than the leaves, unbranched, peduncular **Bra** longer than the internodes, leaf-like, fertile part few- to many-flowered, lax or dense; **Fl** shortly pedicellate or sessile, glabrous; **Sep** free, ± symmetrical, red; **Pet** free, symmetrical, bright purple, with 2 scales at the base; **St** included; **Fil** free; **Ov** completely inferior; **Fr** fleshy berries.

*Neoglaziovia* is easily recognized by the rosettes with few ascending to erect, narrowly linear and succulent leaves. Its systematic position within *Bromelioideae* is not well-resolved. Schulte & al. (2009) found it as basal sister of the “core bromelioids”, but with limited support. Evans

& al. (2015) did not even find the 2 studied species (*N. variegata*, *N. burle-marxii*) to form a monophyletic clade, and both appear as separate entities as part of an extensive polytomy in their Eubromelioid clade.

Leal & al. (2006) and Lemos Pereira & Maciel Quirino (2008) report hummingbird pollination (mainly by *Chlorostilbon aureoventris*) for *N. variegata*. — An intergeneric hybrid with *Orthophytum* has been formally named ×*Orthoglaziovia*.

**N. burle-marxii** Leme (J. Bromeliad Soc. 40(3): 101–103, ill., 1990). **Type:** Brazil, Bahia (*Burle-Marx* s.n. [HB, RB]). — **Distr:** Brazil (Bahia); Caatinga vegetation, sandy soil.

**L** to 3 m, lamina linear, narrowing gradually to the tip, 2.5 cm wide at the base, very rigid and thick, strongly canaliculate, upper face inconspicuously white-lepidote, lower face uniformly densely white-lepidote in longitudinal rows; **Inf** to 70 cm, erect, peduncular **Bra** not completely covering the peduncle, lower ones leaf-like, upper ones narrowly lanceolate, reddish, densely white-lepidote on both faces; fertile part of the **Inf** dense, 30- to 40-flowered, with an apical tuft of small bracts; **Fl** sessile, spreading-ascending; **Sep** sub-orbicular; **Pet** long obovate, 13–18 mm.

**N. concolor** C. H. Wright (Curtis’s Bot. Mag. 136: t. 8348 + text, 1910). **Type:** K, GH [photo]. — **Distr:** NE Brazil (Bahia); Caatinga vegetation, sandy soils.

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**Fig. 1** *Neoglaziovia variegata*. (Copyright: U. Eggli)

**L** to 0.6 m but probably becoming longer, lamina to 2.5 cm wide, long-acuminate, both faces uniformly appressedly white-lepidote; **Inf** erect, peduncular **Bra** not described; lower floral **Bra** linear, longer than the flowers, upper ones to 4 mm, triangular; **Ped** 5–7 mm; **Fl** spreading; **Sep** broadly ovate, rounded; **Pet** broadly round, to 20 mm.

**N. variegata** (Arruda) Mez (in Martius, Fl. Bras. 3(3): 427, t. 80, fig. 1, 1894). **Type:** not typified. — **Distr:** NE Brazil (Piauí, Ceará, Rio Grande do Norte, Paraíba, Bahia, Minas Gerais); Caatinga vegetation on stony to sandy ground. **I:** Leme & Marigo (1993: 156–157). – Fig. 1.

≡ *Bromelia variegata* Arruda (1810) ≡ *Billbergia variegata* (Arruda) Schultes fil. (1830) ≡ *Agallostachys variegata* (Arruda) Beer (1856); **incl.** *Bromelia linifera* hort. ex Beer (1856) (*nom. inval.*, Art. 34.1c); **incl.** *Dyckia glaziovii* Baker (1889).

**L** to 1.5 m, lamina 1.5–2 cm wide, acuminate-pungent, both faces laxly lepidote, upper face

green to brown-green, smooth, lower face with broad white bands, margins somewhat revolute; **Inf** erect to ± inclined, densely white-floccose; peduncular **Bra** narrow, entire or slightly serrulate; fertile part of the **Inf** lax, 10- to 60-flowered; lower floral **Bra** ± as long as the flowers, linear, upper to 3 mm, triangular; **Ped** to 4 mm; **Fl** somewhat spreading; **Sep** obtuse to minutely mucronate, 6–7 mm; **Pet** obtuse, to 13 mm. — **Cytology:** 2n = 100 (tetraploid) (Gitaí & al. 2014).

The species is has been extensively used as a source for fibre for making textiles especially in rural areas (Xavier 1942), and fibres are classified as having low to medium strength in comparison with other lignocellulosic fibres (Almeida & al. 2008). The leaves are also harvested to feed to animals, and overharvesting has caused the disappearance of the species from some areas in Bahia (Silveira & al. 2011).

## References

- Almeida, J. R. M. d' [ & al. 2008], Almeida, A. L. F. S. d' & Carvalho, L. H. (2008) Mechanical, morphological, and structural characteristics of Caroa *Neoglaziovia variegata* fibres. *Polymers & Polymer Composites* 16(9): 589–595. <https://doi.org/10.1177/096739110801600902>
- Evans, T. M. [ & al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>.
- Gitaí, J. [ & al. 2014], Paule, J., Zizka, G., Schulte, K. & Benko-Iseppon, A. M. (2014) Chromosome numbers and DNA content in *Bromeliaceae*: Additional data and a critical review. *Bot. J. Linn. Soc.* 176(3): 349–368, ills. <https://doi.org/10.1111/boj.12211>.
- Leal, F. C. [ & al. 2006], Lopes, A. V. & Machado, I. C. (2006) Polinização por beija-flores em uma área de caatinga no Município de Floresta, Pernambuco, Nordeste do Brasil. *Revista Brasil. Bot.* 29(3): 379–389. <https://doi.org/10.1590/S0100-84042006000300005>.
- Leme, E. M. C. & Marigo, L. C. (1993) *Bromeliads in the Brazilian wilderness*. Rio de Janeiro (BR): Marigo Comunicação Visual.
- Lemos Pereira, F. R. de & Maciel Quirino, Z. G. (2008) Fenologia e biologia floral de *Neoglaziovia variegata* (*Bromeliaceae*) na caatinga paraibana. *Rodriguésia* 59(4): 835–844, ills.
- Schulte, K. [ & al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromeliaceae*) inferred

- from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylogen. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>.
- Silveira, D. G. [ & al. 2011], Pelacani, C. R., Antunes, C. G. C., Rosa, S. S., Duarte Souza, F. V. & Santana, J. R. F. de (2011) Resposta germinativa de sementes de caroá [*Neoglaziovia variegata* (Arruda) Mez]. *Ci. Agrotecnol.* 35 (5): 948–955. <https://doi.org/10.1590/S1413-70542011000500012>.
- Smith, L. B. & Downs, R. J. (1979) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4399940>.
- Xavier, L. P. (1942) O caroá, história, cultura e distribuição geográfica. Rio de Janeiro (BR): Ministerio da Agricultura.







## × *Neophytum* BROMELIACEAE

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× ***Neophytum*** M. B. Foster (Bromeliad Soc. Bull. 8: 73, 1958). — **Distr:** Cultivated only.

= *Neoregelia* × *Orthophytum*. Smith & Downs (1979: 2064) mention the hybrid *N. bahiana* × *O. navioides* (now classified as *Sincoraea*), for which the formal name × *Neophytum lymanii* M. B. Foster was published in 1964 (illustrated by Roguenant & al. (2016: 587)). Many more cultivars are offered in the horticultural trade, many of them producing rosettes with numerous gracefully ascending to arching leaves that turn red in strong light.

### References

- Roguenant, A. [ & al. 2016], Lecoufle, M. & Raynal-Roques, A. (2016) Les Broméliacées. Approche panoramique d'une grand famille "américaine". Paris (FR): Belin.
- Smith, L. B. & Downs, R. J. (1979) Flora Neotropica. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>

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## Ochagavia BROMELIACEAE

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**Ochagavia** Philippi (Anales Univ. Chile 13: 168, 1856). **Type:** *Ochagavia elegans* Philippi. — **Bromelioideae** — **Lit:** Smith & Downs (1979: 1527–1533, Fl. Neotropica); Zizka & al. (2002: monograph). **Distr:** C to S-C Chile (incl. Juan Fernández archipelago). **Etym:** For Silvestre Ochagavía Errázuriz (1820–1883), Chilean lawyer, politician and businessmen, minister of education 1853–1854, and founder of the Ochagavia Winery in 1851.

**Incl.** *Rhodostachys* Philippi (1858). **Type:** *Rhodostachys andina* Philippi.

**Incl.** *Ruckia* Regel (1868). **Type:** *Ruckia ellemetii* Regel.

**Incl.** *Placseptalia* Espinosa (1947). **Type:** *Placseptalia rebecca* Espinosa.

Perennial terrestrial rosette plants, shortly to distinctly caulescent, forming extensive stands through offsetting; **L** numerous, quite densely arranged, **L** sheath ovate to orbicular, merging into the lamina, conspicuously veined, coriaceous, quite succulent, marginally spinose, **L** lamina narrowly triangular to linear, gradually attenuate towards the tip, to 80 (–120) cm, rigid, coriaceous and quite succulent, canaliculate or flat, upper

face glabrous or sparsely lepidote near the base, lower face densely to sparsely white-lepidote to glabrescent, marginal spines 1–4.5 mm, antrorse to spreading, innermost **L** at flowering time rose-red, with reduced lamina; **Inf** terminal, single, condensed and capitate to subcorymbose, with 7–>50 densely arranged flowers, sessile or to 17.5 cm pedunculate, peduncular **Bra** similar to innermost rosette leaves; floral **Bra** shorter than the flowers, acute, pungent, membranous, rose-red to white, with spinose margins; **Fl** 3.5–7.9 cm, hermaphrodite, actinomorphic, sessile, with a conspicuous epigynous tube to 19 mm; **Sep** free, ± symmetrical, chartaceous, whitish to pale rose-red; **Pet** free, erect, obovate to spatulate, without basal appendages, rose-red; **St** usually exerted; **Fil** free or basally united with the petals (only *O. elegans*); **Ov** inferior; **Sty** exerted and longer than the stamens; **Sti** lobes conduplicate, hardly contorted; **Fr** berries, 2–4.5 cm (without the persistent perianth remains), brown to black when dry; **Se** numerous, flattened, glabrous, unappendaged, dark brown to black.

A small genus of 4 species, endemic to Chile between 31° 33' and 38° 14' S, essentially confined to the mediterranean climate zone. The leaves are distinctly succulent, with a water storage volume of 66% reported for *O. litoralis* (Horres & Zizka 1995: as *O. carnea*).

*Ochagavia* is closely related to the monotypic genus *Fascicularia*, which differs by retuse or

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praemorse sepals, blue-violet petals with appendages, and included stamens and style, but sterile plants are virtually impossible to distinguish. The molecular phylogenetic analysis of Horres & al. (2007) confirms the long-suspected close relationship between the two genera. They are, together with *Deinacanthon*, *Greigia* and *Bromelia*, part of a weakly supported clade that is sister to the remaining genera of *Bromelioideae* (Givnish & al. 2011), confirming similar placements in the phylogenies of Schulte & al. (2005), Schulte & Zizka (2008), and Schulte & al. (2009). The phylogeny of Silvestro & al. (2014) places *Fascicularia* within *Ochagavia*, and the combined clade is sister to *Greigia*. Evans & al. (2015) confirm the inclusion of *Fascicularia* and *Deinacanthon* in *Ochagavia* (*Greigia* not studied). Plants are only occasionally found in cultivation, esp. in Botanical Gardens.

Hummingbird pollination has been reported for *O. elegans* (Skottsberg 1928, Bernardello & al. 2001).

The following names are of unresolved application but are referred to this genus: *Rhodostachys leiboldiana* Mez (1896)  $\equiv$  *Ochagavia leiboldiana* (Mez) L. B. Smith & Looser (1934).

**O. andina** (Philippi) Zizka & al. (Willdenowia 32(2): 343, 2002). **Type:** Chile (*Germain* s.n. [SGO 46378, FR [photo]]). — **Distr:** C-S Chile (Región VI O'Higgins: Cachapoal to Región VIII: Biobío); 700–2500 m.

$\equiv$  *Rhodostachys andina* Philippi (1858).

**L** lamina (14.3–) 30–40 cm, (0.5–) 0.9–1.7 cm wide, linear, faintly canaliculate, upper face glabrous to lepidote near the base, lower face densely white-lepidote; **Inf** globose to ovoid,  $\pm$  30-flowered, to 15 cm pedunculate; **Fl** 5.3–6.8 cm, epigynous tube 5–7 mm; **St** exserted.

Insufficiently known. Most collections date from the 19. or early 20. century, and the taxon is likely very rare today.

**O. carnea** (Beer) L. B. Smith & Looser (Revista Univ. (Santiago) 18(8): 1078, 1934).

**Type:** [lecto — icono]: Paxton's Fl. Gard. 2, t. 65, 1851. — **Distr:** C to S-C Chile (Región V Valparaíso to Región IX Araucanía); understory of woodlands, in ravines and on riverbanks, (60–) 200–1080 m. **I:** Rauh (1990: 212: fig. 97); Roguenant & al. (2016: 607).

$\equiv$  *Bromelia carnea* Beer (1856)  $\equiv$  *Rhodostachys carnea* (Beer) Mez (1896); **incl.** *Bromelia longifolia* Lindley (1851) (*nom. illeg.*, Art. 53.1); **incl.** *Bromelia lindleyana* Lemaire (1853) (*nom. inval.*, Art. 34.1b); **incl.** *Rhodostachys grandiflora* Philippi (1859)  $\equiv$  *Ochagavia grandiflora* (Philippi) Mez (1934); **incl.** *Hechtia ellemeetii* Hort. Utrecht (1866) (*nom. inval.*, Art. 32.1c); **incl.** *Ruckia ellemetii* Regel (1867); **incl.** *Pourretia argentea* hort. ex Wittmack (1895) (*nom. inval.*, Art. 32.1c); **incl.** *Rhodostachys chamissonis* Mez (1896)  $\equiv$  *Ochagavia chamissonis* (Mez) L. B. Smith & Looser (1934).

Stems to >25 cm; **L** lamina (38–) 50–80 (–120) cm, 1.2–3.4 (–4.8) cm wide, linear, conspicuously canaliculate, upper face glabrescent, lower face sparsely lepidote to glabrescent, only near the base more densely lepidote; **Inf** globose to elongate, to >50-flowered, to 17.5 cm pedunculate; **Fl** (3.5–) 4.5–7.9 cm, epigynous tube 3–7 mm; **St** exserted.

**O. elegans** Philippi (Anales Univ. Chile 13: 168, 1856). **Type:** Chile, Juan Fernández (*Philippi* 941 [B, F, GH [photo], W †]). — **Distr:** Chile: Juan Fernández archipelago: Isla Robinson Crusoe, endemic; rocky exposed cliffs, 200–600 m. **I:** Wilkin (1996).

Stems to 72 cm; **L** lamina (7.5–) 10–24 cm, 1–2.9 cm wide, narrowly triangular, upper face flat or slightly canaliculate, glabrous to  $\pm$  lepidote, lower face densely white-lepidote; **Inf** capitate, to 20-flowered, 2.5 cm pedunculate; **Fl** 5–7 cm, epigynous tube 10–19 mm; **St** included or slightly exserted.

**O. litoralis** (Philippi) Zizka & al. (Willdenowia 32(2): 340, 2002). **Type:** Chile, Colchagua (*Volckmann* s.n. [SGO 46374]). — **Distr:** Coastal C Chile (Región IV Coquimbo to Región VI



**Fig. 1** *Ochagavia litoralis* (Engraving from *Revue Horticole*, sér. 4, 40: facing p. 211, as *Hechtia pitcairniifolia*, 1868). (Copyright: Public Domain)

O'Higgins: Colchagua); coastal rocks and cliffs, often in extensive stands, 10–250 m. **I**: Roguenant & al. (2016: 608). – Fig. 1.

≡ *Rhodostachys litoralis* Philippi (1859) ≡ *Fascicularia litoralis* (Philippi) Mez (1896); **incl.** *Hechtia pitcairniifolia* Hort. Berol. ex B. Verlot (1868) ≡ *Bromelia pitcairniifolia* (Hort. Berol. ex B. Verlot) K. Koch (1868) ≡ *Rhodostachys pitcairniifolia* (Hort. Berol. ex B. Verlot) Benth (1883) ≡ *Fascicularia pitcairniifolia* (Hort. Berol. ex B. Verlot) Mez (1896); **incl.** *Ochagavia lindleyana* Mez (1934); **incl.** *Placseptalia rebecca* Espinosa (1947).

Stems to >20 cm; **L** lamina 17–40 cm, 1–3 cm wide, narrowly triangular, not or only slightly

canaliculate, upper face glabrous to sparsely lepidote, lower face densely white-lepidote; **Inf** globose to ovoid, 15- to 35-flowered, 8–12 cm pedunculate; **Fl** 4–6.3 cm, epigynous tube 3–6 mm; **St** exserted.

## References

- Bernardello, G. [ & al. 2001], Anderson, G. J., Stuessy, T. F. & Crawford, D. J. (2001) A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *Bot. Rev. (Lancaster)* 67(3): 255–308. <https://doi.org/10.1007/BF02858097>.
- Evans, T. M. [ & al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromelioideae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. *Syst. Bot.* 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>.
- Givnish, T. J. [ & al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromelioideae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ills., maps. <https://doi.org/10.3732/ajb.1000059>.
- Horres, R. & Zizka, G. (1995) Untersuchungen zur Blattsukkulenz bei *Bromelioideae*. *Beitr. Biol. Pfl.* 69(1): 43–76, ills.
- Horres, R. [ & al. 2007], Schulte, K., Weising, K. & Zizka, G. (2007) Systematics of *Bromelioideae* (*Bromelioideae*) — evidence from molecular and anatomical studies. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution: Poales*. *Aliso* 23(1): 27–43, ills. <https://doi.org/10.5642/aliso.20072301.05>
- Rauh, W. (1990) *Bromelien*. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Roguenant, A. [ & al. 2016], Lecoufle, M. & Raynal-Roques, A. (2016) *Les Broméliacées. Approche panoramique d'une grande famille "américaine"*. Paris (FR): Belin.
- Schulte, K. & Zizka, G. (2008) Multi locus plastid phylogeny of *Bromelioideae* (*Bromelioideae*) and the taxonomic utility of petal appendages and pollen characters. *Candollea* 63(2): 209–225. [http://www.ville-ge.ch/cjb/publications\\_candollea\\_632.php](http://www.ville-ge.ch/cjb/publications_candollea_632.php)
- Schulte, K. [ & al. 2005], Horres, R. & Zizka, G. (2005) Molecular phylogeny of *Bromelioideae* and its implications on biogeography and the evolution of CAM in the family. *Senckenberg. Biol.* 85(1): 113–125, maps.
- Schulte, K. [ & al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromelioideae*) inferred



- from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylogen. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>.
- Silvestro, D. [ & al. 2014 ], Zizka, G. & Schulte, K. (2014) Disentangling the effects of key innovations on the diversification of *Bromelioideae* (*Bromeliaceae*). *Evolution* 68(1): 163–175. <https://doi.org/10.1111/evo.12236>.
- Skottsberg, C. (1928) Pollinationsbiologie und Samenverbreitung auf den Juan Fernández-Inseln. In: Skottsberg, C. (ed.): *The natural history of Juan Fernández and Easter Island*, Botany, 2(4): 503–547, ills. Uppsala (SE): Almqvist & Wiksells Boktryckeri. <http://biodiversitylibrary.org/page/28693416>
- Smith, L. B. & Downs, R. J. (1979) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/3999940>
- Wilkin, P. (1996) *Ochagavia elegans*. *Curtis's Bot. Mag., ser. nov.*, 13(1): 22–26, t. 287. <https://doi.org/10.1111/j.1467-8748.1996.tb00532.x>.
- Zizka, G. [ & al. 2002 ], Trumpler, K. & Zöllner, O. (2002) Revision of the genus *Ochagavia* (*Bromeliaceae*, *Bromelioideae*). *Willdenowia* 32(2): 331–350, ills., map, key. <http://www.jstor.org/stable/3997641>.



## × *Orthocohnia* BROMELIACEAE

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× ***Orthocohnia*** G. Lawn (J. Bromeliad Soc. 63 (2): 138, 2013). — **Distr:** Cultivated only.

= *Orthophytum* × *Deuterocohnia*. The only known hybrid is the cultivar ‘Surprise’, raised in a Florida nursery in 1996 from the cross

*Deuterocohnia lorentziana* (treated as synonym of *D. brevifolia* in this handbook) × *Orthophytum estevesii* (pollen parent). It is similar to *D. brevifolia*, but forms larger plants.

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## × *Orthoglaziovia* BROMELIACEAE

U. Eggli

× *Orthoglaziovia* Lawn (J. Bromeliad Soc. 61(5): 234, 2012). — **Distr:** Cultivated only.

= *Orthophytum* × *Neoglaziovia*. A single cultivar 'Rosita' has been named for the cross *N. variegata* × *O. albopictum* (now classified as

*Sincoraea*), obtained in cultivation. The plants are roughly intermediate between the parents, with an almost sessile, cone-shaped inflorescence with pale pinkish flowers.

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## × *Orthomea* BROMELIACEAE

U. Eggli

× ***Orthomea*** E. L. Smith (J. Bromeliad Soc. 33 (2): 75, 1983).  
= *Orthophytum* × *Aechmea*. Reported combinations include *A. fasciata* var. *purpurea* × *O. navioides* (the latter now classified as *Sincoraea*) (introduced into cultivation as cultivar ‘Powder-puff’) and *A. recurvata* var. *benrathii* × *O. vagans* (unnamed).

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## Orthophytum BROMELIACEAE

U. Eggli and E. J. Gouda

**Orthophytum** Beer (Flora 37: 347, 1854). **Type:** *Prantleia glabra* Mez [typification according to L. B. Smith & Downs, Fl. Neotrop. 14(3): 1696, 1979]. — **Bromelioideae** — **Lit:** Smith & Downs (1979: 1696-1710, Fl. Neotropica); Leme (2008: key to the *mello-barretoii*-complex); Louzada & al. (2010: cytology); Louzada & Wanderley (2010: partial monograph of the *vagans*-clade); Louzada (2012: unpublished monograph, with key); Louzada & al. (2014: molecular phylogeny); Leme & al. (2017: classification). **Distr:** E Brazil; Atlantic Forest, Cerrado and Caatinga vegetations, usually saxicolous. **Etym:** Gr. 'orthos', erect, straight; and Gr. 'phyton', plant; for the erect stems with well-spaced leaves of the type species.

**Incl.** *Prantleia* Mez (1891). **Type:** *Prantleia glabra* Mez.

**Incl.** *Cryptanthopsis* Ule (1908). **Type:** *Cryptanthopsis saxicola* Ule.

Perennial terrestrial or saxicolous rosette plants; **Ros** sessile or short- to long-caulescent, sometimes elongating-desintegrating when flowering,

monocarpic but offsetting, sometimes with short stolons; **L** few to many, laxly to densely rosulate or spirally arranged on elongate stems, sheath inconspicuous or  $\pm$  indistinctly separated from the lamina, **L** lamina linear to narrowly triangular, or ovate-triangular, coriaceous to succulent, flat or canaliculate, glabrous to densely lepidote, margins serrate and with antrorse to retrorse spines, apex acuminate,  $\pm$  pungent; **Inf** terminal, elongate and rosette desintegrating with inflorescence growth, and then with spikes, spikes of spikes, or glomerules in the axils of the primary bracts, or congested and sessile in the centre of the caulescent rosette; peduncular **Bra** resembling the leaves but progressively diminishing in size; floral **Bra** subcoriaceous to coriaceous, narrowly triangular to ovate-triangular, sometimes strongly carinate, shorter to longer than the sepals, green to green-yellowish or red to dark wine-red, margins serrate, apex acuminate and/or pungent; **Fl** sessile to shortly pedicellate, hermaphrodite; **Sep** narrowly triangular to ovate-triangular, free or rarely forming a short tube, acuminate and/or pungent; **Pet** often spatulate, free or forming an epigynous tube to 2 mm long, white to green, greenish-yellow or lilac-rose, upper  $\frac{1}{3}$  spreading or erect, obtuse to obtuse-cucullate or acute, basal appendages echinatiform, cupuliform, scutelliform or sacciform (absent in Subgen. *Orthocryptanthus*); **St** included; **Fil** of the inner whorl adnate to the petals; **Ov** inferior,  $\pm$  trigonous, glabrous to densely lanate-lepidote; **Sty** long and slender; **Sti** lobes simple, erect, narrow; **Fr** subglobose to

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globose capsules, with persistent sepals; **Se** ovoid, striate, few to numerous per fruit.

The majority of the  $\pm 55$  species has been described in the past 20 years or so (Leme & al. 2017). There are two centres of diversity, one in the Serra do Espinhaço Range in Bahia and Minas Gerais, the other in the inselberg regions of Minas Gerais and Espírito Santo. Many of the species are narrow endemics.

Until recently, the genus also included species with sessile rosettes with congested, sessile inflorescences and white flowers now segregated as *Sincoraea* (see separate treatment in this handbook). *Orthophytum* is placed in subfamily *Bromelioideae*, where it belongs to a group of early-diverging genera (Schulte & Zizka 2008, Schulte & al. 2009). Schulte & al. (2009) found a position as sister group of *Ananas* for the 3 taxa of *Orthophytum* s.s. analyzed, though with low support. Silvestro & al. (2014) and Evans & al. (2015) analyzed more species and found that *Orthophytum* is not monophyletic. In the analysis of Silvestro & al. (2014) *Orthophytum* s.l. falls in 2 clades (*Orthophytum* s.s. versus the taxa now segregated as *Sincoraea*), being sister to *Cryptanthus* p.p. and the combined clade sister to *Ananas*. The phylogeny obtained by Evans & al. (2015) differs insofar as the species now segregated as *Sincoraea* appear in sister-group position to 2 *Aechmea* species and *Ronnbergia petersii* (as sister to *Lapanthus*, within a well-supported “*Hohenbergia-Orthophytum* clade”), while the species of *Orthophytum* s.s. form a well-supported clade with *Aechmea floribunda* and *Canistrum triangulare* in the extensive polytomy that makes up their Eu-Bromelioid clade. The most detailed analysis is that of Louzada & al. (2014), which is largely congruent with the clades found by Silvestro & al. (2014). *Orthophytum* s.s. accordingly is closely related to the morphologically often similar genera *Cryptanthus* (see separate treatment in this handbook) and *Lapanthus* (2 species, not considered to include succulents). The traditional distinction of *Orthophytum* s.s. (petals with basal appendages) from *Cryptanthus* (petals without basal appendages) is thus probably not warranted, esp. because the presence/absence

of petal appendages is not phylogenetically informative according to Schulte & Zizka (2008). On the other hand, *Cryptanthus* appears to differ consistently from *Orthophytum* in its generally low chromosome numbers ( $2n = 34, 36, \text{ or } 54$ , vs. a polyploid series of  $2n = 50, 100, 150$  in *Orthophytum* and the species now segregated as *Sincoraea*) (Louzada & al. 2010, Louzada & al. 2014). *Lapanthus* is similar to *Orthophytum* s.s. but differs by completely erect petals, free filaments of the inner whorl, and lanceolate (vs. saccate or cupuliform) petal appendages (Louzada & Versieux 2010). More detailed analyses and a more complete study of *Cryptanthus* are necessary to further elucidate the relationship between that genus and *Orthophytum* s.s.

Traditionally, *Orthophytum* was divided into 2 main groups, based on whether the inflorescence is sessile or long-pedunculate, and Leme (2004) provided a further break-down into 6 “subcomplexes”. These groupings were only partly recovered in the molecular phylogenies of Louzada & al. (2014) and Leme & al. (2017). Based on their results, Leme & al. (2017) divide *Orthophytum* into 5 subgenera, but only Subgen. *Orthophytum* (in terminal sister-position to Subgen. *Clavanthus*) is strongly supported, while the topology of the remaining clades is less clearly resolved, and Subgen. *Capixabanthus* is shown as polyphyletic in the molecular data. All subgenera are morphologically well circumscribed and (with the exception of the wide-spread Subgen. *Orthophytum*) show neatly defined geographical ranges:

- [1] Subgen. *Orthophytum*: Plants (nearly) stemless; **L** thin to thick-coriaceous; **Sep** free; **Pet** erect except the suberect to recurved apical part, white or green, appendage echinatifform; **Sti** simple-dilated (rarely simple-patent). — 43 spp., widespread throughout the range of the genus, to 500 (rarely 600–1200) m.
- [2] Subgen. *Clavanthus* Leme & al. 2017: Plants stemless; **L** strongly coriaceous; **Sep** free; **Pet** erect and corolla tubular-clavate, green, green with white apex, or greenish-yellow, appendages scutelliform (rarely sacciform); **Sti**

simple-dilated. — 6 species from Minas Gerais 650–1300 m.

- [3] Subgen. *Orthocryptanthus* Leme & al. 2017: Plants long-caulescent; **L** coriaceous; **Sep** free; **Pet** spreading-recurved, lilac-rose or white, appendages absent; **Sti** simple-erect to simple-patent. — 2 species from Minas Gerais, 1000–1400 m.
- [4] Subgen. *Capixabanthus* Leme & al. 2017 (= “*Vagans*-clade of earlier classifications): Plants stemless to long-caulescent; **L** thin to thick-coriaceous; **Sep** free; **Pet** suberect or rarely spreading, green with with apex or white, appendages cupuliform or sacciform; **Sti** simple-dilated. — 7 species from Espírito Santo and neighbouring Bahia and Minas Gerais, to 600 m.
- [5] Subgen. *Krenakanthus* Leme & al. 2017: Plants caulescent; **L** thin; **Sep** connate for  $\frac{1}{6}$ – $\frac{1}{4}$  of their length; **Pet** spreading, rose-lilac to purple towards the apex, appendages cupuliform; **Sti** conduplicate-spiral. — Only *O. roseolilacinum* from Minas Gerais, 250–810 m, not succulent.

**Succulence:** The degree of succulence varies throughout the genus, but can be very strongly pronounced in taxa from more xeric habitats. Horres & Zizka (1995) specifically mention *O. disjunctum*, but their material was probably misidentified as cultivated plants of this species are hardly succulent.

**Horticulture:** Horticulturally, *Orthophytum* s.s. is of limited importance, and its species are not commonly seen in cultivation. Due to the small size and the xeromorphic features, many species are well-adapted to cultivation together with other xerophytes and succulents. Plants can easily be propagated from the short basal shoots produced before flowering, or from shoots arising at the base of the inflorescence, depending on the species.

The following intergeneric hybrids have been recorded: *Orthophytum* × *Aechmea* = ×*Orthomea* (see separate entry in this handbook); *Orthophytum* × *Cryptanthus* = ×*Orthoanthus* (see

separate entry in this handbook); and *Orthophytum* × *Nidularium* = ×*Ortholarium* (not involving succulent taxa).

**O. argentum** Louzada & Wanderley (Phytotaxa 28: 27–29, ills., 2011). **Type:** Brazil, Bahia (Louzada & al. 110 [SP, HUEFS]). — **Distr:** E Brazil (Bahia: Rio de Contas); quartzite rock outcrops in Campo Rupestre vegetation, shaded or rarely open places, 900–1300 m.

**Incl.** *Orthophytum toscanoi* ssp. *atropurpureum* P. J. Braun & Esteves (2010).

[1] **Ros** open, shortly caulescent, 24–34 cm tall, with short rhizomatose offsets, stems completely covered by the leaves; **L** arching, sheath distinguishable from the lamina, chartaceous, ovate, castaneous, both faces glabrous, margins serrulate, **L** lamina narrowly triangular, 15–20 × 2–2.5 cm, rigid, coriaceous, canaliculate, with long attenuate pungent tip, cinereous, densely lepidote on both faces, margins densely serrate, **Sp** slender, dark brown, 3.5–4 mm but gradually shorter towards the leaf tip, retrorse; **Inf** pedunculate, branched with sessile glomerate branches; peduncle elongate, erect, 11–18 cm, woolly-lepidote, dark wine-red; peduncular **Bra** narrowly triangular with long-attenuate pungent tip, divergent, much exceeding the internodes, leaf-like, coriaceous, margins densely serrate and lepidote; fertile **Inf** part ±12 cm, with 7–8 condensed spicate branches, lax but dense at the tip, axis wholly exposed, slender, straight, glabrescent, dark wine-red; primary **Bra** leaf-like, linear-triangular or ovate-lanceolate with pungent tip, patent or reflexed, the lower longer than the subtended branch, the upper shorter, coriaceous, both faces subdensely lepidote, margin serrate; floral **Bra** triangular, ±15 × 10 mm, clasping the flowers, coriaceous, with pungent tip, prominently veined, carinate, dark wine-red, sparsely lepidote, margins serrate or serrulate; **Fl** ±17 mm, sessile; **Sep** triangular, ±10 × 4 mm, asymmetrical, coriaceous, dark wine-red, glabrous, entire, adaxial ones carinate, abaxial one ecarinate; **Pet** elliptic, ±13 × 5 mm, obtuse, green with white blades, apically spreading to recurved, with 2 fimbriate appendages well above the base and conspicuous callosities; **St** included, exceeding the stigma; outer **Fil** free, inner **Fil** adnate



to the petals,  $\pm 8$  mm; **Anth** 3–4 mm, elliptic; **Ov** trigonous,  $\pm 3$  mm, green; **Sti** simple, erect; **Fr** and **Se** not known.

**O. braunii** Leme (Pabstia 5(1): 14–15, 1994).

**Type:** Brazil, Bahia (*Pereira & Braun* E343 [HB]). — **Distr:** E Brazil (Bahia); on quartzitic sandstone rocks and sandy soils, 400–1250 m.

[1] **Ros** distinctly elongate, caulescent,  $\pm 20$  cm at flowering time; **L**  $\pm 10$ , suberect to curved, rosulate, sheath inconspicuous, outer face furrowed, **L** lamina narrowly triangular,  $\pm 13 \times 2.5$  cm, canaliculate, leathery, abaxially distinctly veined, both faces greenish and very densely white-lepidote with strongly appressed membranous scales, upper face becoming glabrescent to the long-caudate tip, margins laxly spinose, **Sp** 3–5 mm; **Inf** to 16 cm, erect; peduncle  $\pm 6$  cm, greenish, white-lanate; peduncular **Bra** leaf like; fertile **Inf** part  $\pm 8$  cm, dense near the tip, with  $\pm 7$  laxly arranged spicate branches at the base with 2 congested flowers each; primary **Bra** suberectly curved, lower ones leaf-like and  $\pm 5 \times$  longer than the subtended branch, upper ones somewhat leaf-like and  $2 \times$  as long as the subtended branch; floral **Bra** ovate,  $\pm 20 \times 9$  mm, acuminate, green, both faces white-lepidote, veined, carinate or ecarinate, laxly spined with 1.5–2 mm long hooked recurved spines; **Fl** subsessile,  $\pm 27$  mm; **Sep** lanceolate,  $\pm 13 \times 4$  mm, almost free, subsymmetrical, slenderly acuminate, whitish, white-lepidote, carinate, margins near the tip very minutely retrorsely spinulose; **Pet** subspatulate with broadly acute and minutely apiculate tip,  $\pm 21 \times 5$  mm, pale greenish but white towards the tip, with 2 fimbriate appendages above the base and 2 elongate acute calli 10 mm long; **St** details not described; **Anth**  $\pm 2$  mm, obtuse; **Ov** broadly obovoid,  $\pm 5 \times 4$  mm, white, white-lepidote; **Sty** not described; **Sti** simple, erect, lobes free, greenish; **Fr** and **Se** unknown.

**O. diamantinense** Leme (J. Bromeliad Soc. 58(6): 257–259, ill., 2008). **Type:** Brazil, Minas Gerais (*Leme & al.* 1825 [HB]). — **Distr:** E Brazil (Minas Gerais); among rocks and in rock crevices in full sun or more often partial shade, 1070–1100 m. **I:** Leme & al. (2017: fig. 14D).

[2] **Ros** acaulescent, with short basal rhizomatous offsets, plants 30–37 cm tall at flowering time; **L**  $\pm 6$ , laxly rosulate but forming a distinct rosette before anthesis, sheath inconspicuous, subreniform,  $\pm 2.7 \times 5.5$  cm, strongly corrugate, densely white-lepidote towards the tip and abaxially, thick, **L** lamina sublinear-attenuate,  $35\text{--}41 \times 2.2\text{--}3.8$  cm, long caudate, thick and strongly coriaceous, subspreading-arcuate, distinctly canaliculate mainly towards the base, dark red, adaxially glabrous, abaxially conspicuously veined and densely appressedly and coarsely white-lepidote, margins densely spinose at the base but more laxly so towards the tip, **Sp** narrowly-triangular, spreading (basal ones) to antrorse-uncinate (apical ones), 2–3 mm, 3–10 mm apart; **Inf** pedunculate, erect, without forming adventive rosettes; peduncle 22–28 cm, greenish to reddish bronze-coloured, densely white-lanate; peduncular **Bra** not distinct from the rosette leaves, well-spaced; fertile **Inf** part subellipsoid to capitate,  $4.5\text{--}6 \times 3.5\text{--}4.5$  cm, branched with 5–6 congested glomerate branches; primary **Bra** spreading or nearly so, the lowest many times longer than the fascicles, canaliculate, the basal ones resembling the peduncular bracts, the upper ones with a broadly ovate sheath and a long, narrowly subtriangular to sublinear-caudate or nearly subulate pungent lamina  $5\text{--}26 \times 1.8\text{--}3$  cm, densely and coarsely white-lepidote abaxially mainly towards the base, glabrescent to glabrous adaxially, greenish at the base and dark red towards the apex, conspicuously veined abaxially, densely to laxly spinose; **Inf** branches densely 3- to 5-flowered, sessile; floral **Bra** ovate-triangular,  $17\text{--}25 \times 8\text{--}17$  mm, acuminate with a short mucro, densely spinulose towards the apex, distinctly carinate mainly towards the apex, glabrescent except the white-lepidote to -lanate tip; **Fl** 38–41 mm, sessile, tubular, with inconspicuous epigynous tube, unscented; **Sep** suboblong,  $18\text{--}23 \times 4\text{--}8$  mm, acute and shortly acicular-mucronulate, subsymmetrical, green except for the hyaline membranous entire to crenulate margins, glabrous except for the white-lanate tip, adaxial ones alate-carinate, abaxial one ecarinate; **Pet** sublinear-subspatulate,  $30\text{--}33 \times 5\text{--}7$  mm, obtuse-cucullate, erect, green except for the white apex, with 2 irregularly shaped broadly

lamine lacinate-crenulate appendages 4–5 mm above the base, and with 2 oblong callosities; outer **Fil** 25–26 mm, inner **Fil**  $\pm 24$  mm and adnate to the petals for 16–17 mm; **Anth** sub-ellipsoid to sublinear, 3.5–4 mm; **Ov** 6–8  $\times$  5–6 mm, trigonous, glabrous, green; **Sty** not described; **Sti** weakly conduplicate,  $\pm 1.5$  mm  $\emptyset$ ; **Fr** trigonous; **Se** reniform, dark brown.

Compared with *O. mello-barretoii* and the non-succulent *O. graomogolense* in the protologue, and differing mostly in leaf characters.

**O. eddie-estevesii** Leme (J. Bromeliad Soc. 50 (2): 55–57, ills., cover-ill., 2000). **Type:** Brazil, Minas Gerais (*Esteves Pereira* 499 in *Lemé* 4693 [HB, UFG]). — **Lit:** Braun & Esteves Pereira (2009: 60–62, with ills.). **Distr:** E Brazil (Minas Gerais); rocky soils in Campo Rupestre grasslands,  $\pm 1300$  m. **I:** Leme & al. (2017: fig. 14E).

[2] **Ros** shortly caulescent, with slender stolons to 10 cm, 17–19 cm tall at flowering time; **L** subdensely arranged, recurved, sheaths inconspicuous, **L** lamina narrowly-triangular, 10–15  $\times$   $\pm 2.5$  cm, attenuate-caudate, strongly coriaceous, distinctly canaliculate, completely covered by a thick layer of white trichomes on both faces, margins densely spinose, **Sp** narrowly triangular, nearly straight to slightly retrorse, densely white-lepidote except for the yellowish apical portion,  $\pm 3 \times 1$  mm; **Inf** erect, to 15 cm; peduncle 6–7 cm, densely white-lanate, green; peduncular **Bra** leaf-like, progressively shorter upwards, almost completely covering the axis; fertile **Inf** part subcorymbose, branched with  $\pm 5$  densely arranged nearly sessile glomerate branches, ellipsoid in overall outline, 5–6  $\times$  2 cm  $\emptyset$ ; primary **Bra** leaf-like with broadly ovate-triangular base, long-caudate, the basal ones distinctly exceeding the subtended branches, the others gradually shorter and only slightly longer than the subtended branch, margins densely spinose; **Br**  $\pm 4 \times 1.5$  cm in outline, densely 2- to 3-flowered; floral **Bra** of the fascicles triangular, 22–23  $\times$  12 mm, acuminate, densely spinulose towards the tip, carinate, reaching the middle of the sepals, greenish-hyaline towards the base and brightly orange-red at the apex, veined, membranous, sparsely white-lepidote, floral **Bra** of the

simple apical inflorescence part broadly oblong,  $\pm 30 \times 20$  mm, equalling  $\frac{3}{4}$  of the sepal length, irregularly curved, ecarinate, with pungent tip, densely spinulose; **Fl**  $\pm 45$  mm, sessile, with a  $\pm 1.5$  mm long epigynous tube, unscented; **Sep** narrowly lanceolate,  $\pm 30 \times 6$  mm, acuminate, entire, reddish-orange towards the apex, submembranous, glabrous, carinate; **Pet** sublinear-spatulate,  $\pm 36 \times 5$  mm, strongly obtuse-cucullate, erect at anthesis, greenish-yellow, with 2 densely fimbriate appendages  $\pm 8$  mm above the base and 2 conspicuous longitudinal callosities which nearly equal the anthers; **Fil** 26 mm, the inner adnate to the petals for  $\pm 20$  mm; **Anth**  $\pm 3$  mm, base obtuse, apex acute; **Ov** trigonous,  $\pm 9$  mm; **Sty** long-filiform; **Sti** simple-erect,  $\pm 2.5$  mm  $\emptyset$ , lobes densely papillose, recurved; **Fr** and **Se** unknown.

This is probably the most attractive species of Subgen. *Clavanthus* due to the conspicuously white-lepidote leaves and the contrasting reddish-orange sepals and the greenish-yellow petals. It is similar to *O. mello-barretoii*.

**O. harleyi** Leme & M. Machado (J. Bromeliad Soc. 56(3): 108–110, ills., 2006). **Type:** Brazil, Bahia (*Machado* 180 [HB, CEPEC]). — **Distr:** E Brazil (Bahia); granite rock outcrops, on rocks or between shrubs, 700–830 m.

[1] **Ros** acaulescent, with slender stolons to 6 cm, 13–15 cm tall at flowering time; **L** 25–35, densely rosulate but becoming well-spaced at flowering time, sheath inconspicuous; **L** lamina narrowly triangular-attenuate, 10–11  $\times$  1.3–1.9 cm, attenuate-caudate, fleshy-coriaceous, suberect-recurved to spreading-recurved, nearly flat near the base to slightly canaliculate towards the tip, densely and coarsely white-lepidote on both faces mainly towards the base, trichomes (almost) totally obscuring the greenish to reddish-brown colour, veined mainly abaxially, margins subdensely spinose, **Sp** triangular, slightly retrorse-uncinate, 3–4 mm, 3–7 mm apart; **Inf**  $\pm 12$  cm, erect; peduncle  $\pm 6.5$  cm, densely white-lanate, pale green but the colour almost completely obscured by the trichomes; peduncular **Bra** leaf-like, suberect-arcuate to nearly spreading, not completely covering the axis; fertile **Inf** part

simple, densely congested, 4.5–5.5 cm, densely  $\pm 25$ - to 35-flowered, without vegetative shoots; basal floral **Bra** like the upper peduncular bracts, almost leaf-like, much exceeding the flowers, upper ones ovate-triangular, 24–35  $\times$  8–13 mm, acuminate-caudate, ecarinate, exceeding the sepals, greenish towards the base, reddish-brown towards the apex, colour in part obscured by a dense layer of coarse white trichomes on both faces, veined, thinly coriaceous, strongly recurved, margins subdensely to densely spinulose; **Fl** 28–34 mm, sessile or nearly so, suberect, tubular with spreading-ascending limb, with an epigynous tube  $\pm 0.5$  mm; **Sep** sublinear-lanceolate, 14–16  $\times$  3–5 mm, acuminate, shortly caudate, entire, pale green, veined, membranous mainly along the margins, white-lanate at the base, subdensely to densely white-floccose towards the apex, shortly fimbriate, obtusely carinate to carinate; **Pet** sublinear-spatulate, 24–28  $\times$  4–6 mm, subobtusely and inconspicuously apiculate, white towards the apex, with 2 densely and irregularly scalloped and long-lacerate predominantly downwardly oriented appendages 2.5–3 mm above the base and 2 conspicuous longitudinal callosities which nearly equal the filaments; outer **Fil** 20–21 mm, inner **Fil**  $\pm 18$  mm, adnate to the petals for 12–13 mm; **Anth** 2–2.5 mm; **Ov** trigonous, 3–5  $\times$  4–5 mm, white-lanate; **Sti** simple-erect,  $\pm 1$  mm  $\varnothing$ , lobes sub-orbicular, remotely crenulate; **Fr** globose,  $\pm 7$  mm  $\varnothing$ , white-lanate, greenish; **Se** reniform, black-purple, striate.

Compared with *O. braunii* and the non-succulent *O. saxicola* in the protologue. According to the original description, flowers in cultivated plants opened in late afternoon and stayed open throughout the night — unique for the genus as far as known.

**O. jacaraciense** Leme (Selbyana 30(2): 144–145, ill., 2010). **Type:** Brazil, Bahia (*Reis* s.n. in Leme 6987 [HB]). — **Distr:** E Brazil (Bahia); on interior sand dunes formed from decomposed quartzite rocks, sun-exposed at the fringe of shrubs, 900–1000 m. — Fig. 1.

[1] **Ros** acaulescent, elongating at flowering time and plants then 20–22 cm tall; **L**  $\pm 5$  at flowering time, in a distinct rosette before



**Fig. 1** *Orthophytum jacaraciense* (type collection). (Copyright: E. M. C. Leme)

flowering, sheath inconspicuous, **L** lamina narrowly lanceolate, 1–12.5  $\times$  2 cm, acuminate-caudate, strongly coriaceous, suberect-arcuate to nearly spreading, nearly flat near the base to canaliculate towards the apex, yellowish-green or sometimes reddish towards the apex, dull, finely veined abaxially, subdensely white-lepidote at the base mainly adaxially and glabrous towards the apex on both faces, margins straight, subdensely to densely spinose, **Sp** narrowly triangular, mostly retrorse-uncinate, pale castaneous towards the apex, 2–3 mm, 3–7 mm apart; **Inf** erect,  $\pm 18$  cm; peduncle  $\pm 12$  cm, erect, light green, finely and sparsely white-lanate to glabrescent; peduncular **Bra** like the rosette leaves, spreading-arcuate, slightly decreasing in size towards the inflorescence tip; fertile **Inf** part branched,  $\pm 6.5$  cm, branches  $\pm 3$ , laxly arranged, strongly condensed and shortly spicate, 0.5–1.5 cm apart, densely 2- to 3-flowered, tip of the main axis similarly

fasciculate-rosulate, to 3 cm, densely  $\pm 8$ -flowered; primary **Bra** spreading-arcuate to reflexed, nearly flat, basal ones resembling the upper peduncular bracts, 3 $\times$  as long as the subtended branches but gradually shorter towards the inflorescence tip, light to yellowish-green, sometimes reddish towards the apex, finely veined abaxially, glabrous, densely to subdensely spinulose; floral **Bra** ovate to ovate-subtriangular or broadly subtriangular, those of the branches 21–22  $\times$  12–13 mm, those of the main axis 30–32  $\times$  18 mm, acuminate, slightly pungent, equalling to exceeding the sepals, strongly suberect-recurved, finely veined, glabrous, margins densely spinulose; **Fl** 34–36 mm, sessile, narrowly tubular, unscented, with inconspicuous epigynous tube; **Sep** narrowly lanceolate,  $\pm 17 \times 5$  mm, acuminate-caudate, entire, green, glabrous, the adaxial ones carinate, the abaxial one ecarinate; **Pet** narrowly sublinear-spatulate, 27–28  $\times$  4–5 mm, obtuse to obtuse-emarginate, slightly cucullate, pale green except for the white apex, with 2 thick scalloped appendages  $\pm 4$  mm above the base and 2 conspicuous longitudinal callosities slightly shorter than the filaments; **Fil** greenish, 20–22 mm, the inner adnate to the petals for  $\pm 13$  mm; **Anth** 2–2.5 mm; **Ov**  $\pm 5 \times 7$  mm, trigonous, glabrous; **Sti** conduplicate,  $\pm 2$  mm  $\varnothing$ , white, lobes obovate, obtuse, suberect, finely and shortly scalloped-lacerate; **Fr** and **Se** unknown.

Compared with the non-succulent *O. maracasense* in the protologue.

**O. lemei** E. Pereira & I. A. Penna (Bol. Mus. Bot. Munic. [Curitiba] 62: 3–4, t. 4 (p. 8), 1985). **Type:** Brazil, Bahia (Leme & al. 440 [HB]). — **Distr:** E Brazil (Bahia, Minas Gerais); arid stony ground, 600–1100 m.

[1] **Ros** largely absent, stoloniferous, plants 50 cm tall at flowering time; lowermost **L** to 26 cm, sheath inconspicuous, 1  $\times$  4 cm, membranous, glabrous, transversely pleated, margins very minutely spinose, **L** lamina very long and narrowly triangular, 25  $\times$  3.5 cm, acuminate, with pungent tip, thick and coriaceous, dark green, canaliculate, both faces densely white-lepidote with scales forming an appressed membrane, abaxially densely veined with prominent veins,

margins spinose, **Sp** to 3 mm, retrorse; **Inf** erect, branched; peduncle erect,  $\pm 15$  cm, red, at first white-lanate but becoming glabrous; peduncular **Bra** similar to the basal leaves but without sheath; fertile **Inf** part lax, 30 cm, rachis red, first white-lanate but later glabrous; **Br** condensed-spicate; lower primary **Bra** similar to the peduncular bracts, much longer than the subtended branches, upper ones ovate-acuminate, much shorter than the spikes; **Br** condensed strobilate spikes, subglobose, 2  $\times$  1.5 cm  $\varnothing$ , subsessile; floral **Bra** ovate,  $\pm 10$  mm, acuminate-spinose, reaching the tips of the sepals, keeled, veined, glabrous, wine-red, margins almost entire or pectinately spinose; **Fl** 10–15 mm, without epigynous tube; **Sep** ovate to narrowly triangular, 7–10  $\times$  3 mm, glabrous, red, adaxial pair at first strongly keeled and later winged, abaxial one ecarinate; **Pet** spatulate, 12 mm, blunt, green with white lobes, with 2 strongly fimbriate appendages  $\pm 4$  mm above the base, without callosities; **St**  $\pm 8$  mm; **Anth** 2 mm; **Ov** subglobose, 3 mm, not further described; **Fr** globose; **Se** reniform.

Flower description completed from Louzada (2012).

**O. mello-barretoii** L. B. Smith (Bol. Mus. Nac. Rio de Janeiro, Bot. ser. 2, 15: 2, t. 1, figs. c–e, 1952). **Type:** Brazil, Minas Gerais (*Mello Barreto* 2121 [R, US [photo]]). — **Lit:** Leme (2008). **Distr:** E Brazil (Minas Gerais); among rocks in campo, 1000–1400 m. **I:** Leme & al. (2017: fig. 14C).

[2] **Ros** somewhat elongating at flowering time, 10–20 cm tall, with stolons; **L** to 25 cm, sheath elliptic, 4 cm, **L** lamina arching-recurved, very narrowly triangular, with pungent tip, strongly canaliculate, adaxially densely and coarsely white-lepidote near the base and subdensely white-lepidote and soon glabrescent towards the tip, margins laxly spinulose, **Sp** straight or curved, 2 mm, 5–10 mm apart; **Inf** branched; peduncle erect, 3.5–16 cm, densely white-lanate; peduncular **Bra** not distinct from the rosette leaves but more laxly arranged; fertile **Inf** part very densely subglobose or slightly interrupted at the base, 3–5 cm  $\varnothing$ , with congested glomerate branches, main axis head-like, densely flowered; primary



**Bra** leaf-like, all but the uppermost with a long lamina; floral **Bra** broadly ovate, 12–15 × 8–10 mm, acuminate, straight, erect or nearly erect, slightly shorter than the sepals, serrulate, with conspicuously white-lanate tip; **Fl** with almost no epigynous tube; **Sep** (sub-) oblong, 17–20 mm, acute and mucronate, densely white-lanate at the tip, serrulate; **Pet** oblong-elliptic, 25 mm, obtuse, white, with 2 fimbriate appendages ±7 mm above the base; inner **Fil** high-connate with the petals; **Ov** subglobose, 6 mm, strongly compressed, glabrous; **Fr** subglobose; **Se** black-purple, striate.

The type locality is Jaboticatubas in the Serra do Cipó according to Leme & Coelho de Paula (2008). — The recently described *O. piranianum* is similar according to its protologue.

**O. piranianum** Leme & C. C. Paula (J. Bromeliad Soc. 58(2): 112–116, ill., 2008). **Type:** Brazil, Minas Gerais (Leme & Paula 7189 [HB, RB]). — **Distr:** E Brazil (Minas Gerais: Grão Mogol); sandy to rocky soils on quartzitic sandstone outcrops in Campo Rupestre vegetation, full sun or partial shade, ±1300 m. **I:** Leme & al. (2017: fig. 14G).

[2] **Ros** stemless, desintegrating-elongating at flowering time and plants to 19 cm tall, offsetting with basal rhizomes, without new shoots from the inflorescence; **L** ±12, laxly arranged, sheath inconspicuous, strongly corrugate, **L** lamina narrowly triangular-attenuate, 15–16 × 3 cm, long-caudate, coriaceous, subspreading-recurved, distinctly canaliculate esp. when water-stressed, both faces coarsely cinereous-lepidote obscuring the bronze leaf colour, abaxially veined, margins (sub-) densely spinose, **Sp** mostly spreading-retrorse, 2–3 mm, 3–7 mm apart; **Inf** erect; peduncle ±9 cm, pale bronze-coloured, densely and finely white-lanate; peduncular **Bra** not distinct from the rosette leaves; **Inf** branched but remaining congested-condensed and capitate in outline, ± 4 × 3.5 cm, rachis not visible; primary **Bra** spreading-recurved, longer than the subtended fascicles, with a suborbicular base and a narrowly triangular-attenuate canaliculate lamina similar to the rosette leaves; **Br** ±4 cm, suberect, sessile, ±2.7 × 2.5 cm in outline, 4- to 5-flowered; floral **Bra** ovate-triangular, 20–24 × 12–16 mm, ± as

long as the sepals but recurved, acuminate with short acicular mucro, distinctly carinate, green, finely veined, abaxially densely and coarsely white-lepidote throughout, adaxially densely and coarsely white-lepidote towards the apex, margins densely and coarsely spinose towards the tip; **Fl** 31–33 mm, narrowly tubular, with inconspicuous epigynous tube, unscented; **Sep** narrowly triangular-lanceolate, 18 × 4.5–5 mm, acuminate and shortly acicular-mucronulate, entire, pale green except for the hyaline membranous margins, subdensely to densely and coarsely white-lepidote abaxially, the adaxial ones alate-carinate, the abaxial one ecarinate; **Pet** sublinear-subspatulate, 24–25 × 4.5–5 mm, obtuse-cucullate, claw green, limb white, with 2 irregularly lacerate-crenulate obovate to suborbicular appendages ±4 mm above the base and 2 conspicuous longitudinal callosities much shorter than the inner filaments; **Fil** greenish, outer ±17 mm, inner ±16 mm, adnate to the petals for ±9 mm; **Anth** suboblong, ±2.5 mm; **Ov** ± 5–6 × 4.5 mm, trigonous, white, densely sublanate; **Sti** ±1.5 mm Ø, white, lobes weakly conduplicate, densely papillose; **Fr** and **Se** unknown.

Similar to *O. mello-barretoii*, but differing by the densely white-lepidote leaves and floral bracts without glabrous tip, different sepals and a white-sublanate ovary. *O. piranianum* grows sympatrically with the hardly succulent *O. graomogolense*, from which it is not easily distinguished.

**O. riocontense** Leme (J. Bromeliad Soc. 55(4): 156–158, ill. (p. 162), 2006). **Type:** Brazil, Bahia (*Reis jr.* s.n. in Leme 5787 [HB]). — **Distr:** E Brazil (Bahia); on quartzitic sandstone rock outcrops in cavities of steep rocks, 700–1200 m.

[1] **Ros** acaulescent, elongating-disintegrating at flowering time and plants then 40–45 cm tall, basally offsetting, without new shoots from the inflorescence; **L** ±10, subdensely arranged, suberect-arcuate, sheath inconspicuous, **L** lamina narrowly triangular, 28–32 × 4 cm, long-caudate, distinctly succulent, distinctly canaliculate esp. towards the tip, adaxially densely white-lepidote near the base but glabrous otherwise, abaxially densely appressedly white-lepidote completely obscuring the leaf colour and forming a membrane, distinctly veined, margins (sub-) densely



spinose, **Sp** distinctly uncinately-retrorse, yellowish to pale brown, 2–3 mm, 4–11 mm apart; **Inf** erect; peduncle dark red, white-lanate; peduncular **Bra** not distinct from the rosette leaves, slightly reduced in size further up; fertile **Inf** part branched,  $\pm 22$  cm; **Br** 10–11, as condensed sessile subglobose-strobilate spikes  $1.7\text{--}2 \times 2\text{--}2.5$  cm  $\varnothing$ , 8- to 15-flowered, laxly (near the base) to densely (more distally) arranged, 1–4 cm apart, at the tip of the main axis forming an inconspicuous head of 2 or 3 fascicles, rachis dark red, white-sublanate to glabrous; primary **Bra** straight or nearly so, spreading or the upper ones reflexed, slightly canaliculate to nearly flat, the basal ones resembling the peduncular bracts, distinctly longer than the subtended fascicles but the distal ones abruptly shorter, the upper ones with a triangular or broadly ovate-triangular base and a long-acuminate lamina,  $2\text{--}6 \times 1.3\text{--}1.6$  cm, distinctly longer to slightly shorter than the subtended fascicles, glabrous adaxially, densely white-lepidote abaxially, green (basal ones) to reddish (upper ones), distinctly veined abaxially, densely to laxly spinulose; floral **Bra** ovate-triangular,  $12\text{--}15 \times 8\text{--}11$  mm, acute-apiculate, densely spinulose, basal ones carinate, the other ecarinate, with strongly recurved tip, dark red, finely veined, glabrescent to glabrous; **Fl** 19–23 mm, densely arranged, tubular with hardly spreading-ascending limb, with inconspicuous epigynous tube, unscented; **Sep** slightly asymmetrical, broadly ovate,  $9\text{--}11 \times 5\text{--}5.5$  mm, entire, red except for the hyaline margins, glabrous, tip with a distinct slightly pungent mucro  $\pm 1.5$  mm long, adaxial ones alate-carinate; **Pet** subspatulate,  $15\text{--}17 \times 4\text{--}4.5$  mm, rounded to inconspicuously cucullate-emarginate, base whitish, central portion green, distally white, with 2 densely scalloped-fimbriate appendages  $\pm 4$  mm above the base and 2 conspicuous longitudinal callosities almost extending to the anthers; **Fil** white near the base, greenish near the tip, outer  $\pm 11$  mm, inner  $\pm 9$  mm, adnate to the petals for  $\pm 5$  mm; **Anth** green,  $\pm 2.5$  mm; **Ov**  $\pm 4$  mm, subtrigonal, greenish-white, glabrous; **Sti**  $\pm 1$  mm, white, with reniform erect lobes; **Fr** and **Se** unknown.

Compared with *O. maracasense* (not considered to be succulent) in the protologue, differing, amongst other characters, by the strongly

succulent leaves. *O. riocontense* is amongst the most succulent members of the genus.

**O. rubrum** L. B. Smith (Smithsonian Misc. Collect. 126: 34, 180, Fig. 83, 1955). **Type:** Brazil, Bahia (*Foster* 2444 [US]). — **Distr:** E Brazil (Bahia); in Caatinga vegetation on a table mountain,  $\pm 600$  m.

[1?] **Ros** distinct but elongating at flowering time and plants 50–60 cm tall; **L** numerous, covered at first with white appressed scales, sheaths suborbicular, 2–3 cm, pale brown, becoming glabrous and glossy, **L** lamina linear-triangular,  $55\text{--}60 \times 2\text{--}3$  cm, long-attenuate and subfiliform-acute, adaxially glabrescent and dark glossy green, abaxially cinereous-lepidote, margins laxly serrate; **Sp** antrorse, greenish or brownish, 2 mm; **Inf** densely conglomerately compound; peduncle elongate, densely white-lepidote, often slightly curved; peduncular **Bra** leaf-like, divergent to spreading; fertile **Inf** part with  $\pm 3\text{--}5$  spikes, ellipsoid to globose in outline, densely many-flowered,  $2\text{--}4 \times 2.5$  cm  $\varnothing$ , red, sometimes the lowest spike somewhat remote from the others; primary **Bra** spreading, lower ones leaf-like, upper soon shorter and triangular, upper ones  $\pm$  as long as the spikes, with pungent tip; floral **Bra** broadly ovate,  $\pm 20$  mm, acuminate, bright pinkish-red, the lower ones divergent, the upper suberect, all with pungent tip, veined abaxially with lines of white trichomes, soon glabrous; **Fl** narrowly tubular and hardly opening; **Sep** triangular, 12 mm, mucronulate, the adaxial ones very broadly alate-carinate, green to red at the tip; **Pet** 15 mm, white, with 2 appendages well above the base; **St** included; **Ov** subglobose, yellowish-green.

Treated as dubious and not recollected since the first description, which was based on cultivated material (Louzada 2012).

**O. schulzianum** Leme & M. Machado (J. Bromeliad Soc. 55(4): 175–177, ill., 2006). **Type:** Brazil, Minas Gerais (*Machado & Schulz* s.n. in *Leme* 5881 [HB]). — **Distr:** E Brazil (C Minas Gerais; Serra do Espinhaço: Diamantina plateau); rock outcrops,  $\pm 1260$  m. — Fig. 2.

[2] **Ros** subdensely few-leaved, elongating-disintegrating at flowering time and plants to



**Fig. 2** *Orthophytum schulzianum*. (Copyright: E. M. C. Leme)

19 cm tall, with slender stolons; **L** spreading to spreading-ascending, sheath inconspicuous, **L** lamina narrowly triangular,  $\pm 12 \times 3$  cm, attenuate-caudate, coriaceous, distinctly canaliculate with upright-incurved margins, completely covered by a thick layer of coarse white trichomes on both faces, distinctly veined abaxially, margins densely spinose, **Sp** narrowly triangular, nearly straight to slightly retrorse,  $\pm 2$  mm, 2–3 mm apart; **Inf** erect; peduncle  $\pm 10$  cm, densely white-lanate, green; peduncular **Bra** leaf-like but gradually reduced in size further up, suberect; fertile **Inf** part densely branched and subcorymbose, ellipsoid-capitate,  $5\text{--}6 \times 3$  cm  $\varnothing$ , with  $\pm 5$  strobilate sessile glomerules, each 2- to 3-flowered; primary **Bra** suberect, completely covered by a dense thick layer of coarse white trichomes on both faces, greenish-white near the base, slightly darker towards the apex, the basal ones  $\pm$  leaf-like, much longer than the fascicles but gradually

shorter higher up, uppermost slightly longer than the fascicles from a broadly ovate-triangular base,  $\pm 2.8 \times 2.5$  cm, margins densely spinose; floral **Bra** suberect, greenish-white, veined, densely and coarsely white-lepidote mainly abaxially, those of the fascicles narrowly triangular, acuminate, strongly carinate, slightly shorter than the sepals, membranous,  $\pm 29 \times 13$  mm, densely spinulose towards the tip, those of the simple main axis narrowly triangular to broadly ovate, long-apiculate, ecarinate, slightly shorter to equalling the sepals,  $31\text{--}35 \times 10\text{--}16$  mm, densely spinulose; **Fl**  $\pm 46$  mm, erect, narrowly tubular, without epigynous tube, unscented; **Sep** subsymmetrical, narrowly lanceolate,  $26\text{--}27 \times 7$  mm, acuminate, entire to remotely denticulate near the apex, greenish-white, membranous, densely to subdensely and coarsely white-lepidote except for the white-lanate apex, carinate; **Pet** sublinear-spatulate,  $\pm 37 \times 6$  mm, obtuse-cucullate, green except for the white apex and apical margins, with 2 laminate obovate and apically denticulate appendages at the base and 2 conspicuous longitudinal callosities  $\pm 25$  mm long; outer **Fil**  $\pm 31$  mm, inner **Fil**  $\pm 28$  mm, adnate to the petals for  $\pm 20$  mm; **Anth**  $\pm 3.5$  mm; **Ov**  $\pm 7$  mm, trigonous; **Sti** simple-erect,  $\pm 1$  mm  $\varnothing$ , lamina green near the base, white towards the apex, suberect; **Fr** and **Se** unknown.

Compared with *O. eddie-estevessii* and *O. mello-barretoii* in the protologue. Versieux & al. (2010: 13) argue that the species is probably closest to *O. diamantinense*, and that the differences need further evaluation.

**O. striatifolium** Leme & L. Kollmann (J. Bromeliad Soc. 57(4): 152–154, ill. (p. 151, 153), 2007). **Type:** Brazil, Espírito Santo (Kollmann & al. 7085 [MBML, HB]). — **Distr:** E Brazil (Espírito Santo); rock outcrops in the Atlantic Forest, in shallow organic soils in full sun. – Fig. 3.

[1] **Ros** subdensely 10- to 14-leaved, elongating-disintegrating at flowering time and plants then to 13 cm tall, with slender rhizomes  $\pm 5$  cm long, without new shoots from the inflorescence; **L** sheath inconspicuous, **L** lamina narrowly triangular-lanceolate,  $8\text{--}11 \times 1.4\text{--}1.5$  cm, long attenuate-caudate, thickly coriaceous, arcuate to



**Fig. 3** *Orthophytum striatifolium*. (Copyright: E. M. C. Leme)

spreading, canaliculate mainly towards the tip, pale reddish-brown, adaxially subdensely white-lepidote with trichomes in rows along the veins, abaxially densely and coarsely white-lepidote completely obscuring the leaf colour, distinctly veined, margins subdensely spinose, **Sp** narrowly triangular, 1.5–2 mm, 4–7 mm apart, basal ones nearly straight, upper distinctly antrorse-uncinate; **Inf** erect; peduncle 4–8 cm, green but densely white-lanate; peduncular **Bra** similar to the rosette leaves, subspreading-arcuate to reflexed, upper ones slightly shorter and congested below the fertile inflorescence part, fertile **Inf** part simple, densely capitate-rosulate, 6- to 9-flowered,  $\pm 2.5$  cm, 3–3.5 cm  $\varnothing$  in outline; floral **Bra** triangular-ovate, 17–23  $\times$  10–13 mm, acuminate, distinctly canaliculate, navicular, ecarinate to obtusely carinate, strongly recurved, yellowish-green to orange (in full sun), (nearly) glabrous, veined, subdensely spinose; **Fl** 32–34 mm, densely

arranged, narrowly tubular with distinctly spreading-recurved limb, with inconspicuous epigynous tube, unscented; **Sep** symmetrical or nearly so, narrowly lanceolate, 15–16  $\times$  4–5 mm, attenuate towards the acuminate-caudate apex, entire, greenish-yellow, veined, glabrous, the adaxial ones carinate, the abaxial one ecarinate; **Pet** sublinear-spatulate, 27–28  $\times$  5–6 mm, obtuse-emarginate, very minutely apiculate-caudate, white except for the pale greenish central portion, with 2 densely and irregularly fimbriate-scalloped appendages  $\pm 3.5$  mm above the base and 2 conspicuous longitudinal callosities reaching the filaments; outer **Fil**  $\pm 18$  mm, inner **Fil**  $\pm 17$  mm, adnate to the petals for 11–12 mm; **Anth** 2.5–3 mm, green; **Ov**  $\pm 5 \times 4.5$ –5 mm, trigonous, greenish-white; **Sti** simple-erect,  $\pm 2$  mm  $\varnothing$ , lobes spreading-recurved, white; **Fr** and **Se** unknown.

Compared with the non-succulent *O. estevesii* in the protologue.

**O. toscanoi** Leme (J. Bromeliad Soc. 53(1): 23–24, 28, ills., cover ill., 2003). **Type:** Brazil, Bahia (*Reis* s.n. [HB]). — **Distr:** E Brazil (Bahia: Poço da Moça); amongst rocks in rather humid forest, 500–900 m.

[1] **Ros** acaulescent, subdensely  $\pm 12$ -leaved, with short basal offshoots,  $\pm 30$  cm tall at flowering time; **L** sheath inconspicuous, lamina narrowly-triangular,  $\pm 10 \times 2.5$  cm, strongly coriaceous, attenuate-caudate, slightly canaliculate to nearly flat, with nearly subulate tip, completely covered by a thick layer of white trichomes on both faces, abaxially distinctly veined, margins densely spinose-serrate for most of the length but entire near the tip, **Sp** triangular, nearly straight to slightly retrorse, 3–5 mm, 1–8 mm apart; **Inf** erect; peduncle  $\pm 13$  cm, densely white-lanate, greenish bronze-coloured; peduncular **Bra** similar to the rosette leaves but upper ones gradually shorter, all white-lanate at the base, exposing the axis, suberect-arcuate; fertile **Inf** part corymbose, laxly branched at least towards the base,  $\pm 15$  cm, **Br**  $\pm 8$ , sessile and shortly rosulate-strobilate spikes, 1–1.2  $\times$  1.5–1.7 cm  $\varnothing$  in outline, 4- to 7-flowered; primary **Bra** like the upper peduncular bracts but gradually smaller, 20–55  $\times$  12–17 mm, distinctly exceeding the subtended branches but



gradually shorter further up, basal ones spreading, the upper slightly reflexed and slightly exceeding the subtended branch, margins on the basal  $\frac{1}{2}$  (sub-) densely spinose; floral **Bra** ovate, 10–11  $\times$  7 mm, acuminate, strongly carinate and recurved, equalling to exceeding the sepals, green, veined, coriaceous, sparsely white-sublanate, subdensely and minutely spinulose; **Fl**  $\pm$ 16 mm, densely arranged, narrowly tubular with hardly flaring limb, with inconspicuous epigynous tube, unscented; **Sep** subsymmetrical, narrowly ovate,  $\pm$ 7  $\times$  3 mm, tip spinescent-acuminate, entire, green, rigid, sparsely white-sublanate, carinate; **Pet** sublinear, 11  $\times$  2–3 mm, obtuse to slightly emarginate and with a hook-like minute apiculus, green except for the white apical part, with 2 densely fimbriate appendages  $\pm$ 3 mm above the base and 2 conspicuous longitudinal callosities which nearly reach the filaments; **Fil**  $\pm$ 6 mm, inner adnate to the petals for  $\pm$ 3 mm; **Anth**  $\pm$ 1 mm; **Ov**  $\pm$ 3 mm, trigonous; **Sti** simple-erect,  $\pm$ 1 mm  $\varnothing$ , lobes suberect; **Fr** and **Se** unknown.

Compared with *O. lemei* in the protologue, but with shorter leaves with longer and more densely arranged marginal spines, shorter inflorescences, and green floral bracts and sepals.

**O. triunfense** J. A. Siqueira & Leme (Fragm. Atlantic Forest N.E. Brazil, 311–312, ill., 2007). **Type:** Brazil, Pernambuco (*Siqueira-Filho* 1255 [UFP, HB]). — **Distr:** E Brazil (Paraíba, Pernambuco); granite outcrops in full sun, 720–1200 m. **I:** Herndon (2015).

[1] **Ros** acaulescent, subdensely 7- to 8-leaved, elongating-disintegrating at flowering time and plants then 10–16 cm tall, propagating with slender stolons, without new shoots from the inflorescence; **L** sheath inconspicuous, **L** lamina narrowly-triangular, 11–20  $\times$  2–3.5 cm, attenuate-caudate and with pungent tip, strongly coriaceous, suberect-arcuate, distinctly canaliculate, densely and coarsely white-lepidote on both faces with the trichomes almost totally concealing the greenish colour, distinctly veined abaxially, margins (sub-) densely spinose, **Sp** acicular, nearly straight to retrorse, 2–3 mm, 3–8 mm apart; **Inf** erect; peduncle 4–6 cm, densely white-lanate, pale green but

colour almost completely concealed by the trichomes; peduncular **Bra** similar to the rosette leaves, exposing the peduncle at the base only, suberect, slightly arcuate; fertile **Inf** part densely branched and subcorymbose, 3.5–4.5  $\times$  2 cm  $\varnothing$  in outline, subdensely  $\pm$ 12-flowered in total; **Br**  $\pm$ 5, almost sessile spikes,  $\pm$ 1.6 cm, each  $\pm$ 2-flowered; primary **Bra** leaf-like but slightly shorter, suberect to nearly spreading, slightly arcuate, greatly exceeding the subtended fascicles, subdensely spinose; floral **Bra** of the fascicles triangular,  $\pm$ 13  $\times$  7 mm, acuminate, densely spinulose, strongly carinate, yellowish, veined, densely and coarsely white-lepidote on both faces, those of the apical part of the main axis more leaf-like, densely spinulose, distinctly exceeding the flowers to about equalling the sepals, suberect, otherwise like the other floral bracts; **Fl**  $\pm$ 26 mm, narrowly tubular, with an epigynous tube  $\pm$ 0.5 mm long, unscented; **Sep** narrowly triangular to ovate-lanceolate,  $\pm$ 11  $\times$  4 mm, acuminate-spinescent, entire, yellowish, submembranous along the margins, densely and coarsely white-lepidote, the adaxial ones carinate, the abaxial one obtusely carinate; **Pet** sublinear-spatulate, 17–20  $\times$  4 mm, acute and minutely apiculate, basal  $\frac{3}{5}$  pale greenish, the apical  $\frac{2}{5}$  white, with 2 shortly scalloped appendages  $\pm$ 3.5 mm above the base and 2 conspicuous longitudinal callosities which nearly reach the anthers; **Fil**  $\pm$ 9 mm, the inner adnate to the petals for  $\pm$ 6 mm; **Anth**  $\pm$ 2 mm, yellowish-green; **Ov**  $\pm$ 5 mm, trigonous; **Sti** simple-erect,  $\pm$ 1 mm  $\varnothing$ , yellowish; **Fr** and **Se** unknown.

Herndon (2015) compares the taxon with the non-succulent *O. magalhaesii*, *O. disjunctum*, *O. gurkenii* and material traded (but most probably incorrectly identified) as *O. leprosum*.

**O. vasconcelosianum** Leme (Phytotaxa 205 (4): 287–289, ills., 2015). **Type:** Brazil, Minas Gerais (*Leme & al.* 8673 [RB, HB]). — **Distr:** E Brazil (Minas Gerais: Alvarenga); on rocks on the summits of inselbergs with Campo Rupestre vegetation, 1060–1440 m. **I:** Leme & al. (2017: fig. 16B-E).

[3] **Ros** long caulescent, stem 20–57 cm long, with 1–2 short shoots produced at the base of the

inflorescence; **L** densely and equally spaced along the stem, spreading, sheath inconspicuous, subtrapeziform, 1–1.3 × 1.8–2 cm, greenish towards the tip, whitish to hyaline towards the base, thin-textured, densely white lepidote and densely spinulose near the apex, glabrous and entire towards the base, densely and conspicuously veined, **L** lamina very narrowly triangular, 5–11 × 0.8–1.3 cm, with attenuate but not pungent apex, coriaceous, canaliculate with upturned margins mainly when water-stressed, densely and coarsely white-lepidote on both faces, green but the colour completely obscured by the trichomes, abaxially veined, margins densely spinulose, **Sp** subtriangular, straight to prevalingly antrorse-uncinate, reddish, 0.5–1 mm, 1.5–4 mm apart; **Inf** sessile at the stem tip, 3–4 cm, corymbose and fasciculately compound at the base but unbranched distally; **Br** 9–12, densely arranged, nearly sessile, slightly pulvinate, 1.7–1.8 cm, 3- to 7-flowered; primary **Bra** leaf-like, gradually shorter towards the tip of the inflorescence, distinctly exceeding the subtended fascicles; floral **Bra** of the fascicles narrowly triangular, 10–12 × 4–8 mm, acute to acuminate, distinctly carinate, ± equalling the middle of the sepals, greenish to wine-coloured, veined, densely and coarsely white-lepidote, not pungent, margins entire, floral bracts of the main axis more leaf-like, equalling to exceeding the flowers; **Fl** 19–24 mm, densely arranged, with inconspicuous epigynous tube, distinctly fragrant; **Sep** narrowly lanceolate, 9–10 × 2.5–3 mm, acuminate, entire, greenish except for the wine-red margins, not pungent, coarsely white-lepidote, (obtusely) carinate; **Pet** lanceolate to narrowly obovate, 15–18 × 4.5–5 mm, acute to inconspicuously emarginate, subspreading-recurved, lilac-rose, without appendages but with 2 conspicuous longitudinal callosities ± as long as the inner filaments, callosities inconspicuously glandulose at the base; outer **Fil** 8–9 mm, inner **Fil** 5–6 mm; **Anth** 2.5–3 mm; **Ov** obovoid, trigonous, 4–6 × 3–4 mm, whitish, coarsely white-lepidote; **Sty** rose-lilac for most of its length; **Sti** simple-erect, somewhat conduplicate-patent, lobes spreading, short to elongate, 0.7–1 mm, rose-lilac with white tip; **Fr** globose, 4–7 × 3.5–6 mm, greenish; **Se** only 3–5 per fruit, 2.2–3 × 1–2 mm.

The species is unique in the genus on the base of several characters and somewhat intermediate between *O. zanonii* of Subgen. *Capixabanthus* and *Cryptanthus* (Subgen. *Hoplocryptanthus*) *glaziovii*, with which it shares fragrant flowers and unappendaged petals. The lilac-rose petals and the few-seeded fruits are also notable.

**O. zanonii** Leme (J. Bromeliad Soc. 54(2): 72–73, ills. (incl. pp. 70–71), 2004). **Type:** Brazil, Espírito Santo (Leme & al. 5930 [HB]). — **Lit:** Louzada & Wanderley (2010: 23–25, with ills.). **Distr:** E Brazil (Espírito Santo: Pancas); slightly inclined rock outcrop in deciduous forest or nearby open sunny places, on rocks, 430–550 m; only known from the type locality. **I:** Leme & al. (2017: fig. 13G). — Fig. 4.

[4] **Ros** forming large and dense clumps, with branched stems 20–50 cm long and 1.5–1.8 cm Ø, propagating by branching and rooting of mature stem sections, as well as new shoots produced at the inflorescence base; **L** densely and



**Fig. 4** *Orthophytum zanonii*. (Copyright: E. M. C. Leme)



equally spaced along the stem, spreading-recurved, sheath broadly ovate,  $\pm 3.5 \times 2.5$  cm, pale-coloured, densely white-lepidote and densely spinulose near the tip, glabrous towards the base, completely covering the stem, coarsely veined, disintegrating into fibres along older stem parts, **L** lamina narrowly-triangular,  $10\text{--}25 \times 1\text{--}1.2$  cm, attenuate-caudate, with a pungent tip, strongly coriaceous, distinctly canaliculate with upturned margins, adaxially densely white-lepidote, abaxially completely covered by a thick layer of white scales, greenish to reddish but the colour  $\pm$  completely obscured by the white scales, sometimes cross-banded, margins densely spinulose, **Sp** uncinata, antrorse, reddish-brown,  $0.5\text{--}1$  mm,  $3\text{--}5$  mm apart; **Inf** sessile, densely compound, corymbose, ellipsoid to subcapitate in outline,  $3\text{--}3.5 \times 2.5\text{--}3$  cm  $\varnothing$ ; **Br**  $5\text{--}8$ , dense, nearly sessile, complanate,  $2\text{--}2.2 \times 1.5$  cm, 2- to 3-flowered; outer primary **Bra** transitional to the inner rosette leaves that sometimes become red-flushed during flowering time, gradually shorter nearer the inflorescence tip but distinctly exceeding the branches; floral **Bra** of the fascicles narrowly triangular,  $18\text{--}19 \times 6\text{--}10$  mm, acuminate with a pungent tip, strongly carinate,  $\pm$  equalling the sepals, greenish, veined, densely white-lanate except for the apical spine, margins spinulose, those of the apical part of the main axis more leaf-like, exceeding the flowers, some rudimentary floral bracts present; **Fl**  $\pm 25$  mm, densely arranged, narrowly tubular and hardly opening, with inconspicuous epigynous tube, unscented; **Sep** narrowly oblong-lanceolate,  $13\text{--}14 \times 3\text{--}4$  mm, acuminate, entire, greenish, rigid but not coriaceous, densely white-lanate, the adaxial ones alate-carinate, the anterior one carinate or nearly so; **Pet** sublinear-spatulate,  $\pm 18 \times 3.5\text{--}4$  mm, obtuse-cucullate, green except for the whitish apical margins, with 2 downwardly oriented cucullate crenulate appendages  $\pm 5$  mm above the base and 2 conspicuous longitudinal callosities  $\pm$  extending to the filaments; outer **Fil**  $\pm 15$  mm, inner **Fil** 6 mm, adnate to the petals; **Anth**  $\pm 3.5$  mm, strongly compressed laterally at anthesis; **Ov**  $\pm 7 \times 6$  mm, trigonous but slightly complanate; **Sty**  $\pm 1.7$  mm; **Sti** simple-erect, lobes suberect, densely papillose, greenish; **Fr** and **Se** unknown.

Compared with the non-succulent *O. vagans* in the protologue but distinct in leaf and inflorescence characters. *O. pseudovagans* is another similar species with elongate stems.

## References

- Braun, P. J. & Esteves Pereira, E. (2009) Succulent and xeromorphic Bromeliads of Brazil: Part 5: *Orthophytum estevesii* & *O. eddie-estevesii*. Cact. Succ. J. (US) 81(2): 59–63, ills. <https://doi.org/10.2985/015.081.0202>.
- Evans, T. M. [ & al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromeliaceae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. Syst. Bot. 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>.
- Herndon, A. (2015) Introducing *Orthophytum triumfense*. J. Bromeliad Soc. 64(4): 264–271, ills.
- Horres, R. & Zizka, G. (1995) Untersuchungen zur Blattsukkulenz bei *Bromeliaceae*. Beitr. Biol. Pfl. 69(1): 43–76, ills.
- Leme, E. M. C. (2004) Studies on *Orthophytum*, an endemic genus of Brazil – Part I. J. Bromeliad Soc. 54(1): 36–43, ills.
- Leme, E. M. C. (2008) Studies on *Orthophytum* — Part IX. The “subcomplex *mello-barreto*” and another new species. J. Bromeliad Soc. 58(6): 257–261, ills., key.
- Leme, E. M. C., Heller, S., Zizka, G. & Halbritter, H. (2017) New circumscription of *Cryptanthus* and new *Cryptanthoid* genera and subgenera (*Bromeliaceae: Bromelioideae*) based on neglected morphological traits and molecular phylogeny. Phytotaxa 318(1): 1–88, ills., maps, key. <https://doi.org/10.11646/phytotaxa.318.1.1>
- Leme, E. M. C. & Coelho de Paula, C. (2008) Studies on *Orthophytum* — Part VIII: Two new species from Grão-Mogol State Park, Minas Gerais, Brazil. J. Bromeliad Soc. 58(3): 106–117, ills.
- Louzada, R. B. (2012) Revisão taxonômica e filogenia de *Orthophytum* (*Bromeliaceae, Bromelioideae*). São Paulo (BR): Universidade de São Paulo, unpublished Ph.D. thesis.
- Louzada, R. B. & Versieux, L. M. (2010) *Lapanthus* (*Bromeliaceae, Bromelioideae*): A new genus from the southern Espinhaço Range, Brazil. Syst. Bot. 35(3): 497–503, ills., key. <https://doi.org/10.1600/036364410792495908>.
- Louzada, R. B. & Wanderley, M. G. L. (2010) Revision of *Orthophytum* (*Bromeliaceae*): The species with sessile inflorescences. Phytotaxa 13: 1–26, ills., key.
- Louzada, R. B. [ & al. 2010], Palma-Silva, C., Corrêa, A. M., Kaltchuck-Santos, E. & Wanderley, M. G. L. (2010) Chromosome number of *Orthophytum* species (*Bromeliaceae*). Kew Bull. 65(1): 53–58. <https://doi.org/10.1007/s12225-010-9175-6>.

- Louzada, R. B. [ & al. 2014], Schulte, K., Wanderley, M. G. L., Silvestro, D., Zizka, G., Barfuss, M. H. & Palma-Silva, C. (2014) Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (*Bromelioideae*, *Bromeliaceae*) and its implications on morphological character evolution. *Molec. Phylogen. Evol.* 77: 54–64. <https://doi.org/10.1016/j.ympev.2014.03.007>.
- Schulte, K. & Zizka, G. (2008) Multi locus plastid phylogeny of *Bromelioideae* (*Bromeliaceae*) and the taxonomic utility of petal appendages and pollen characters. *Candollea* 63(2): 209–225. [http://www.ville-ge.ch/cjb/publications\\_candollea\\_632.php](http://www.ville-ge.ch/cjb/publications_candollea_632.php)
- Schulte, K. [ & al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromeliaceae*) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylogen. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>.
- Silvestro, D. [ & al. 2014], Zizka, G. & Schulte, K. (2014) Disentangling the effects of key innovations on the diversification of *Bromelioideae* (*Bromeliaceae*). *Evolution* 68(1): 163–175. <https://doi.org/10.1111/evo.12236>.
- Smith, L. B. & Downs, R. J. (1979) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 3: *Bromelioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399940>
- Versieux, L. M. [ & al. 2010], Louzada, R. B., Lage Viana, P., Mota, N. & Wanderley, M. G. L. (2010) An illustrated checklist of *Bromeliaceae* from Parque Estadual do Rio Preto, Minas Gerais, Brazil, with notes on phytogeography and one new species of *Cryptanthus*. *Phytotaxa* 10: 1–16, ills. <https://doi.org/10.11646/phytotaxa.10.1.1>





## × *Orthotanthus* BROMELIACEAE

U. Eggli

× ***Orthotanthus*** L. E. Smith (J. Bromeliad Soc. 38(2): 75, 1983). — **Distr:** Cultivated only.

= *Orthophytum* × *Cryptanthus*. Smith (1983) lists the cultivar ‘What’ with the parentage *O. saxicola* var. *rubra* × *Cryptanthus* ‘It’, and Giroux (2009) described the cultivar ‘Blazing Bonsai’ with the parentage *O. navioides* (now classified as *Sincoraea*) × *C. microglazioui*.

### References

- Giroux, L. (2009) An unusual bigeneric hybrid with *C. [ryptanthus] microglazioui* [sic!]. *Cryptanthus Soc. J.* 24(1): 18–19, ills.
- Smith, E. L. (1983) Bigeneric hybrids — A listing. *J. Bromeliad Soc.* 33(2): 69–75. <http://journal.bsi.org/V33/2/>

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## × *Puckia* BROMELIACEAE

N. Schütz and F. Krapp

× ***Puckia*** D. Butcher (J. Bromeliad Soc. 52: 52, 2002). — **Distr:** Cultivated only.

**Incl.** × *Dyckipu* hort. (*nom. inval.*, ICN Art. 29.1).

= *Puya* × *Dyckia*. The only known cultivar is the hybrid ‘Sparkle’ (= *P. laxa* (female) × (*D. fosteriana* × *D. platyphylla*)). It originated in a nursery in Venice, Florida, and was first invalidly named × *Dyckipu*.

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## × *Pucohnia* BROMELIACEAE

N. Schütz and F. Krapp

× ***Pucohnia*** G. H. Anderson *ex* D. A. Beadle (Prelim. List. Cult. Grex Bromeliad, 200, 1991).

— **Distr:** Cultivated only.

= *Puya* × *Deuterocohnia*. The only known cultivar is ‘George Anderson’ (= *P. laxa* (female) × *D. schreiteri*) (Anderson 1986: 103). The greenish-grey leaves are said to be longer than

those of either parent. Plants produce numerous offsets at their base.

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### References

Anderson, G. H. (1986) Hybrids by design and by chance. *J. Bromeliad Soc.* 36(3): 99–103, 109, ill.

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## Puya BROMELIACEAE

J. M. Manzanares

**Puya** Molina (Sag. Stor. Nat. Chili, 160, 351, 1782). **Type:** *Puya chilensis* Molina. — **Puyoideae** — **Lit:** Gilmartin (1972: synopsis Ecuador); Smith & Downs (1974: 66–190, Fl. Neotropica); Gómez & Grau (2009: synopsis Argentina); Jabaily & Sytsma (2010: phylogeny Chile); Jabaily & Sytsma (2013: biogeography and evolution); Zizka & al. (2013: taxonomy Chile). **Distr:** C America to C-S Chile. **Etym:** Span. ‘puya’, tip of the lancet used to drive oxen; probably for the pungent leaf tips or the leaf marginal teeth.

**Incl.** *Pourretia* Ruiz & Pavón (1794) (*nom. illeg.*, ICN Art. 52.1). **Type:** *Pourretia lanuginosa* Ruiz & Pavón.

Monocarpic or polycarpic rosette-forming dwarf to giant herbs, terrestrial, sometimes on rocks, monocarpic taxa with solitary sessile or single-stemmed rosette, polycarpic taxa with usually offsetting rosettes with short to long branched stems, stems sometimes fleshy; **Ros** few- or more often many-leaved; **L** with a distinct wide and usually slightly to strongly fleshy sheath, **L** lamina narrowly triangular, coriaceous to slightly or rarely distinctly succulent, persisting for several

years, young ascending, becoming increasingly spreading to reflexed with age, adaxially usually glabrous, abaxially completely or at least between the veins covered with a cinereous indumentum, tip attenuate, pungent in the majority of the species, margins spinose-serrate, **Sp** retrorse or antrorse, or both; **Inf** terminal, usually pedunculate, erect, simple racemes or spikes, or branched, lax or dense, cylindrical or pyramidal in outline, or strobiliform, axes covered with a lanate, ferruginous, tomentose or floccose indumentum, or glabrous, peduncle usually exceeding the leaves; peduncular **Bra** leaf-like or reduced; lower primary **Bra** similar to the peduncular bracts or reduced, branches when present stipitate (i.e. with the basal portion sterile), polystichous, dense, subdense or lax; floral **Bra** longer or shorter than the sepals, imbricate or remote, persistent, entire or serrulate; **Fl** actinomorphic, hermaphrodite, subsessile or pedicellate, mostly diurnal; **Sep** free, convolute, entire, symmetrical or  $\pm$  asymmetrical; **Pet** free, frequently in shades of dark green or purple, without appendages at the base, becoming spirally contorted after anthesis; **Ov** superior; **Fr** loculicidal and septicidal capsules; **Se** alate.

The genus is composed of 223 species and 7 varieties of which 55 species and 5 varieties are considered succulent. The degree of succulence is comparable to that of many bona-fide succulents from other families. Usually, succulence is confined to the leaf sheaths, and/or to the fleshy stems. CAM is present in about  $\frac{1}{4}$  of

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all taxa, and has been found to have evolved repeatedly (Jabaily & Sytsma 2010).

**Classification:** *Puya* was traditionally included in subfamily *Pitcairnioideae*. All recent molecular phylogenetic studies of the family agree, however, that the genus is sister to the *Bromelioideae* (Givnish & al. 2007, Schulte & Zizka 2008, Schulte & al. 2009, Jabaily & Sytsma 2010, Givnish & al. 2011). To accommodate this finding, the monotypic subfamily *Puyoideae* was erected by Givnish & al. (2007: 16). The genus has been found to be monophyletic by Jabaily & Sytsma (2010), while Givnish & al. (2011) found some support that the genus rather represents a paraphyletic grade at the base of the *Bromelioideae*, but monophyly cannot be rejected. Monophyly is also supported by the diagnostic character of the petals that form a tightly coiled spiral after anthesis. The 2 subgenera traditionally recognized have not been confirmed by the molecular phylogeny of Jabaily & Sytsma (2010), but they are here maintained on practical grounds.

*Puya* represents one of the largest radiations in the family and spans a wide ecological amplitude in a diversity of wet to dry habitats. Its species are often characteristic elements of the Páramo floras. *Puya* is also a good example of a rapid species-level radiation in the Andes (Jabaily & Sytsma 2013): The greatest diversity is found at middle elevations and mid-latitudes in S America. The origin of the genus is in present-day C Chile, and speciation progressed from S to N tracking the final Andean uplift. Pleistocene glaciation cycles are the likely drivers for speciation. Hybrid speciation also appears to play a considerable role (Jabaily & Sytsma 2010, Jabaily & Sytsma 2013: 214).

The genus is traditionally divided in 2 subgenera based on the inflorescence architecture:

- [1] Subgen. *Puya*: **Inf** branched, branches sterile in their apical parts.
- [2] Subgen. *Puyopsis* (Baker) L. B. Smith 1970: **Inf** unbranched or branched, fertile over the whole length.

**Ecology:** *Puya* species native to high-elevation Páramo vegetations in the Andes often have compact

inflorescences with a dense woolly indumentum. Miller (1994) measured flower temperatures and found them to be above ambient temperatures in the species studied. Hypothetically, the dense indumentum serves for thermal insulation and protects the flowers from freezing damage.

Hornung-Leoni & al. (2013) report that the flowers of species of subgen. *Puyopsis* (e.g. *P. coerulea*, *P. venusta*) are visited by specialist nectarivorous hummingbirds, while species of subgen. *Puya* (e.g. *P. chilensis*, *P. alpestris*) are visited by more generalist passerine birds that perch on the sterile distal branch parts to exploit the flowers with their generally highly diluted but abundant nectar. According to Salinas & al. (2007) High Andean *Puya* species are an important source of nutrients for hummingbirds, at least in Peru.

**Horticulture:** *Puya* has limited horticultural potential due to the large size of many of its species. The smaller-growing species are sometimes encountered in specialist collections. In cultivation, hybrids with *Dyckia* (= ×*Puckia*, see separate entry) and *Deuterocohnia* (= ×*Pucohnia*, see separate entry) have been obtained.

The following names are of unresolved application but are referred to this genus: *Pourretia aurucensis* Linden (1853); *Pourretia lepidota* Linden (1853); *Pourretia speciosa* Linden (1853); *Pourretia yuccoides* Linden (1871); *Puya acris* hort. ex Gentil (1907) (*nom. inval.*, ICN Art. 32.1c).

**P. adscendens** L. B. Smith (Phytologia 17: 76, t. 1: figs. 17–18, 1968). **Type:** Peru, Amazonas (*Sagástegui* 6073 [TRP, US [photo]]). — **Distr:** Peru (Amazonas: small area in Chachapoyas); ravines, semi-desert areas, 2800 m.

[2] Polycarpic, forming dense groups, 2 m tall at flowering time; **L** sheath fleshy, lamina 40–60 × 1.5–2 cm, adaxially glabrous, abaxially covered with appressed cinereous scales, margins laxly serrate with brown antrorse **Sp** 5 mm long; **Inf** laxly branched, pyramidal, greenish, except for the petals densely cinereous-tomentose with finely stellate scales, peduncle exceeding the leaves; peduncular **Bra** leaf-like; primary **Bra** broadly ovate, 5 cm, with an attenuate apex,

shorter than the subtended branches but slightly exceeding the naked sterile branch bases; **Br** divergent, ascending, 15–30 cm, laxly flowered with  $\pm$  secund flowers; floral **Bra** broadly ovate, 20 mm, with an attenuate brown apex, covering the lower  $\frac{1}{2}$  of the sepals; **Ped** rather slender, 5 mm; **Sep** oblanceolate, 23 mm, broadly rounded and mucronulate; **Pet** green-bluish, 45 mm; **St** included; **Anth** yellow; **Sty** as long as the petals; **Sti** yellow.

As in many other Andean species, the inflorescence is totally covered by dense cinereous scales, and only the petals are glabrous. Only few inflorescences are present in a dense group of plants. The flowers are pollinated by hummingbirds.

**P. aequatorialis** André (Énum. Bromél., 5, 1888). **Type:** Ecuador, Imbabura (*André* 3564 [K]). — **Distr:** N Ecuador (Carchi, Imbabura, Pichincha, Azuay, Loja); dry inter-Andean valleys, 2200–2400 m.

[2] Polycarpic, forming dense groups, 1.5–2 m tall at flowering time, stem  $40 \times 20$ –25 cm, branched; **L** sheath 5.5–4.5 cm, fleshy, lamina  $35$ – $50 \times 1.5$ –2 cm, adaxially green, abaxially with appressed cinereous scales, margins serrate with yellow retrorse hooked **Sp** 5 mm long; **Inf** peduncle exceeding the leaves, 60–90 cm, floriferous part 50–100 cm, simple, cylindrical, lax, red-violet or green, glabrous; peduncular **Bra** small, exposing most of the peduncle; **Br** divergent, 30–50 cm, laxly flowered; floral **Bra** ovate, 9–10 mm, attenuate towards the tip, much shorter than the sepals, margins entire; **Ped** rather slender, to 15 mm; **Sep** linear, 5 mm, broadly rounded and apiculate; **Pet** white, green or violet, 45 mm; **St** included; **Anth** yellow; **Sty** included; **Sti** surrounded by the anthers.

Very common in the Andes of N Ecuador. Natural hybrids between green- and violet-flowered populations result in an array of different flower colours from green to violet. The plants are used locally to plant fences. This is also one parent of the natural hybrid *P. ×pichinchae* (see there).

**P. aequatorialis** var. **aequatorialis** — **Distr:** N Ecuador (Carchi, Imbabura, Pichincha, Azuay, Loja); dry inter-Andean valleys, 2200–2400 m. **I:**

Oliva-Esteve (2002: 228); Manzanares (2005: 304–305).

[2] Floral **Bra** merely reaching to the base of the sepals, to 10 mm; **Ped** 2–6 mm at anthesis; **Pet** green or violet.

**P. aequatorialis** var. **albiflora** André (Énum. Bromél., 5, 1888). **Type:** Ecuador, Pichincha (*André* 3596 [K]). — **Distr:** N Ecuador (Pichincha). **I:** Gilmartin (1972: Fig. 8); Manzanares (2005: 306).

$\equiv$  *Puya aequatorialis* fa. *albiflora* (André) Gouda (s.a.) (*nom. inval.*, ICN Art. 29.1).

[2] Floral **Bra** exceeding the base of the sepals, to 22 mm; **Ped** 9–15 mm at anthesis; **Pet** white.

White-flowering plants commonly grow among populations with violet flowers. Populations from the area of the Río Pisque (Pichincha) have longer and more slender peduncles than those registered elsewhere.

Gouda & al. (2012+) treat this variety as a mere form of *P. aequatorialis*.

**P. alpestris** (Poeppig) Gay (Fl. Chil. 6: 12, 1853). **Type:** Chile, Bío Bío (*Poeppig* 891 p.p. [W †, BM]). — **Lit:** Zizka & al. (2013: with ills.). **Distr:** C to S-C Chile; stony arid to semi-humid habitats, 0–2200 m.

$\equiv$  *Pourretia alpestris* Poeppig (1833).

[1] Polycarpic, forming dense groups, 1.5–2.5 (–5) m tall at flowering time, stems prostrate, covered with old leaves; **L** arched and recurving, sheath fleshy,  $2.5$ – $9.5 \times 1.8$ –10 cm, margins in the upper part laxly serrate, **L** lamina  $50$ – $130 \times 1.5$ –4.5 (–5) cm, adaxially green with  $\pm$  cinereous scales, abaxially with dense coating of white scales, margins laxly serrate with uncinat **Sp** 4 mm long; **Inf** peduncle to 2.5 m, exceeding the leaves, floriferous part 0.25–1 m, pyramidal in outline, with 15–100 racemose branches, axes greenish, cinereous-tomentose; peduncular **Bra** oblong, reflexed,  $\pm$  deciduous; primary **Bra** like the upper peduncular **Bra**, shorter than the subtended branch; **Br** divergent, 25–30 cm, laxly to densely flowered in the lower  $\frac{1}{3}$ – $\frac{1}{4}$ , distally sterile with reduced bracts; floral **Bra** elliptic, 15 mm, shorter than the sepals; **Ped** slender, 10 mm; **Sep** oblong, acute, 20–25 mm; **Pet** blue-green, 50 mm;

**St** included; **Anth** yellow-orange; **Sty** included; **Sti** yellow, surrounded by the anthers.

**P. alpestris** ssp. **alpestris** — **Lit:** Zizka & al. (2013: with ills.). **Distr:** C-S Chile (Maule, Bío Bío, Araucanía), Argentina (San Juan)?; 0–2000 m.

**Incl.** *Puya whytei* Hooker fil. (1868); **incl.** *Puya pumila* Ravenna (2000).

[1] Plants 1.2–1.5 (–2) m tall at flowering time; **L** lamina 1.5–2.5 (–3.2) cm wide; **Inf** with 20 (–40) laxly few-flowered branches.

Gómez & Grau (2009) report the taxon from S Argentina (Neuquén), and Subils (2009: 346) from C Argentina (San Juan). The Neuquén record appears doubtful according to Zizka & al. (2013: 391), since the plants were described with violet petals. The plants from San Juan are described with white to lead-blue flowers.

**P. alpestris** ssp. **zoellneri** Zizka & al. (Brittonia 65(4): 393, 2013). **Type:** Chile, Valparaíso (Zizka 8004 [FR]). — **Distr:** C to C-S Chile (Coquimbo, Valparaíso, Libertador O’Higgins, Maule: N of La Serena to E of Curicó); 0–2200 m.

**Incl.** *Pitcairnia alpestris* L. H. Bailey (1916) (*nom. inval.*, ICN Art. 38.1a).

[1] Plants (2–) 2.5–5 m tall at flowering time; **L** lamina to 5 cm wide; **Inf** with (40–) 50–80 (–100) densely many-flowered branches.

**P. asplundii** L. B. Smith (Phytologia 6: 439, t. 2: figs. 14–15, 1959). **Type:** Ecuador, Imbabura (*Asplund* 20222 [S]). — **Distr:** N-C Ecuador (Pichincha, Cañar); shrub and Páramo vegetations, 3000–4000 m. **I:** Manzanares (2005: 364–365).

[2] Polycarpic, forming dense groups, 2–3 m tall at flowering time; **L** sheath fleshy, orbicular, 6–7 × 5 cm, margins in the upper part serrate, **L** lamina 40–50 × 2–3 cm, adaxially glabrous, abaxially covered with cinereous scales, margins serrate with brown antrorse and retrorse **Sp** 5–7 mm long; **Inf** peduncle exceeding the leaves, 0.7–0.9 m, fertile part 0.5–0.7 m, laxly branched, cylindrical, covered with cinereous indumentum; peduncular **Bra** leaf-like, remote; primary **Bra** broadly ovate, 3–4 cm, margins in the upper part serrulate, with an attenuate apex, shorter than the subtended branch; **Br** divergent, strobilaceous or

ellipsoid, 5–9 × 1–4 cm, densely flowered, with a distinct stipe 1–4 cm long; floral **Bra** ovate, 25 × 15 mm, acute, reaching the middle of the sepals, margins entire; **Ped** stout, 5–7 mm; **Sep** obovate, 23 × 8 mm, rounded and ± retuse; **Pet** green or bluish, 50 mm; **St** exposed; **Anth** green; **Sty** included.

Gilmartin (1972: 30) treats this species as synonym of *P. glomerifera* based on an examination of the floral bracts (size and margins) and the margins of the primary bracts. Manzanares (2005: 364–365) discusses the differences between the two species in detail. Plants with a globose spike are often mis-identified as *P. glomerifera*, but careful examination of the flowers allows to easily distinguish between the species. — Locally used for fences as the groups grow very dense and are impossible to penetrate.

**P. ×berteroniana** Mez pro sp. (in A. & C. de Candolle, Monogr. Phan. 9: 477, 1896). **Type:** Chile, Valparaíso (*Bertero* 115 [P, B, G]). — **Lit:** Zizka & al. (2013: with ills.). **Distr:** C Chile (Valparaíso: Quillota); dry and rocky areas near sea-level. **I:** Oliva-Esteve (2002: 230).

[1 + 2] Polycarpic, forming dense groups, 5 m tall at flowering time, stems prostrate, simple or branched, covered with the bases of old leaves; **L** arched and recurving, sheath fleshy, 7 × 6 cm, margins entire, **L** lamina 100 × 2.5–5 cm, adaxially green and glabrous, abaxially with white appressed scales, margins laxly serrate with antrorse and retrorse yellow-green uncinat **Sp** 5–10 mm long; **Inf** peduncle exceeding the leaves, 0.6 m, densely white-lanate when young, floriferous part 0.6–1 m, densely branched with 80–100 branches, slenderly pyramidal in outline; peduncular **Bra** broadly lanceolate, reflexed, ± deciduous; primary **Bra** like the upper peduncular **Bra**, much shorter than the subtended branch; **Br** 25–35 cm, densely flowered in the lower 1/3–1/2, sterile on the remainder with reduced bracts; floral **Bra** elliptic, acute, 30 mm, shorter than the sepals, white-lepidote; **Ped** slender, 15 mm; **Sep** narrowly oblong, 20–25 × 6.5 mm, broadly acute or obtuse, green; **Pet** elliptic, 50 mm, blue-green; **St** included; **Fil** blue-green; **Anth** orange; **Sty**

included; **Sti** green, surrounded by the anthers; **Fr** ovoid, as long as the sepals.

The correct identification of this name has been problematic for a long time. According to Zizka & al. (2013: 399–400), it should be considered to represent a natural hybrid, based on the observation of a plant intermediate between the locally sympatric *P. alpestris* ssp. *zoellneri* and *P. venusta* in the Pichidanguí area (Zizka 8119, CONC, FR). Its inflorescence resembled that of *P. alpestris* but without the sterile terminal parts. Plants identified as *P. berteroniana* are also reported from the region of Coliguay (Varadarajan & al. 1490, SEL) from open cliffs in forest vegetation, sympatric with *P. chilensis*. More studies are needed to clarify the existence of natural hybridization, and the application of the name. According to the taxonomy of Zizka & al. (2013), material usually named *P. berteroniana* is attributable to *P. alpestris* ssp. *zoellneri*.

**P. boliviensis** Baker (Handb. Bromel., 126, 1889). **Type:** Chile, Antofagasta (*Gaudichaud* s.n. [P, B, F, US]). — **Lit:** Jabaily & Sytsma (2010). **Distr:** N Chile (Antofagasta); stony coastal deserts and hills, 0–670 m.

**Incl.** *Puya copiapina* Philippi (1895).

[1] Polycarpic, forming dense groups, 2 m tall at flowering time; **L** sheath fleshy, **L** lamina 100 × 6 cm, succulent, both faces green and sparsely lepidote when young but soon completely glabrous, margins serrate with green uncinately stout **Sp** 10 mm long; **Inf** peduncle to 60 cm, exceeding the leaves, fertile part 50–70 cm, laxly branched, with 20–25 branches, broadly pyramidal in outline, green, tomentose-lepidote; lower peduncular **Bra** narrowly triangular and coarsely serrate, upper broadly lanceolate and entire, reflexed, primary **Bra** like the upper peduncular bracts, much shorter than the subtended branch; **Br** shortly stipitate, 20–30 cm, laxly flowered in the lower ½, sterile distally with reduced bracts; floral **Bra** lanceolate-elliptic, acute, 25–30 mm, shorter than the sepals, brown, tomentose-lepidote; **Ped** slender, 15 mm, tomentose-lepidote; **Sep** oblong-lanceolate, 30 × 6 mm, broadly acute, green, tomentose-lepidote; **Pet** elliptic, 50 mm, yellow or green-yellow, with a dark green spot at

the base; **St** included; **Anth** dark; **Sty** included, longer than the stamens; **Sti** green; **Fr** subglobose.

Despite the name, the taxon is endemic to Chile, but at the time when it was discovered, that part of Chile belonged to Bolivia. Flowering appears to be restricted to years with above-average precipitation associated with El Niño events.

**P. bravoii** Aráoz & A. Grau (J. Bromeliad Soc. 58(5): 199–200, ills., 2008). **Type:** Argentina, Salta (Aráoz & al. 1596 [LIL, LPB, MO]). — **Lit:** Gómez & Grau (2009: with ill.). **Distr:** Argentina (Salta: near Santa Victoria); rocky-grassy slopes and on rock walls, 3100 m; only known from the type locality.

[2] Monocarpic, 1.5–2 m tall at flowering time; **Ros** solitary, stemless; **L** numerous, sheath fleshy, suborbicular, 9 cm, **L** lamina 60 × 6 cm, adaxially green, abaxially white-lepidote, margins entire except at the base and the top and there with few **Sp** 2–3 mm long; **Inf** peduncle as long as the leaves or shorter, 20–60 cm, stout, brown, floriferous part 100 cm, densely branched, cylindrical, brown, strobiliform, compact, all brown-lanate except for the petals; peduncular **Bra** densely imbricate making the peduncle appear nearly as thick as the inflorescence proper, apex reflexed; primary **Bra** ovate with triangular apex, longer than the subtended branch, lanate, brown, margins entire; **Br** shortly stipitate, spreading, densely 2- to 3-flowered; floral **Bra** 5 mm, elliptic, acute, shorter than sepals and the pedicel, lanate, brown; **Ped** fleshy, 12 mm, lanate; **Sep** elliptic, acute, 35 × 8 mm, brown, lanate; **Pet** elliptic, blue, 60–70 mm; **St** included; **Anth** yellow; **Sty** included, longer than the stamens; **Sti** green; **Fr** ellipsoid, 15–35 mm; **Se** alate, 4–5 × 2.5–3.5 mm.

An extraordinary monocarpic species, known from a single population with a few hundred individuals only.

**P. cardenasii** L. B. Smith (Lilloa 14: 94, fig. 6, 1948). **Type:** Bolivia, Cochabamba (*Cárdenas* 4082 [US, GH]). — **Distr:** Bolivia (Cochabamba); rocky-grassy slopes in moderately moist open puna, (2950–?) 3800–3900 m.

[2] Polycarpic, 1.5 m tall at flowering time; **L** sheath fleshy, **L** lamina 50 × 3 cm, arching,



green, sparsely lepidote, margins laxly serrate with broad straight or curved brown **Sp** 8 mm long; **Inf** peduncle exceeding the leaves, to 75 cm, stout, lanate, floriferous part 25–50 cm, densely branched, cylindrical, pale lanate, glabrous at fruiting time; lower peduncular **Bra** leaf-like, the upper reflexed, base ovate and apex long attenuate, margins laxly serrate; primary **Bra** ovate, acuminate, 6 × 5 cm, ± as long as the subtended branch, pale lanate, margins obscurely serrulate; **Br** shortly stipitate, densely 5- to 7-flowered; floral **Bra** ovate, acute or acuminate, 35–40 × 25–30 mm, exceeding the sepals; **Ped** slender, obconical, 10 mm; **Sep** broadly lanceolate, acute, 25 × 7 mm, thinly coriaceous; **Pet** blue, 45 mm; **Fr** subglobose.

Insufficiently known and only collected twice recently. Petal colour was described as blue in the protologue, but as pale green in one of the recent collections (*Solomon* 9682, MO), made at a lower altitude (2950 m).

**P. castellanosii** L. B. Smith (*Phytologia* 18: 140, 1969). **Type:** Argentina, Salta (*Castellanos* s.n. [BA 45819]). — **Lit:** Gómez & Grau (2009: with ill.). **Distr:** N Argentina (Salta: Valles Calchaquies); dry mountain slopes with Monte vegetation, 2800–3000 m. **I:** Varadarajan (1989: 4); Grau & al. (2010: 12). — Fig. 1.

**Fig. 1** *Puya castellanosii* (Argentina, Salta, Valle de Lerma, beyond El Alisal, 2800 m). (Copyright: G. Rivera)



[1] Polycarpic, forming dense colonies of 3–8 rosettes aggregated into a massive clump, 1–2 m tall at flowering time; **L** sheath fleshy, reniform, 6 × 8 cm, **L** lamina 60–80 × 4.5 cm, broadly channelled, both faces densely lepidote, margins serrate with retrorse and antrorse curved **Sp** 5 mm long; **Inf** peduncle exceeding the leaves, 0.6 m, stout, green, lepidote, floriferous part 1–1.5 m, laxly branched, with 25–30 branches, pyramidal in outline, dark purplish, densely tomentose-lepidote; lower peduncular **Bra** narrowly triangular, upper deltoid, reflexed, purplish; primary **Bra** ovate, with acute apex, much shorter than the subtended branch, lepidote, purplish; **Br** shortly stipitate, 25–30 cm, spreading, subdensely flowered in the lower ½, sterile distally with reduced bracts; floral **Bra** lanceolate, acute, 30 mm, shorter than the sepals, purplish, lepidote; **Ped** slender, 15 mm, tomentose-lepidote; **Sep** triangular-ovate, acute, 30 × 7 mm, purplish, lepidote; **Pet** elliptic, white-blue, 50–60 mm, **St** included; **Anth** yellow; **Sty** included; **Sti** green; **Fr** subglobose, shorter than the sepals.

**P. cerrateana** L. B. Smith (*Contr. US Nation. Herb.* 29: 533, fig. 88, 1954). **Type:** Peru, Ancash (*Cerrate* 369 [US, USM]). — **Distr:** N & C Peru (Cajamarca, Ancash); rocky ground, 2000–3560 m.



[2] Polycarpic, forming dense groups united by thick stems, 1–1.5 m tall at flowering time; **L** sheath fleshy, elliptic,  $9 \times 6$  cm, mostly glabrous, margins serrate in the upper part, **L** lamina  $40\text{--}50 \times 3\text{--}5$  cm, adaxially glabrous, abaxially covered with fine white appressed scales, margins laxly serrate, **Sp** red-brown, uncinata, 7 mm; **Inf** peduncle exceeding the leaves, erect, 1–1.2 m,  $\pm$  lepidote, glabrous at anthesis, floriferous part 0.3–0.4 m, 7–10 cm  $\varnothing$ , simple, cylindrical, densely flowered, densely cinereous-lepidote; lower peduncular **Bra** leaf-like, upper quickly deciduous, lanceolate, attenuate,  $5\text{--}9 \times 1.5$  cm, longer than the internodes, margins  $\pm$  denticulate esp. in the lower part; floral **Bra**  $50\text{--}70 \times 30$  mm, ovate, acuminate, adaxially glabrous and nearly black, abaxially covered with a short-lanose dusty-white tomentum, longer than the sepals but with the upper  $\frac{1}{2}$  coiling-reflexed at anthesis, margins entire; **Fl** tubular; **Ped** obconical, 10–15 mm, lanate; **Sep** elliptic,  $35\text{--}40 \times 12$  mm, broadly acute, adaxially glabrous, abaxially lanate; **Pet** olive-green turning brown, 56 mm, apex recurved; **St**  $\pm$  exserted.



**Fig. 2** *Puya chilensis*. (Copyright: M. Wisnev)

**P. chilensis** Molina (Sag. Stor. Nat. Chili, 160, 351, 1782). **Type** [neo]: Chile, Bío Bío (*Quezada* 174 [CONC]). — **Lit**: Zizka & al. (2013: 396–398, ills. p. 392). **Distr**: C to C-S Chile (Coquimbo, Valparaiso, Libertador O’Higgins, Maule, Bío Bío); dry stony ground, 0–900 m. **I**: Rauh (1990: 128: fig. 131, 437); Duval (1990: 118: figs. 43–44); Oliva-Esteve (2000: 404). — **Fig. 2**.

$\equiv$  *Pitcairnia chilensis* (Molina) Cat. Loddiges ex Loudon (1830); **incl.** *Pourretia coarctata* Ruiz & Pavón (1798)  $\equiv$  *Pitcairnia coarctata* (Ruiz & Pavón) Persoon (1805)  $\equiv$  *Puya coarctata* (Ruiz & Pavón) Fischer (1846); **incl.** *Puya suberosa* Molina (1810); **incl.** *Puya gigantea* Philippi (1864)  $\equiv$  *Puya chilensis* var. *gigantea* (Philippi) Baker ex Mez (1896); **incl.** *Puya quillotana* W. Weber (1984).

[1] Polycarpic, forming dense masses, 4–4.5 m tall at flowering time, stems prostrate, simple or branched, to 5 m; **L** sheath fleshy, broad, **L** lamina  $80\text{--}100 \times 5$  cm, strongly channelled, adaxially soon glabrous, abaxially densely lepidote, margins serrate with antrorse and retrorse curved **Sp**

5–10 mm long with white scales; **Inf** peduncle exceeding the leaves, 1–1.5 m, stout, green, soon glabrous, floriferous part 1–1.5 m, densely branched, with 80–100 branches, cylindrical in outline, green, sparsely tomentose-lepidote; lower peduncular **Bra** leaf-like, upper broadly ovate, acute, reflexed, brown, lepidote; primary **Bra** triangular-ovate, acute, much shorter than the subtended branch, margins sparsely serrate, lepidote, brown-green; **Br** shortly stipitate, 30–40 cm, spreading, subdensely flowered in the lower  $\frac{1}{2}$ , sterile distally with reduced bracts; floral **Bra** 50 mm, narrowly elliptic, acute or acuminate, as long as or shorter than the sepals, green, lepidote; **Ped** slender, 15 mm, lepidote; **Sep** elliptic-oblong, broadly acute or obtuse,  $35 \times 13$  mm, green, lepidote; **Pet** elliptic, yellow or yellow-green, 50 mm; **St** included; **Anth** yellow; **Sty** included, longer than the stamens; **Sti** green.

One of the best-known and most widespread species of *Puya*. When grazing too close to the plants, sheep sometimes get trapped by the heavily

armed leaves with their mix of antrorse and retrorse spines.

Quezada & al. (2014) studied photosynthesis over the whole range of the species. Populations from northern (more arid) sites had a predominance of CAM, those of the southern (wetter) sites had weakly expressed CAM.

**P. claudiae** Ibisch & al. (Revista Soc. Boliv. Bot. 2(1): 131–132, ills., (incl. p. 127), 1998). **Type:** Bolivia, Santa Cruz (*Ibisch & Ibisch* 98040 [LPB]). — **Distr:** Bolivia (Santa Cruz); disturbed shrub areas, 2000 m.

[2] Polycarpic, forming small clusters, 1.5 m tall at flowering time, stem simple or branched, to 0.5–1 m; **L** sheath fleshy, broad, **L** lamina 100–150 × 5 cm, green, adaxially glabrous, abaxially lepidote, margins serrate with antrorse curved **Sp** 15 mm long, black, white-lepidote at the base; **Inf** peduncle as long as or longer than the leaves, 0.4–0.5 m, stout, red-green, soon glabrous, floriferous part 1–1.5 m, densely branched, with 17–20 branches, pyramidal in outline, red, densely covered with white scales; lower peduncular **Bra** leaf-like, upper triangular, attenuate, lepidote, margins serrulate; primary **Bra** triangular, apiculate, 2.3–7 × 3–3.5 cm, much shorter than the subtended branch, glabrous, red, margins serrulate-denticulate; **Br** shortly stipitate for 5 cm, 20–40 cm, spreading, laxly flowered, red; floral **Bra** 10–15 × 8–10 mm, triangular, acute, longer than the pedicels, green-red, margins entire; **Ped** slender, 5–13 mm, white-tomentose; **Sep** elliptic, apiculate, 20–30 × 6–7 mm, red, green at the base, lepidote; **Pet** oblong, green, 50 mm; **St** included, 45 mm; **Anth** yellow; **Sty** included, 50 mm; **Sti** green; **Fr** 13 mm; **Se** broadly triangular, white-alate.

After flowering, the very robust plants produce 2 new shoots at the base of the inflorescence, and thus form branched stems. The green leaves with the contrasting black marginal spines covered with white woolly scales at their base are very attractive.

**P. cochabambensis** R. Vázquez & Ibisch (Bromelie 2000(1): 16–18, ills., 2000). **Type:** Bolivia, Cochabamba (*Vásquez* 3493 [LPB]). —

**Distr:** Bolivia (Cochabamba: Ayopaya; La Paz); on rocks, 3200–3600 m.

[2] Polycarpic, forming dense colonies of several individuals, branched, 0.8 m tall at flowering time; **L** sheath fleshy, white, 2.5 × 2.5 cm, **L** lamina 18 × 1.5 cm, green, adaxially glabrous, abaxially completely covered by white scales, margins serrate with antrorse and retrorse **Sp** 2–3 mm long; **Inf** peduncle erect, to 50 cm, green, covered with russet stellate hairs, floriferous part 20–30 cm, simple, few-flowered, ± secund, axis, bracts, pedicels and sepals covered with ochre-brown to russet stellate hairs, tomentum easily detached; lower peduncular **Bra** leaf-like, upper lanceolate; floral **Bra** 23 × 8 mm, shorter than the pedicels, lanceolate, acute, papery, margins entire; **Ped** slender, 3–3.3 mm; **Sep** rounded-triangular, 28 × 10 mm, apex round; **Pet** linear, 70–75 mm, green; **St** included, 63 mm; **Anth** green-yellow; **Sty** 64 mm; **Sti** green; **Fr** and **Se** not described.

Related to *P. ferruginea*, but differing by the unbranched inflorescence with half-erect to horizontally spreading flowers.

**P. coerulea** Lindley (Bot. Reg. 26: t. 11 + text, 1840). **Type:** Chile (*Lambert* s.n. [[lecto — icono]: l.c. t. 11]). — **Lit:** Zizka & al. (2013). **Distr:** Chile (Coquimbo, Valparaíso, Libertador O'Higgins, Maule, Bío Bío); dry open rocky ground, 400–1200 m.

≡ *Pitcairnia coerulea* (Lindley) Bentham (1883).

[2] Polycarpic, forming dense groups, 1–2 m tall at flowering time; caudex erect or prostrate with time, branched; **L** sheath 2–8.5 × 1–7 cm, fleshy, suborbicular, dark castaneous, **L** lamina 11–62 × 0.4–3.5 cm, both faces with appressed cinereous scales, margins laxly serrate with red-brown antrorse uncinat **Sp** 3–5 mm long; **Inf** peduncle exceeding the leaves, 0.7–0.8 m, red, tomentulose-lepidote, floriferous part 1–1.2 m, laxly branched, cylindrical, red, white tomentulose-lepidote when young; peduncular **Bra** leaf-like, lower lanceolate-ovate, with filiform or laminate apex, upper ovate with apiculate apex; primary **Bra** broadly ovate, with attenuate apex, 5–6 cm, much shorter than the subtended branch,

margins in the upper part serrulate; **Br** spreading, laxly or sub-laxly flowered, 20–30 × 4–5 cm, with a long or short distinct stipe 5–20 cm long; floral **Bra** ovate, 5–44 × 1–15 mm, shorter than the pedicel, tip apiculate or acute, margins entire; **Ped** 10–20 mm; **Sep** lanceolate-triangular to oblong-ovate, 12–24 × 10 mm, rounded and apiculate; **Pet** dark blue, 50 mm, erect and forming a tube; **St** exposed; **Anth** yellow; **Sty** exerted, green; **Fr** ovoid or ellipsoid, shorter than the sepals.

A beautiful and variable species that is divisible into 4 varieties:

**P. coerulea** var. **coerulea** — **Distr:** C Chile (Coquimbo, Valparaiso, Libertador O'Higgins: Coastal cordillera); stony semi-arid areas, (20–) 500–2000 m. **I:** Zizka & al. (2013: 392).

**Incl.** *Pourretia coerulea* Miers (1826) (*nom. inval.*, ICN Art. 38.1a).

[2] Plants 2–2.5 m tall at flowering time; **L** sheath fleshy, 4.5 × 5.3–13 cm, **L** lamina 36–62 × 1.5–3.5 cm; **Inf** white tomentose-lepidote; **Fl** ± upwardly secund; floral **Bra** 10–44 × 4–15 mm, acuminate or apiculate, exceeding the pedicel and reaching the lower 1/3 of the sepals; **Ped** 3–15 × 1.5–2.5 mm.

**P. coerulea** var. **intermedia** (L. B. Smith & Looser) L. B. Smith & Looser (Phytologia 19: 287, 1970). **Type:** Chile, Libertador O'Higgins (Looser 2015 [GH]). — **Distr:** C Chile (Valparaiso, Libertador O'Higgins, Maule); stony hills, 0–1100 m.

≡ *Puya violacea* var. *intermedia* L. B. Smith & Looser (1935).

[2] Plants 2–2.3 m tall at flowering time; **L** sheath fleshy, 2.6–8.5 × 3.4–5.7 cm, **L** lamina 45–47 × 1–1.9 cm; **Inf** densely and persistently white-tomentose; **Fl** polystichously arranged; floral **Bra** 12–18 × 3–6 mm, exceeding the pedicel and shorter than the sepals; **Ped** 5–15 × 1.5–2 mm.

**P. coerulea** var. **monteroana** (L. B. Smith & Looser) L. B. Smith & Looser (Phytologia 19: 287, 1970). **Type:** Chile, Libertador O'Higgins (Montero 26 [GH]). — **Distr:** C Chile (Libertador O'Higgins, Maule); 400–1200 m.

≡ *Puya violacea* var. *monteroana* L. B. Smith & Looser (1935).

[2] Plants 1–1.4 m tall at flowering time; **L** sheath fleshy, 2–4.7 × 2.3–3.3 cm, **L** lamina 19–48 × 0.8–1.1 cm; **Inf** glabrous at anthesis; **Fl** polystichously arranged; floral **Bra** 5–25 × 2–6 mm, exceeding the pedicel and shorter than the sepals; **Ped** 9–12 × 1.5–2 mm.

This is the smallest variety. It is additionally characterized by having arching leaves.

**P. coerulea** var. **violacea** (Brongniart) L. B. Smith & Looser (Phytologia 19: 287, 1970). **Type:** Ex cult. Hort. Paris (*Anonymus* s.n. [P]). — **Distr:** C Chile (Libertador O'Higgins, Maule, Bío Bío); stony areas, 100–1300 m.

≡ *Pitcairnia violacea* Brongniart (1847) ≡ *Pourretia violacea* (Brongniart) Linden (1853) ≡ *Puya violacea* (Brongniart) Mez (1896); **incl.** *Pourretia rubricaulis* Miers (1826) (*nom. inval.*, ICN Art. 38.1a) ≡ *Puya rubricaulis* (Miers) Steudel (1841) (*nom. inval.*, ICN Art. 38.1a); **incl.** *Puya paniculata* Philippi (1864); **incl.** *Pitcairnia philippii* Baker (1889); **incl.** *Puya glabrata* Philippi ex Baker (1889) (*nom. inval.*, ICN Art. 36.1c).

[2] Plants 1–2.7 m tall at flowering time; **L** sheath fleshy, 3–6.5 × 1.5–7 cm, **L** lamina 11–56 × 0.4–1.6 cm; **Inf** white-tomentulose, soon glabrous; **Fl** polystichously arranged; floral **Bra** 3–12 × 1–3 mm, shorter than the pedicel; **Ped** 10–24 × 1.5–2 mm.

This variety is characterized by the long pedicels.

**P. densiflora** Harms (Notizbl. Bot. Gart. Berlin-Dahlem 10: 791, 1929). **Type:** Peru, Cuzco (Herrera 1954 [B, F [photo]]). — **Distr:** SE Peru (Cuzco, Arequipa); on rocks and rocky slopes, under shrubs and cacti, 2000–3000 m.

[1] Polycarpic, forming dense clusters, 1–1.5 m tall at flowering time; **L** arching, sheath fleshy, broadly ovate, 4–5 cm, densely serrulate, **L** lamina 40–60 × 3–4 cm, green, adaxially covered with a membrane of white scales, abaxially glabrous, margins laxly serrate, **Sp** slender, antrorse, red-brown, 10 mm; **Inf** peduncle ± equalling the leaves, 0.4–0.6 m, stout, 15 mm Ø, densely and finely white stellate-tomentose, floriferous part 0.5–0.7 m, densely branched,

subcylindrical-attenuate, finely white stellate-tomentose including the flowers except the petals; lower peduncular **Bra** leaf-like, upper broadly ovate-lanceolate, long-caudate, imbricate, lepidote, margins serrate; primary **Bra** ovate-lanceolate, 4–8 × 2.5–3 cm, attenuate, much shorter than the subtended branch, papery, light brown, margins spinose-serrate; **Br** shortly stipitate, 4–10 cm, suberect, subdensely ±10-flowered, green, terminal part of the main axis longer and attenuate; floral **Bra** 20–30 × 8 mm, from slightly longer than the pedicels to 3 × as long, oblong-lanceolate, aristate, green, margins entire; **Ped** slender, 15 mm; **Sep** lanceolate, 25–30 × 5 mm, aristate, green, glabrous; **Pet** narrowly oblong, 40–50 mm, subobtusate, green-bluish; **St** exserted; **Anth** green, falcate, 40–50 mm; **Sty** exserted; **Sti** yellow.

**P. dyckioides** (Baker) Mez (in A. & C. de Candolle, Monogr. Phan. 9: 486, 1896). **Type:** Bolivia, Chuquisaca (*Weddell* 3739 [P, GH [photo]]). — **Lit:** Gómez & Grau (2009: with ill.). **Distr:** S Bolivia (Chuquisaca, Tarija), NW Argentina (Jujuy, Salta, Tucumán, Catamarca); Yungas vegetation and grassy mountain slopes, between rocks, 1500–3500 m. **I:** Grau & al. (2010).

≡ *Pitcairnia dyckioides* Baker (1889).

[2] Polycarpic, forming small clusters, 0.8–1 m tall at flowering time, stem branched, to 40–50 cm; **L** sheath fleshy, broadly ovate, 3–5 cm, dark castaneous, **L** lamina 60–80 × 1.5–2 cm, green, adaxially glabrous, abaxially covered with pale appressed scales, margins serrate with antrorse uncinata **Sp** 3 mm long; **Inf** peduncle shorter than the leaves, 20–30 cm, stout, furfuraceous, floriferous part 40–80 cm, subdensely branched, cylindrical in outline, axes furfuraceous; lower peduncular **Bra** leaf-like, upper broadly ovate, acuminate or linear, imbricate, lepidote, margins serrulate; primary **Bra** ovate, acuminate, 4.5–6 cm, much shorter than the subtended branch, pink, margins coarsely serrulate; **Br** shortly stipitate, 10–20 cm, erect or divergent, subdensely few-flowered, pink; floral **Bra** 20 × 8 mm, longer than the pedicels, ovate-elliptic, apiculate, pink, margins entire or serrulate; **Fl** tubular; **Ped** slender, 5–7 mm; **Sep** ovate-elliptic, 12 × 6 mm,

obtuse, pink, glabrous; **Pet** oblong, 40 mm, green-bluish; **St** included, 35 mm; **Anth** orange; **Sty** included, 35 mm; **Sti** yellow.

A very attractive species, esp. at flowering time, due to the pinkish inflorescences with contrasting dark blue-green flowers with orange anthers. After flowering, 1–2 offsets are formed.

**P. eryngioides** André (Énum. Bromél., 5, 1888). **Type:** Ecuador, Loja? (*André* 4542 [K, K [photo]]). — **Lit:** Manzanares (2011: 233). **Distr:** Ecuador (Azuay, Loja); open slopes and shrubby Páramo vegetation, 2700–3100 m. **I:** Oliva-Esteve (2002: 231); Manzanares (2005: 309–310).

[2] Polycarpic, forming small dense groups from a very short fleshy stem, 30–40 cm tall at flowering time; **L** sheath orbicular, 2 × 3 cm, chestnut-brown, margins entire, **L** lamina 15–20 × 1–1.5 cm, both faces glabrous, margins serrate with yellow-brown **Sp** 2–3 mm long; **Inf** peduncle exceeding the leaves, 20–25 cm, completely covered by the bracts, lepidote, red, floriferous part 7–10 cm, with 7–14 branches, globose or cylindrical in outline, dense, glabrous, reddish to violet; peduncular **Bra** ovate, with attenuate tip, red to violet, sparsely lepidote, margins serrate; primary **Bra** ovate to orbicular, acuminate, 1.5 × 0.9 cm, almost completely covering the subtended branch, glabrous, margins serrate; **Br** reduced or aborted, 2- to 3-flowered, fasciculate, 1 × 1.5 cm, glabrous; floral **Bra** 7 × 5 mm, ovate, cuspidate, ± shorter than the sepals, red, covering the pedicel, margins serrulate; **Ped** only 1 mm; **Sep** ovate, 15 × 8 mm, acute, glabrous; **Pet** dark blue, 20 mm; **St** included; **Anth** yellow.

The stems remain hidden by the predominant grass of the Páramos. *P. eryngioides* can be confused with *P. exigua*, but differs by forming groups with an above-ground stem and branched inflorescences.

**P. ferruginea** (Ruiz & Pavón) L. B. Smith (Phytologia 16: 461, 1968). **Type:** Peru, Lima (*Ruiz & Pavón* s.n. [BM]). — **Distr:** Ecuador (Bolívar, Chimborazo, Morona Santiago, Loja, Zamora Chinchipe), Peru (Amazonas, Cajamarca, La Libertad, Huánuco, Pasco, Lima, Junín, Cusco, Apurímac, Puno), Bolivia (La Paz,





**Fig. 3** *Puya ferruginea* (Peru: Arequipa). (Copyright: I. Treviño)

Cochabamba); dry rocky slopes in the Andes and Ecuadorian Amazonia, 1800–3800 m. **I:** Rauh (1990: 435); Manzanares (2005: 319–320); Wisnev (2016: 172–174). – Fig. 3.

≡ *Pitcairnia ferruginea* Ruiz & Pavón (1802) ≡ *Pourretia ferruginea* (Ruiz & Pavón) Sprengel (1825) ≡ *Hepetis ferruginea* (Ruiz & Pavón) Mez (1896); **incl.** *Pitcairnia asterotricha* Poeppig & Endlicher (1838); **incl.** *Puya grandiflora* Hooker (1861); **incl.** *Pitcairnia consimilis* Baker (1881) ≡ *Hepetis consimilis* (Baker) Mez (1896); **incl.** *Puya echinotricha* André (1888) ≡ *Pitcairnia echinotricha* (André) Baker (1889); **incl.** *Pitcairnia weberbaueri* Mez (1904); **incl.** *Pitcairnia viridis* Mez (1919); **incl.** *Pitcairnia cotahuasiana* Harms (1929); **incl.** *Pitcairnia herrerae* Harms (1929); **incl.** *Pitcairnia imperialis* Harms (1929); **incl.** *Pitcairnia latibracteata* Harms (1929); **incl.** *Pitcairnia laresiana* Harms (1930).

[2] Monocarpic or polycarpic, 2–5 m tall at flowering time, solitary or forming dense groups, stem branched, procumbent or ascending; **L** sheath fleshy, broadly orbicular, 15 × 10 cm,

white, glabrous, **L** lamina 80–100 × 5 cm, green, adaxially glabrous, abaxially grey-lepidote, margins serrate with antrorse **Sp** 15 mm long; **Inf** all parts and including pedicels and sepals with ferruginous indumentum, peduncle exceeding the leaves, 1 m, stout, floriferous part 1.5–3 m, laxly branched, pyramidal in outline; lower peduncular **Bra** leaf-like, upper shorter than the internodes, basal part ovate and with serrate margins, acuminate towards the tip and serrulate; primary **Bra** ovate, acuminate, 3–5 × 2 cm, shorter than the stipe, margins entire; **Br** 50–80 cm, with a distinct stipe 3–11 cm long, spreading, laxly 20- to 30-flowered; floral **Bra** 20 × 11 mm, ovate, acute, shorter than the pedicel, margins entire; **Fl** tubular, secundly arranged and pendulous after anthesis; **Ped** slender, 25–40 mm; **Sep** oblong, 45–50 × 5–8 mm, obtuse; **Pet** linear, 58–70 mm, initially violet at the start of anthesis changing to green to cream; **St** included, 50–60 mm; **Sty** included, 55–65 mm.

The plants of the populations of Ecuadorian Amazonia are monocarpic, while those of the Andean populations of Ecuador, Peru and Bolivia from dry rocky slopes are polycarpic. According to Smith & Downs (1974), there is considerable variation between populations. Common to all forms is the dense ferruginous indumentum of all parts of the inflorescence and flowers except the petals.

**P. gilmartiniae** G. S. Varadarajan & A. R. Flores (J. Bromeliad Soc. 40(4): 161–163, ills., 1990). **Type:** Chile, Coquimbo (Varadarajan & al. 1481 [GH, MO, WS]). — **Lit:** Zizka & al. (2013: 398). **Distr:** C Chile (Coquimbo: N of La Serena); coastal scrub, 50–520 m; critically endangered.

[1] Polycarpic, forming dense masses, 1.5 m tall at flowering time, caulescent, stem prostrate, branched, 30–50 cm, covered with dry and persistent leaf sheaths; **L** sheath fleshy, 4–4.5 cm wide, ovate, dark castaneous, densely lepidote, **L** lamina 50–60 × 2.5 cm, arching, towards the base densely covered with cinereous white scales, both faces densely cinereous-lepidote (more densely along the margins), margins serrate with uncinat antrorse and retrorse **Sp** 10 mm long; **Inf**



peduncle exceeding the leaves, 0.45 m, stout, green, persistently lanate esp. close to the bracts, fertile part 0.6–1 m, branched, with  $\pm 20$  branches and a long terminal part of the main axis, ellipsoid or ovoid in outline, green, sparsely tomentose-lepidote; lower peduncular **Bra** leaf-like, upper broadly lanceolate, acuminate, reflexed, brown, papyraceous, persistently lanate, margins entire; primary **Bra** broadly ovate-lanceolate, acuminate, covering from nearly  $\frac{1}{3}$  to  $> \frac{1}{2}$  of the subtended branch, coriaceous, strongly veined, persistently lanate, brown, margin entire; **Br** 30–35 cm, stipitate for 2 cm, spreading, densely flowered in the lower  $\frac{1}{2}$ , sterile distally with reduced bracts; floral **Bra** broadly ovate, 30 mm, acuminate, as long as the sepals, green in the lower part, brown above, sparsely lanate; **Ped** slender, 10 mm, tomentose-lepidote; **Sep** elliptic to lanceolate, 15–20  $\times$  11 mm, obtuse, yellow-green, sparsely lanate at the apex; **Pet** yellow-green, 50 mm; **St** included; **Fil** yellow-green; **Anth** yellow; **Sty** included, as long as or  $\pm$  longer than the stamens; **Sti** green.

Already in the protologue, a probable hybrid origin with *P. chilensis* and *P. boliviensis* as possible parents was discussed, and such an origin is supported in the molecular study of Jabaily & Sytsma (2010). The plants are very ornamental due to the dense greyish-white tomentum that covers the young leaves completely, and becomes restricted to the areas along the leaf margins.

**P. glomerifera** Mez & Sodiro (Bull. Herb. Boissier, sér. 2, 4: 630, 1904). **Type:** Ecuador (Sodiro P-2 [B]). — **Distr:** N-C to S-C Ecuador (Pichincha, Tungurahua, Chimborazo, Azuay); very common in desert and semi-desert vegetation of the inter-Andean valleys, 2800–3900 m. **I:** Gilmartin (1972: Fig. 5); Oliva-Esteve (2002: 231); Manzanares (2005: 327). — Fig. 4.

[2] Polycarpic, forming dense groups, 2–3 m tall at flowering time; **L** sheath fleshy, orbicular, 10  $\times$  8 cm, margins entire, **L** lamina 50–80  $\times$  2–3.5 cm, adaxially glabrous, abaxially densely lepidote, margins serrate with castaneous-brown antrorse and retrorse **Sp** 13 mm long; **Inf** peduncle exceeding the leaves, 0.7–1 m, floriferous part 0.5–0.8 m, dense, cylindrical, lanate with brown



**Fig. 4** *Puya glomerifera* (Ecuador: Pichincha, around Quito). (Copyright: J. Manzanares)

indumentum; lower peduncular **Bra** leaf-like, upper remote, 5–9  $\times$  2.5 cm; primary **Bra** ovate, 5–7  $\times$  2 cm, with triangular apex,  $\pm$  shorter than the subtended branch, margins serrulate; **Br** globose, 3–5  $\times$  4.5 cm, densely 6- to 9-flowered, stipe nearly none; floral **Bra** obovate, 30  $\times$  25 mm, rounded or apiculate at the tip, shorter than the sepals, margins entire; **Ped** stout, 7 mm; **Sep** obovate, 25  $\times$  15 mm, rounded and apiculate at the apex; **Pet** cream, 50 mm; **St** exposed; **Anth** yellow; **Sty** included.

Forms dense groups and commonly used by native people as fence and to delineate borders. Flowering plants form a veritable “nectar oasis” with many visiting hummingbirds.

**P. grafii** Rauh (Trop. subtrop. Pfl.-welt 52: 5–11, ill., 1985). **Type:** Venezuela, Amazonia (Graf s.n. in *BG Heidelberg* 64663 [HEID]). — **Lit:** Rauh (1985); Oliva-Esteve & Steyermark (1987); both with ill. **Distr:** Venezuela (Amazonia); grassy rocky slopes, 1200 m. **I:** Rauh (1990: 275, fig. 356).

[2] Polycarpic, with long runners that form new plants, 80 cm tall at flowering time, stem base forming a thick pseudobulb of  $6 \times 5$  cm; **L** sheath fleshy, conspicuous, covering the pseudobulb, white,  $3.5\text{--}4 \times 2$  cm, densely lepidote in the upper  $\frac{1}{2}$ , **L** lamina  $20\text{--}30 \times 0.5\text{--}1$  cm, spreading to recurved, green, canaliculate, both faces densely silvery-white lepidote when young, upper face soon becoming glabrous, margins laxly serrate with antrorse uncinata **Sp** 2 mm long; **Inf** peduncle erect, 70 cm, greenish, with white-woolly indumentum, floriferous part 10–20 cm, simple, racemose, laxly cylindrical, with up to 15 flowers; lower **Bra** leaf-like, upper lax, much longer than the internodes, long triangular, reddish-green, lepidote; floral **Bra**  $35 \times 8$  mm, lanceolate, acute, longer than the pedicel but shorter than the sepals, white-woolly lepidote, margins entire; **Ped** thick, 8–10 mm, densely lepidote; **Sep** long lanceolate,  $35 \times 8$  mm, acute, green, densely grey-lepidote; **Pet** pale yellow with wine-red lines at the margin,  $60 \times 10$  mm, outer face along the midrib with white stellate scales; **St** included; **Anth** white; **Sti** white.

The plants form a pseudobulb at the base of the stem which is densely covered by the leaf sheaths. Due to the small size very suitable for cultivation in xerophyte gardens.

**P. gutteana** W. Weber (Cat. Herb. Lips. Pl. Peruv. II: 42, ill., 1984). **Type:** Peru, Cusco (Gutte & Gutte 3308 [LZ]). — **Distr:** Peru (Cusco: Fundo Bellavista); hanging from rocks, 3200 m; known only from the fragmentary type.

[2] Plants 70–80 cm tall at flowering time; **L** sheath fleshy, ovate, margins serrulate, **L** lamina  $40\text{--}50 \times 3$  cm, narrowly triangular with a long-acuminate apex, adaxially densely white-lepidote, abaxially glabrous, margins densely serrate with dark brown antrorse **Sp** 10 mm long; **Inf** peduncle shorter than or equalling the leaves, 30 cm, scatteredly white-tomentose, floriferous part  $25 \times 10$  cm, dense, cylindrical, densely lepidote; lower peduncular **Bra** leaf-like, upper not imbricate but longer than the internodes,  $8 \times 2.5$  cm, ovate-lanceolate, white-tomentose, margins densely serrate with **Sp** 2–3 mm long; primary **Bra** similar to the peduncular bracts, slightly longer than or as

long as the subtended branch, margins serrate; **Br** suberect, 4–8 cm, to 4-flowered, subdensely tomentose-lepidote, stipe nearly none; floral **Bra** lanceolate-ovate,  $23 \times 8$  mm, acute, much shorter than the sepals, margins minutely serrulate; **Ped** slender, 10 mm, tomentose-lepidote; **Sep** narrowly lanceolate,  $35 \times 8$  mm, long-acuminate, the adaxial pair obtusely carinate with fleshy midvein area; **Pet** green-violet, 63 mm, lanceolate; **St** exposed; **Anth** yellow; **Sty** exposed.

Related to *P. densiflora*, which is also native to the Cusco region, and similar in many details (indumentum, densely serrate leaf margins with antrorse spines 10 mm long, exposed stamens and style), but differing in the peduncle (longer than the leaves in *P. densiflora*, as long as or shorter than the leaves in *P. gutteana*).

**P. harmsii** (A. Castellanos) A. Castellanos (Anales Mus. Nac. Hist. Nat. Buenos Aires, ser. 3, 37: 497, 1933). **Type:** Argentina, Catamarca (Schreiter s.n. [LIL 34524]). — **Distr:** N Argentina (Catamarca, Tucumán); ravines of arid mountain slopes in the Monte - Prepuna ecotone, 2500 m. **I:** Gómez & Grau (2009: 200). – Fig. 5.   
≡ *Puya spathacea* var. *harmsii* A. Castellanos (1929).

[1] Polycarpic, forming dense circular groups, 2 m tall or more at flowering time; **L** sheath fleshy, broadly ovate, 7 cm, brown and serrulate towards the apex, lower part white with entire margins, **L** lamina  $100 \times 3$  cm, recurving, acuminate to pungent, both faces covered with a membrane of white appressed scales, margins laxly serrate, **Sp** antrorse, uncinata, red-brown, 4 mm; **Inf** peduncle equal or shorter than the leaves, 1.2 m, branched with at least 10 branches, lax, purple, appressedly pubescent with fine white stellate trichomes; lower peduncular **Bra** leaf-like, triangular with a long leaf-like lamina,  $4\text{--}7 \times 2.5$  cm, margins serrate; primary **Bra** triangular,  $6 \times 5$  cm, veined, apex acute, margins serrulate; **Br** subspreading, linear, 18 cm, laxly 10- to 18-flowered; floral **Bra** lanceolate,  $14\text{--}20 \times 7$  mm, acute,  $\pm$  shorter than the pedicels, margins entire; **Fl** divergent to spreading; **Ped** curved, slender, 15–17 mm; **Sep** triangular,  $18\text{--}20 \times 10$  mm, acute, carinate, sulcate when dry, thick;



**Fig. 5** *Puya harmsii* (Argentina, Tucumán, Tafi del Valle, S of Mollar, 2000 m). (Copyright: G. Rivera)

**Pet** black, appearing velvety with a pale blue tinge, 25 mm; **St** included, 18 mm; **Anth** green-olive, 5 mm; **Sty** included, 20 mm; **Fr** globose, 13 × 10 mm.

**P. harry-lutheri** Gouda (J. Bromeliad Soc. 62 (6): 255, 2013). **Type:** Venezuela, Amazonas (*Anonymus* s.n. in *BG Utrecht* 2005GR01559 [L, VEN]). — **Distr:** Venezuela (Amazonas: Savana near Puerto Ayacucho near the Colombian border).

[2] Polycarpic, acaulescent, 1.4 m tall at flowering time; **Ros** 30 cm tall; **L** spreading-arching, sheath fleshy, broadly obovate, pale brown and castaneous, 2–2.5 × 5 cm, whitish with closely appressed scales, **L** lamina 50–60 × 2–2.5 cm, channelled, both faces very densely lepidote to partly glabrescent with closely appressed, pruinose, white scales, margins laxly serrate with narrow, dark brown, antrorse **Sp** 1–3 mm long; **Inf** peduncle erect, exceeding the leaves, 45 cm,

greenish and brownish at the nodes, glabrous, floriferous part 65 cm, simple or with a rudimentary branch at the base, laxly cylindrical, 40- to 50-flowered, greenish to brownish, glabrous; lower peduncular **Bra** leaf-like, upper lax, attenuate, all exceeding the internodes but so narrow to expose part of the peduncle, brownish-red and green, margins serrulate; floral **Bra** 11.5 × 8 mm, ovate, obtuse, shorter than the pedicels and shorter than the sepals, diverging from the pedicel, green and partly black, glabrous; **Ped** thick, 18 mm, fleshy and cuneate towards the ovary; **Sep** ovate-lanceolate, 40 × 11 mm, obtuse, ± cucullate at the very apex, green tinged reddish, glabrous; **Pet** obovate-lanceolate, 68 × 14 mm, brown and adaxially green-veined to wholly green towards the base; **St** included but longer than the style, 60 mm; **Anth** cream-green; **Sti** cream.

The original habitat remained unknown, and the plant was described from cultivated material at the Utrecht Botanical Garden, who obtained the plants from the Dutch Corn. Bak Nursery. The species has nocturnal flowers (otherwise in the genus only known from *P. wrightii*) that are probably pollinated by bats.

**P. hofstenii** Mez (Repert. Spec. Nov. Regni Veg. 3: 8, 1906). **Type:** Argentina, Jujuy (*Hofsten* 1710 [B, F [photo]]). — **Distr:** S Bolivia (Potosí), NW Argentina (Jujuy); dry rocky slopes, 3400–3500 m. **I:** Gómez & Grau (2009: 200).

**Incl.** *Puya hauthalii* Mez (1919).

[1] Polycarpic, forming dense groups, 1 m tall or more at flowering time; **L** sheath fleshy, ovate, 6 cm, serrulate towards the apex, **L** lamina 50 × 5 cm, recurving, pungent, cinereous-lepidote esp. abaxially, margins laxly serrate, **Sp** antrorse, 5 mm; **Inf** peduncle shorter than the leaves, 0.7 m, branched with up to 11 branches, lax, red, glabrous; lower peduncular **Bra** leaf-like, the upper ones ovate, acute, 4–7 cm, ± equalling the sterile branch base, margins entire; primary **Bra** ovate, 4 × 3.8 cm, acute, margins entire, red-pink; **Br** spreading to suberect, linear, 20 cm, laxly 12- to 20-flowered; floral **Bra** ovate-elliptic, 15–18 × 12 mm, acute, ± equalling the pedicels, margins entire; **Fl** suberect to deflexed; **Ped** slender, 15–18 mm; **Sep** lanceolate, 26 × 9 mm,

rounded and apiculate, carinate at the base; **Pet** green-lavender, 30 mm; **St** included, 35 mm; **Anth** yellow, 4 mm; **Sty** exerted, 37 mm.

Related to *P. harmsii* but distinguished by leaves green adaxially and densely lepidote abaxially (vs. adaxially and abaxially covered with a membrane of white appressed scales) and the pink glabrous inflorescence (vs. purple, appressed-pubescent with fine white stellate trichomes), as well as the green-lavender flowers with included stamens and styles (vs. velvet-black with a pale blue tinge and exerted stamens and style).

**P. hoxeyi** Janeba (Cact. Succ. J. (US) 89(4): 178–181, ill. (pp. 176–182), 2017). **Type:** Peru, Moquegua (*Hoxey & Loayza Hoxey* 1275.01 [HUSA]). — **Distr:** S Peru (Moquegua: N of Ilo); W- and NW-facing slopes of coastal loma hills, 700–900 m.

[1] Polycarpic, to 4 m tall at flowering time, forming dense clumps to 2 m Ø; **L** numerous, sheath not described, lamina to 100 cm, to 6 cm wide at the base, spreading, narrowly triangular tapering into a sharp tip, glabrous, upper face green, slightly glossy, lower face green with white longitudinal lines, margin serrate, **Sp** brown-tipped from pale base, ±5 mm long and retrorse near the leaf base, higher up antrorse, to 2 mm long near the leaf tip, 15–20 mm apart; **Inf** 1.5–2.5 m, floriferous in the upper ½ to ⅓ with 20–100 branches, finely white-tomentose; lower peduncular **Bra** leaflike but smaller, to 30 × 5 cm, upper peduncular **Bra** to 4 × 3 cm, softly papery, first green but rapidly drying and becoming brownish; **Br** 15–18 cm, spreading to slightly ascending, up to 30-flowered, terminal part sterile or floriferous; floral **Bra** 10 × 3 mm, acuminate; **Fl** tubular-funnelshaped, 45 × 15–20 mm; **Ped** 7 mm, tomentose; **Sep** 25 × 7 mm, greenish-yellow; **Pet** 40 × 15 mm, yellow-greenish, with faint longitudinal veins and outer face with greenish midvein area; **St** included but well visible in the throat; **Fil** 20 mm, greenish-cream; **Anth** 5 mm, greenish, pollen orange; **Ov** conical, 8 × 3–5 mm; **Sty** 25 mm; **Sti** lobes 2 mm, greenish-yellow, connivent.

Compared with *P. boliviensis* and *P. chilensis*. The taxon is only known from 2 restricted populations. In both, ±90% of all individuals are dead, and probably <100 living individuals are left. — [U. Eggl]

**P. humilis** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 498, 1896). **Type:** Bolivia, Cochabamba (*Kuntze* s.n. [NY]). — **Distr:** Bolivia (Cochabamba, Chuquisaca, Potosí); rock crevices and rocky slopes, 2800–4200 m. **I:** Wisnev (2016: 170).

**Incl.** *Puya werdermannii* Harms (1929); **incl.** *Puya butcheriana* H. Luther (1995).

[2] Polycarpic, caespitose with a rizome to 15 cm Ø, 15–25 cm tall at flowering time; **L** sheath ovate, 15 mm, fleshy, **L** lamina 10–15 × 0.7 cm, cinereous-lepidote esp. abaxially, margins laxly serrate, **Sp** spreading, 3 mm; **Inf** peduncle erect, very short, white-tomentellous but becoming glabrous, shorter than the leaves, fertile part 6–8 × 2.5 cm, simple, strobilate, fusiform, densely few-flowered, axis densely white-tomentose; peduncular **Bra** broadly ovate-elliptic, with leaf-like lamina; floral **Bra** 20–28 × 15 mm, broadly ovate, acuminate, pungent, margins entire, appressedly lepidote, becoming glabrous, pink, veined, longer than the sepals; **Ped** short, 2–3 mm; **Sep** subtriangular, 12–13 mm, acute, carinate, sparsely lepidote, becoming glabrous esp. towards the apex; **Pet** green becoming blue or violet, 15–20 mm; **St** included; **Anth** yellow; **Sty** included; **Fr** ovoid, 11 mm.

A very beautiful small species with compact rosettes and a — compared with the rosette size — large pink inflorescence.

**P. ibischii** R. Vásquez (J. Bromeliad Soc. 54(3): 99–102, ill., 2004). **Type:** Bolivia, Cochabamba (*Vásquez* 4457 [LPB, SEL, VASQ]). — **Distr:** Bolivia (Cochabamba: Chaparé); steep slopes above the cloud forest, 3100–3300 m.

[2] Polycarpic, forming dense groups, 2.5–2.8 m tall at flowering time; **L** sheath fleshy, **L** lamina 80–100 × 3–3.5 cm, adaxially glabrous, abaxially densely cinereous-lepidote, margins serrate with light brown antrorse **Sp** 7–10 mm long; **Inf** peduncle exceeding the leaves, 1.8–2 m, stout,



inclined at an angle of  $45^\circ$ , white-lanate, becoming glabrous with age, floriferous part 0.5 m, dense, simple, nutant, cylindrical, densely white-lanate, brown; lower peduncular **Bra** leaf-like, upper exceeding the internodes, 15 cm, reflexed, margins laxly serrate; floral **Bra** ovate,  $95 \times 45$  mm, apiculate, exceeding the sepals at anthesis, dark brown, fleshy at the base, both faces white-lanate, margins laxly serrulate; **Ped** stout, 15–20 mm, obconical; **Sep** obovate, apiculate,  $50 \times 25$  mm, greenish-yellow, brown towards the apex, both faces densely white-lanate; **Pet** greenish-yellow, fleshy at the base,  $65 \times 33$  mm; **St** included, 50–55 mm, white; **Anth** yellow; **Sty** included, 60 mm; **Sti** green.

The long curved peduncle orients the inflorescence away from the mountain slope so that the flowering part becomes pendulous over the abyss. The flowers are positioned erect on the inflorescence axis but hang down in their general aspect, to facilitate pollination by hummingbirds.

**P. lanata** (Kunth) Schultes *fil.* (in Roemer & Schultes, *Syst. Veg.* 7(2): 1233, 1830). **Type:** Peru, Cajamarca (*Humboldt & Bonpland* 3713 [P, F [photo]]). — **Lit:** Gilmartin (1972: 28, fig. 4). **Distr:** S Ecuador (Cañar, Azuay, Loja), N Peru (Cajamarca); dry open sites in semi-deserts of the Inter-Andean valleys, 350–2250 m. **I:** Rauh (1990: t. 132); Oliva-Esteve (2002: 232); Manzanares (2005: 303). — Figs. 6 and 7.

≡ *Pourretia lanata* Kunth (1816) ≡ *Pitcairnia lanata* (Kunth) Dietrich (1820).

[2] Polycarpic, forming dense groups united by thick creeping or upright stems, 1.5–2.5 m tall at flowering time; **L** sheath fleshy, orbicular,  $10 \times 8$  cm, chestnut-brown, margins entire, **L** lamina  $40\text{--}60 \times 2.5$  cm, canaliculate, arching, adaxially glabrous, abaxially with cinereous indumentum, margins strongly serrate with yellow antrorse **Sp** 10 mm long; **Inf** peduncle exceeding the leaves, erect, green, 1 m,  $\pm$  lepidote, floriferous part 0.4–0.5 m, simple, cylindrical, densely 60- to 90-flowered, densely cinereous-lepidote; lower peduncular **Bra** leaf-like, upper lanceolate, attenuate,  $5\text{--}9 \times 1.5$  cm, shorter than the internodes, margins serrate; floral **Bra**  $25 \times 10$  mm, lanceolate, attenuate, black at anthesis, longer than the



**Fig. 6** *Puya lanata* (Ecuador: Azuay, Oña valley). (Copyright: J. Manzanares)

pedicel but shorter than the sepals, margins entire; **Ped** obconical, 6–7 mm; **Sep** lanceolate, attenuate,  $30 \times 14$  mm, abaxially lanate, lepidote; **Pet** greenish-white, 80 mm, apex recurved; **St** included.

The flowers are pendent during anthesis. Flowering plants (usually several rosettes of a group flower synchronously) constitute an important “nectar oasis” for the local hummingbird fauna.

**P. laxa** L. B. Smith (*Phytologia* 6: 195, t. 1: figs. 7–8, 1958). **Type:** Bolivia, Santa Cruz (*Cárdenas* 5092 [US]). — **Distr:** Bolivia (Santa Cruz: near Pulquina), N Argentina?; stony soil, 1500 m. **I:** Rauh (1990: Fig. 276); Oliva-Esteve (2002: 233).

[1] Polycarpic, forming dense groups, 1 m tall at flowering time; **L** arching or straight, sheath fleshy, suborbicular, brown, densely serrulate towards the apex, 3 cm, **L** lamina  $27 \times 1\text{--}1.5$  cm,





**Fig. 7** *Puya lanata* (Ecuador: Loja, Catamayo valley). (Copyright: J. Manzanares)

narrowly triangular, caudate-acuminate with a long entire apex, adaxially and abaxially densely tomentose with coarse white scales esp. abaxially, laxly serrate below with slender antrorse brown **Sp** 5 mm long; **Inf** peduncle exceeding the leaves, erect, 1 m, soon glabrous except for the white-puberulent pedicels, floriferous part 0.4–0.5 m, branched, lax; lower peduncular **Bra** leaf-like, upper ovate, acuminate, 2 × 1.5 cm, shorter than the internodes, margins entire; primary **Bra** ovate, 2.5 × 1.5 cm, ovate, apiculate, abaxially white-puberulent, membranous, margins entire; **Br** long stipitate, 20–30 cm, laxly 10- to 20-flowered, spreading, straight or ± arching with time; floral **Bra** 13 × 10 mm, ovate, apiculate, green with pink apex, longer than the pedicel but shorter than the sepals, membranous, margins entire; **Ped** cylindrical, slender, 5–8 mm; **Sep** lanceolate-oblong, 17 × 9 mm, apiculate, thin, sulcate, ± carinate at the base, abaxially white-puberulent; **Pet** dark violet with a greenish base, 30 mm; **St** included.

Forming impenetrable spiny thickets. Fruiting branches become pendent. The species is very commonly cultivated in desert gardens.

**P. lopezii** L. B. Smith (Phytologia 8: 501, t. 2: figs. 11–12, 1963). **Type:** Peru, La Libertad (*López & Sagástegui* 3549 [US, TRP]). — **Distr:** Peru (La Libertad: Huaylillas, Pataz); dry slopes, 2300 m.

[2] Polycarpic, forming groups, 1 m tall at flowering time; **L** sheath fleshy, suborbicular, 10 × 11 cm, lower part yellow, upper part dark castaneous, **L** lamina 40–50 × 5 cm, both faces covered with appressed white scales, margins laxly serrate with flat, brown, uncinatae, antrorse and retrorse **Sp** 8 mm long; **Inf** peduncle 0.5 m, erect, green, soon glabrous, floriferous part 0.5 m, simple, cylindrical in outline, subdense, densely and finely white-stellate; lower peduncular **Bra** leaf-like, upper ovate with a long narrowly triangular apex, margins entire; floral **Bra** 17 × 6 mm, broadly ovate, with a narrowly triangular apex, margins entire, the lower exceeding the sepals, the upper shorter than the sepals but longer than the pedicel; **Ped** obconical, 6 mm; **Sep** oblong, acute, 26 × 6 mm, lepidote; **Pet** yellowish, 40 mm; **St** included.

A little-known species, notable for its attractive whitish foliage.

**P. macrura** Mez (Repert. Spec. Nov. Regni Veg. 3: 13, 1906). **Type:** Peru, Ancash (*Weberbauer* 3022 [B, F [photo]]). — **Distr:** Peru (Ancash, La Libertad: Cordillera Blanca); rocky ground, 2200–2500 m. **I:** Rauh (1966: 37).

[2] Polycarpic, forming groups, 1–1.5 m tall at flowering time, stem decumbent, thick; **L** sheath fleshy, ovate, short, **L** lamina 40 × 3.5 cm, recurved, both faces covered with a membrane of pale appressed scales, margins serrate with spreading, curved, fuscous-castaneous or dark antrorse **Sp** 9 mm long; **Inf** peduncle erect, as long as or ± longer than the leaves, densely white-lanate, floriferous part 0.35–0.6 m, simple, cylindrical-scepteriform in outline, very densely subspiculate, axis densely white-lanate; peduncular **Bra** ovate, lower ones laminate, upper with acute apex, glabrous, margins minutely crenulate; floral **Bra**

40 × 16 mm, broadly ovate, acuminate, exceeding the sepals, brown, densely lanuginose, margins entire; **Ped** only 2–3 mm, densely lanuginose; **Sep** triangular, attenuate, 26 × 7 mm, densely lanuginose; **Pet** dark violet, 47 mm; **St** included.

**P. medica** L. B. Smith (Phytologia 4: 216, t. 2: figs. 1–2, 1953). **Type:** Peru, Ancash (*Cerrate* 1333 [US, USM]). — **Distr:** Peru (Ancash, La Libertad); rocks and rocky slopes, 2950–3800 m.

[2] Polycarpic, caulescent, 20–37 cm tall at flowering time, stem 3 cm Ø; **L** sheath sub-orbicular, 2.5 cm, fleshy, apical  $\frac{1}{3}$  serrulate and densely lepidote, **L** lamina 10–15 × 1.2 cm, green, adaxially glabrous, abaxially covered with appressed white scales, margins laxly serrate, **Sp** slender, spreading, white, 3 mm; **Inf** peduncle erect, very short, white-flocculose,  $\pm$  longer than the leaves, floriferous part branched in the lower  $\frac{2}{3}$ , 10–20 × 2–3 cm, slenderly cylindrical; peduncular **Bra** subfoliaceous, the upper ones with thin rose-coloured sheaths; primary **Bra** triangular-ovate, 3–4 cm, acuminate, exceeding the few-flowered axillary branches, margins pectinate-serrate, pink, covered with appressed scales; **Br** very short, few-flowered; floral **Bra** ovate, 25–30 × 16 mm, acuminate, margins pectinate-serrate, pink, covered with appressed scales, equalling or  $\pm$  longer than the sepals; **Ped** short, 3 mm; **Sep** lanceolate-oblong, 18–20 mm, with acicular tip, carinate, densely white-flocculose; **Pet** blue-green, 34–40 mm; **St** and **Sty** included.

A very attractive (esp. when flowering, due to the compact pink inflorescence) species forming dense groups amongst rocks. The white spines on the margins of the green leaves are conspicuous.

**P. mirabilis** (Mez) L. B. Smith (Phytologia 16: 461, 1968). **Type:** Bolivia, Tarija (*Fiebrig* 2320 [B]). — **Lit:** Gómez & Grau (2009: with ill.). **Distr:** C-S Bolivia (Cochabamba, Tarija), NW Argentina (Jujuy, Tucumán); rocky slopes, 750–2590 m. **I:** Rauh (1990: 276: Figs. 361–362); Oliva-Esteve (2000: 408). — Fig. 8.

$\equiv$  *Pitcairnia mirabilis* Mez (1906); **incl.** *Pitcairnia mirabilis* var. *tucumana* A. Castellanos (1929).

[2] Polycarpic, forming dense groups, 30–150 cm tall at flowering time, stem short; **L** sheath fleshy, ovate, forming an above-ground pseudo-bulb, 3–3.5 × 3–4 cm, margins serrulate towards the apex, **L** lamina 22–65 × 0.8–1.5 cm, linear, with acuminate apex, arching, both faces soon glabrous, margins serrate with dark antrorse and retrorse **Sp** 1–2 mm long; **Inf** peduncle erect, 30–100 cm, exceeding the leaves, floriferous part 8–50 cm, simple, cylindrical, laxly few-flowered, with a terminal coma of sterile bracts, glabrous; peduncular **Bra** ovate, lower ones laminate, upper with ovate sheath extending into a long-attenuate lamina, glabrous, margins minutely serrate; floral **Bra** 30–45 × 10–16 mm, ovate-elliptic, acuminate, longer than the pedicel but shorter than the sepals, margins laciniate-spinose;

**Fig. 8** *Puya mirabilis*.  
(Copyright: U. Eggli)



**Ped** 12 mm, suberect during anthesis, later arching-decurved; **Sep** subtriangular, 40–60 × 7–9 mm, obscurely mucronulate; **Pet** yellow-green or white-cream, broadly linear, 90 mm, upper part recurved; **St** included, 60–80 mm; **Anth** yellow; **Sty** included; **Fr** ellipsoid, 20–30 mm; **Se** alate, triangular, 3–4.5 mm.

Flowering is often synchronous in up to 10 rosettes of large plants. The inflorescence becomes arched at times due to the weight of the flowers, which are somewhat spreading-pendent at anthesis.

**P. mitis** Mez (Repert. Spec. Nov. Regni Veg. 3: 10, 1906). **Type:** Peru, Junín (*Weberbauer* 2094 [B, F [photo]]). — **Distr:** Peru (Amazonas?, Junín: mountains W of Huacapistana); rock crevices and rocky slopes, 3000–3100 m.

[2] Polycarpic, forming groups, 70 cm tall at flowering time; **L** sheaths forming a large ellipsoid pseudo-bulb, fleshy, margins entire, **L** lamina 15 × 0.5 cm, subulate-convolute, green, both faces glabrous, margins entire; **Inf** peduncle 30–50 cm, erect, exceeding the leaves, floriferous part 20 cm, simple, cylindrical in outline, laxly racemose, to 15-flowered, glabrous; lower peduncular **Bra** with long entire lamina, middle and upper ones ovate with serrulate lamina, glabrous; floral **Bra** 25–35 mm, broadly ovate-elliptic, apex acute and pungent, the lower with serrulate margins and the upper entire, shorter than the sepals but longer than the pedicel; **Fl** tubular, erect; **Ped** 15 mm, suberect; **Sep** elliptic, obtuse, 16 × 10 mm, fleshy, glabrous except for the apex; **Pet** yellow-green, 32 mm, obtuse; **St** and **Sty** included.

One of the few species with entire leaf margins. The flowers are pendent at the time of anthesis.

**P. navarroana** Manzanares & W. Till (Jewels Jungle Bromeliac. Ecuador II, Pitcairnioideae, 342–344, ill., 2005). **Type:** Ecuador, Azuay (*Manzanares & al.* 7529 [QCNE, MO, SEL, WU]). — **Distr:** Ecuador (Azuay: Sigsig); shrubby vegetation of the cloud forest, 2870 m.

[2] Polycarpic, forming dense groups, 2.5–4 m tall at flowering time, stem evident, to 30 cm Ø; **L** sheath fleshy, orbicular, 6 × 9 cm, margins entire, **L** lamina 100–150 × 3.5–4 cm, adaxially

glabrous, abaxially sparsely lepidote between the veins, margins serrate with chestnut-brown antrorse **Sp** 3–4 mm long; **Inf** peduncle exceeding the leaves, 1–1.5 m, floriferous part 1.4–1.5 m, dense, cylindrical in outline, with 40–50 branches, somewhat lax, green, lepidote; lower peduncular **Bra** leaf-like, upper remote, pendent, 4–7 × 2.5 cm, margins serrate; primary **Bra** ovate, 3.5–4.5 × 2 cm, with attenuate apex, to ½ as long as the subtended branch, tomentose, margins serrate; **Br** at an angle of 90° with the axis, ovate, 7–8 × 5 cm, densely 15- to 22-flowered, stipe lacking, tomentose; floral **Bra** orbicular to reniform, 10 × 20 mm, acute, not covering the sepals, margins entire; **Ped** stout, 5 mm; **Sep** elliptic, acuminate, 23 × 10 mm; **Pet** white, 50 mm; **St** exposed; **Anth** green; **Sty** included.

Can be confused with *P. glomerifera* from which it differs by larger inflorescences with lax branches. Flowering plants are an important food source for the local hummingbird populations.

**P. nigrescens** L. B. Smith (Publ. Mus. Hist. Nat. “Javier Prado”, Ser. B, Bot. 16: 4, figs. 6–8, 1964). **Type:** Peru, Ancash (*Cerrate* 4103 [US, USM]). — **Distr:** Peru (Ancash: between San Cristobal and Mangas); mountain slopes, 1100–1200 m.

[2] Polycarpic, 1.5 m tall at flowering time; **L** sheath reniform, 13 cm wide, fleshy, castaneous, lustrous, glabrous, **L** lamina 50–60 × 1–1.5 cm, green, adaxially glabrous, abaxially covered with cinereous appressed scales, margins serrate with antrorse castaneous **Sp** 7 mm long; only immature **Inf** known, peduncle erect or ascending, 0.8 m, exceeding the leaves, white-tomentose at the nodes, floriferous part 0.4–0.8 m, simple, cylindrical, lax to sublax during anthesis, white-tomentose, soon glabrous; lower peduncular **Bra** leaf-like, upper ones soon deciduous; floral **Bra** 50 mm, lanceolate, acute, blackened along the margins at anthesis and soon completely black, longer than the sepals; **Ped** slender, 10 mm; **Sep** narrowly oblong, obtuse, 40 × 7 mm; remaining flower details unknown.

**P. ×pichinchae** Mez & Sodiro (Bull. Herb. Boissier, sér. 2, 4: 633, 1904). **Type:** Ecuador, Pichincha (*Sodiro* P-4 p.p. [B]). — **Lit:** Gilmartin

(1972: 32–33). **Distr:** N Ecuador (Pichincha); arid inter-Andean areas, in ravines, 2900–3200 m. **I:** Oliva-Esteve (2002: 235); Manzanares (2005: 359–360).

[2] Polycarpic, forming dense groups, 1.5–2 m tall at flowering time, stem 50–60 × 2 cm Ø; **L** sheath fleshy, orbicular, 10 × 5–7 cm, margins entire or laciniate near the apex, white, adaxially glabrous, abaxially lepidote, **L** lamina 60–80 × 3 cm, adaxially glabrous, abaxially cinereously lepidote, margins serrate with brown or yellow hooked antrorse **Sp** 4–9 mm long; **Inf** peduncle exceeding the leaves, 0.8–1 m, floriferous part 0.9–1.25 m, laxly branched, pyramidal in outline, with a long terminal part, ± cinereously lepidote; lower peduncular **Bra** leaf-like, upper shorter than the internodes, 10–20 cm, tomentose, margins serrulate; primary **Bra** elliptic, with attenuate apex, 5 × 2.2 cm, recurved, longer or shorter than the stipe, tomentose, margins serrulate; **Br** cylindrical in outline, 30–60 cm, laxly 20- to 40-flowered, suberect or spreading, with a distinct stipe 1–2 cm long; floral **Bra** ovate or deltoid, 12 × 3 mm, acute or acuminate, shorter than the sepals but as long or longer than the pedicel, margins entire; **Ped** stout, 7–10 mm; **Sep** elliptic, 22–24 × 8–10 mm, with rounded apex; **Pet** green or violet, 50 mm; **St** exposed; **Anth** yellow; **Sti** included.

According to Manzanares (2005), this is the natural hybrid *P. aequatorialis* × *P. sodiroana*, which occur together and flower at the same time. The inflorescences of the hybrid are variable and vary from richly branched as in *P. sodiroana* to few- and laxly branched as in *P. aequatorialis*.

**P. pitcairnioides** L. B. Smith (Publ. Mus. Hist. Nat. “Javier Prado”, Ser. B, Bot. 16: 5, 1964). **Type:** Peru, Amazonas (*Weberbauer* 4268 [B]). — **Distr:** Peru (Amazonas: Bagua, Chachapoyas); slopes, 1100–1200 m.

≡ *Pitcairnia grandiflora* Mez (1906).

[2] Polycarpic, caulescent, 2–3 m tall at flowering time, stem decumbent, branched, 8–9 cm Ø; **L** sheath fleshy, **L** lamina 60–80 × 3.6 cm, both faces densely cinereous-lepidote, margins serrate with **Sp** 10 mm long; **Inf** peduncle exceeding the leaves, 1.5–2 m, floriferous part 0.3–0.5 m,

simple, cylindrical in outline, axis stout, densely flowered, glabrous at anthesis; lower peduncular **Bra** leaf-like; floral **Bra** lanceolate, acute, 45 × 12 mm, shorter than the sepals, reflexed or revolute, margins entire; **Ped** 15 mm; **Sep** narrowly triangular, acuminate, 35 mm; **Pet** reddish-brown, 70 mm; **St** exposed; **Anth** yellow; **Sty** included.

The label of a collection from Prov. Bagua (*P. Barbour* 4224, MO) notes that the flowers are yellowish-green, and that the yellow anthers are visible.

**P. prosanae** Ibisch & E. Gross (J. Bromeliad Soc. 43(5): 211–215, ills., 1993). **Type:** Bolivia, Cochabamba (*Ibisch* 625A [HEID, LPB]). — **Distr:** Bolivia (Cochabamba); slopes, 3500–3700 m.

[2] Polycarpic, forming cushions with radial growth, dying from the centre in age, 20–30 cm Ø, with >20 rosettes, 14 cm tall at flowering time; **Ros** stemless, with a fleshy bulbous base, bulb 2.5 × 1.5 cm Ø; **L** sheath fleshy, conspicuous, broadly ovate, 1.5 × 2 cm, light brown on both faces, upper part lustrous dark brown esp. beneath, membranous, veined, margin near the transition to the lamina serrate, above sparsely brown-lepidote, **L** lamina narrowly triangular, acuminate, 6–8 × 0.2–0.3 cm, both faces lepidote, adaxially soon glabrous, margins with light brown retrorse **Sp** 1–2 mm long, 5 mm apart and almost opposite; **Inf** peduncle erect, 6–9 cm, brown, densely lepidote, floriferous part simple, shortly cylindrical, 5 × 2.5 cm, ± densely spirostichously 5- to 15-flowered; peduncular **Bra** densely imbricate, erect, the basal ones subfoliate, with filamentous and serrate lamina, the middle and upper ones ovate-lanceolate, acuminate, 1.5–2 cm, margins finely serrate, veined, with a conspicuous midrib, abaxially reddish; floral **Bra** erect, ovate, acuminate, 20 × 10 mm, rose-red, membranous when dry, veined, sparsely lepidote, margins inconspicuously serrate; **Ped** almost absent and **FI** subsessile; **Sep** narrowly triangular, acuminate, 11–12 × 2–3 mm, free to the base, with hyaline margin, rose-reddish, sparsely lepidote, margins apically inconspicuously serrate, carinate; **Pet** erect, tongue-shaped, 16–17 mm, red-violet, darker after anthesis; **St** included; **Sty** included; **Fr** 15 mm.



Ideally suited for small gardens of succulents due to the small size, and outstanding because of the fleshy bulbous rosette base.

**P. raimondii** Harms (Notizbl. Bot. Gart. Berlin-Dahlem 10: 213, 1928). **Type:** Peru, Ancash (*Weberbauer* 2955 [B, F [photo]]). — **Lit:** Salazar Castillo & al. (2012). **Dist:** Peru (La Libertad, Ancash, Lima, Junín, Huancavelica, Ayacucho, Apurímac, Cusco, Moquegua, Puno), Bolivia (La Paz, Cochabamba); rocky slopes and páramos, 2400–4200 (–4460) m. **I:** Rauh (1990: 271–273, 397); Baensch (1994: 153); Oliva-Esteve (2000: 409–410); Grau & al. (2010). — Fig. 9.

**Incl.** *Pourretia gigantea* Raimondi (1874).

[1] Monocarpic, 8.3–9.5 (–15) m tall at flowering time; **Ros** solitary, caulescent, trunk 1–2 m, covered by old leaves; **L** very numerous, sheath fleshy, ample, 15–22 × 16 cm, **L** lamina 100–125 × 9 cm, stiff, adaxially green, abaxially white-lepidote, margins laxly serrate with antrorse and retrorse uncinat dark brown **Sp** 10–15 mm

long; **Inf** peduncle exceeding the leaves, 0.6–0.9 m, very stout and 20–40 cm Ø, brown, floriferous part 4–5 (–8) m, densely branched, cylindrical in outline, green, white-lanate; lower peduncular **Bra** leaf-like, upper ovate, attenuate towards the tip, reflexed, brown, lepidote; primary **Bra** broadly ovate, apiculate, much shorter than the subtended branch, subglabrescent, green with brown apex, margins entire; **Br** shortly stipitate, 20–30 cm, spreading or reflexed, densely flowered in the lower part, sterile distally with reduced bracts; floral **Bra** 50–60 mm, ovate-lanceolate, acuminate, longer than the sepals, green, subglabrescent; **Ped** stout, 15 mm, lepidote; **Sep** lanceolate, acute, 40 mm, green; **Pet** elliptic, white, 60–80 mm; **St** included; **Anth** yellow; **Sty** included, longer than the stamens; **Sti** green; **Fr** globose-ovoid.

This massive plant is the queen of the genus, and by far the largest-growing taxon of the family. The massive inflorescence produces thousands of flowers whose abundant nectar attracts numerous birds, both specialized hummingbirds and more generalist passerine birds (Salinas & al. 2007, Hornung-Leoni & al. 2013).

The life-span of a plant is estimated to be in the range 40–100 years, and 28 year old plants can reach a height of 3.36 m (Salazar Castillo & al. 2012). The total reproductive output is estimated to be 12 million seeds (Salazar Castillo & al. 2012). The species is a protected plant in Peru, and is commonly regarded as being threatened or in danger of extinction. Population-level reports (summarized by Salazar Castillo & al. (2012)) give a mixed image, with some populations showing a steep decline in plant numbers (attributed to various causes, including burning of plants to regenerate pastures and stop animals being trapped or hurt by the spiny leaves), while others appear to be stable or increase.

**P. retrorsa** Gilmartin (Phytologia 57: 455, 1985). **Type:** Ecuador, Tungurahua (*Gilmartin* 1103 [US]). — **Dist:** Ecuador (Pichincha, Cotopaxi, Tungurahua, Chimborazo); shrubby Páramo vegetation, and as living fences in the inter-Andean valleys, in ravines, 2800–3400 m. **I:** Manzanares (2005: 347–348).



**Fig. 9** *Puya raimondii* (Peru, Arequipa, Cotahuasi, Lauripampa). (Copyright: I. Treviño)



[2] Polycarpic, forming dense groups, 2–3 m tall at flowering time, stem 30–40 cm  $\varnothing$ ; **L** sheath fleshy, orbicular, 10  $\times$  9 cm, margins entire, **L** lamina 40–60  $\times$  2.5–3 cm, adaxially glabrous, abaxially densely lepidote, margins serrate with chestnut-brown **Sp** 6–8 mm long, retrorse at the base and antrorse in the upper part; **Inf** peduncle exceeding the leaves, 1–1.5 m, floriferous part 0.4–0.8 m, dense, cylindrical in outline, with 80–120 branches, tomentose with brown indumentum; lower peduncular **Bra** leaf-like, upper remote, 10–13  $\times$  2.5 cm, lamina pendent; primary **Bra** orbicular, 4–8  $\times$  5–6 cm, lower with attenuate apex, upper with acuminate apex, at anthesis shorter than the subtended branch, margins serrulate in the upper part; **Br** fasciculate, 3–9  $\times$  2–4 cm, densely 9- to 15-flowered, stipe nearly none; floral **Bra** elliptic to obovate, 30–35  $\times$  10–15 mm, with rounded and acuminate apex, exceeding the sepals, margins sparsely serrate; **Ped** stout, 3 mm; **Sep** elliptic, with rounded apex, 20  $\times$  11 mm; **Pet** cream to green, 40 mm; **St** exposed; **Anth** yellow; **Sty** included.

The plants form dense groups united by branched stems. Growth is moderately slow: A shoot branch of 50 cm takes 7 years to grow, and the thickly branched groups, with arms to 150 cm long (including branches) need  $\pm$ 25 to 35 years to form (Manzanares 2005).

**P. robinfosteri** G. S. Varadarajan & H. Luther (Selbyana 16(2): 235–238, ill., 1995). **Type:** Peru, Pasco (*Foster* 9062 [MO, SEL]). — **Distr:** Peru (Pasco: Cordillera Yanachaga); in seepage area, 2700–2800 m.

[1] Polycarpic, solitary or mat-forming, 25–30 cm tall at flowering time; **Ros** stemless, forming a globose pseudobulb 2–3 cm  $\varnothing$ ; **L** sheath fleshy, 1–1.2  $\times$  0.8–1.2 cm, blackish-brown, inflated, **L** lamina very narrowly triangular to linear, attenuate, pungent, 6–10  $\times$  0.75 cm, involute, subappressedly white-lepidote esp. abaxially, margins serrulate towards the base but entire towards the apex, **Sp** filiform, brown, antrorse, 6–15 mm; **Inf** peduncle erect, 15–18  $\times$  0.5 cm, white-floccose, floriferous part simple, 4–7 cm, green, often subsecund, 5- to 10-flowered; lower peduncular **Bra** subfoliaceous,

upper ones ovate, margins serrate, equalling to exceeding the internodes; floral **Bra** ovate, 10–17  $\times$  9–14 mm, acute to attenuate, margins entire to inconspicuously and minutely serrulate, veined, lustrous, castaneous; **Ped** straight to curved-ascending, 6–13 mm, sparsely floccose; **Sep** oblong-lanceolate, 10–13 mm, broadly acute to retuse, veined, subcarinate, lustrous, castaneous; **Pet** 16–20 mm, green; **St** and **Sty** deeply included; **Fr** 8–10 mm.

**P. roezlii** E. Morren (Belgique Hort. 35: 80, 1885). **Type:** Peru ('Andes') (*Roehl* s.n. [LG, GH [photo]]). — **Distr:** Peru (Lima); on rocks and sandy ground, 2200–2800 m.

**Incl.** *Pitcairnia megastachya* Baker (1889); **incl.** *Puya pectinata* L. B. Smith (1932).

[1] Polycarpic, forming groups, caulescent with short and stout ascending stem, 0.5–1.2 m tall at flowering time; **L** sheath fleshy, broadly ovate, merging with the lamina, dark, lustrous, abaxially  $\pm$  lepidote, **L** lamina narrowly triangular, attenuate to a pungent apex, recurving, 100  $\times$  3 cm, adaxially glabrous, abaxially covered beneath with pale appressed scales, margins laxly serrate, **Sp** antrorse, uncinat, 8 mm; **Inf** peduncle exceeding the leaves, erect, stout, floriferous part laxly and amply 1  $\times$  branched, 50 cm, sordidly pruinose-lepidote; lower peduncular **Bra** foliaceous with long lamina, dense, margins coarsely serrate; primary **Bra** broadly ovate, 3 cm, margins serrate with **Sp** 4 mm long, subcoriaceous, the lowest with narrow decurved lamina; **Br** 15 cm, scorpioid-decurved, flowers to the apex, lowest branches 15- to 25-flowered, subdense to lax at anthesis; floral **Bra** broadly ovate, acute, 10 mm, margins serrulate, equalling or shorter than the sepals, strongly convex; **Ped** very short and stout; **Sep** lanceolate, 16–18 mm, attenuate, mucronulate; **Pet** deep blue or purple, 28 mm; **St** included; **Anth** linear, 5 mm; **Sty** included; **Fr** subglobose, 10 mm.

Strongly succulent and comparable to *Ochagavia* (Zizka & al. 2002).

**P. roldanii** Betancur & Callejas (Caldasia 19: 78, ill., 1997). **Type:** Colombia, Antioquia (*Callejas* 11158 [HUA, COL, SEL]). — **Distr:**

Colombia (Antioquia: Belmira, Río Chico); shrubby Páramo vegetation, 2400–3110 m.

[2] Polycarpic, forming very dense cushions, 0.7–1 m tall at flowering time, stem short, prostrate, covered by old leaves; **L** sheath fleshy, oblong, 3–4 × 1.8–2.5 cm, margins serrate at the top, dark coffee-brown towards the top, with brown indumentum, **L** lamina 28–34 × 1–1.3 cm, triangular, with attenuate apex, adaxially glabrous and mottled with wine-red, abaxially lepidote with grey indumentum becoming denser towards the apex, margins with wine-red lines, serrate with dark antrorse and retrorse **Sp** 3–5 mm long; **Inf** peduncle exceeding the leaves, 30–50 cm; floriferous part 12–16 cm, simple, cylindrical in outline, at anthesis lax, 16- to 23-flowered, tomentose; lower peduncular **Bra** leaf-like, green-yellow, lepidote, upper ovate-elliptic, 5–7 × 2.4–3.1 cm, both faces lepidote with brown indumentum, margins minutely serrate; floral **Bra** 40–45 × 15–20 mm, ovate, acute, longer than the sepals, adaxially pubescent, abaxially tomentose, margins entire; **Ped** 8–16 mm, ascending, lepidote with brown indumentum; **Sep** oblong, truncate, 25–30 × 7–8 mm, ± fleshy, adaxially glabrous, abaxially tomentose; **Pet** green-blue, spatulate, 60–68 mm, ± fleshy; **St** included, 44–47 mm; **Anth** yellow; **Sty** as long as the stamens, included.

Forming dense groups and easily recognizable by the leaves, which are all ascending-erect and mottled with wine-red. The young fleshy inflorescences are often eaten by the cattle of the local farmers.

**P. roseana** L. B. Smith (Phytologia 7: 421, t. 1: fig. 13, 1961). **Type:** Ecuador, Loja (*Rose* 23210a [US]). — **Lit:** Gilmartin (1972). **Distr:** Ecuador (Loja); shrubby vegetation, in ravines, and as living fences, 2400–2600 m. **I:** Manzanares (2005: 361–362).

[2] Polycarpic, forming dense groups, 1.5–2 m tall at flowering time, stem 30–50 cm, branched, ascending; **L** sheath fleshy, orbicular, 8 × 8.5 cm, margins entire, white, **L** lamina 50 × 2–2.5 cm, adaxially glabrous, abaxially with brown indumentum, margins serrate with chestnut-brown **Sp** 4 mm long; **Inf** peduncle exceeding the leaves, 0.6–0.8 cm, lepidote, floriferous part

0.5–1.5 m, dense, cylindrical in outline, with 20–25 branches, with ferruginous indumentum; lower peduncular **Bra** leaf-like, upper triangular, remote, 5–15 × 1.5 cm, apex attenuate and pungent, margins serrate; primary **Bra** 2.5 × 1.5 cm, with an orbicular sheath, margins ± serrate, apex long attenuate, shorter than the subtended branch during anthesis; **Br** 19–30 × 3.7 cm, at an angle of 90° with the axis, subdensely 20- to 25-flowered, with a distinct sterile base 3 cm long; floral **Bra** ovate, 10 × 11 mm, with apiculate apex, as long as or longer than the pedicel but shorter than the sepals, adaxially glabrous, abaxially with ferruginous indumentum, margins entire; **Ped** stout, 7–9 mm; **Sep** oblong, obtuse, 20–22 × 12 mm, fleshy, adaxially glabrous, abaxially with ferruginous indumentum; **Pet** bluish, 30 mm; **St** exposed; **Anth** yellow; **Sty** included; **Fr** 20 mm.

The inflorescence architecture is very variable and depends on the plant's vegetative size. Inflorescences vary between 0.5 and 1.5 m long, with branches 19–30 cm long. Short branches have densely polystichously arranged flowers, long branches have subdensely or occasionally laxly arranged flowers.

**P. schuencasensis** R. Vásquez & al. (Bromelie 2007(3): 150–155, ills., 2007). **Type:** Bolivia, Cochabamba (*Vásquez & Lara* 5279 [LPB, BOLV, MO, SEL]). — **Distr:** Bolivia (Cochabamba); slopes in cloud forest, 2050–2100 m.

[2] Polycarpic, forming dense groups, branched, 2 m tall at flowering time; **L** sheath orbicular, 5–6 × 8–9 cm, white towards the base, dark chestnut-brown at the apex, **L** lamina 50–70 × 5–8 cm, recurving, adaxially glabrous, abaxially densely cinereous-lepidote, margins serrate with dark brown antrorse flat **Sp** 8 mm long; **Inf** peduncle exceeding the leaves, 0.6–0.8 m, lepidote with white stellate scales but then glabrous, floriferous part 1–1.2 m, lax, pyramidal in outline, paniculate with 8 branches; lower peduncular **Bra** leaf-like, upper oblong-elliptic, longer than the internodes, 5–20 cm, margins entire near the base, densely serrate towards the apex; primary **Bra** triangular, spreading, 10 cm, as long as the sterile base of the subtended branch, green, margins densely serrate with antrorse and retrorse spines

near the pungent apex; **Br** 38–45 cm, pendent, subdense, densely covered with white stellate scales, stipe distinct, 10 cm; floral **Bra** triangular, 50 × 20 mm, attenuate, longer than the pedicel, densely white-stellate, margins serrate towards the apex with antrorse and retrorse spines; **Ped** stout, 12 mm, densely white-stellate; **Sep** triangular, attenuate, 40 × 8 mm, densely covered by the white-stellate indumentum; **Pet** blue and green at the base, 56 mm, apex recurved; **St** exserted, 70 mm, blue; **Anth** yellow; **Sty** as long as the stamens; **Fr** 20 mm.

**P. sodiroana** Mez (Bull. Herb. Boissier, sér. 2, 4: 630, 1904). **Type:** Ecuador, Pichincha? (*Sodiro* P-5 [B]). — **Lit:** **Distr:** N Ecuador (Pichincha, Azuay); arid inter-Andean areas, ravines, and also as living fences, 2800–2900 m. **I:** Manzanares (2005: 357).

**Incl.** *Puya gummifera* Mez & Sodiro (1904).

[2] Polycarpic, forming dense groups, 2–2.5 m tall at flowering time, stem 25 cm Ø, branched; **L** sheath fleshy, ovate, 4.5 × 5 cm, white above and chestnut-brown below, with entire margins, **L** lamina 40–60 × 2.5–3.5 cm, adaxially glabrous, abaxially densely lepidote, margins serrate with brown **Sp** 6–10 mm long, retrorse in the lower part and antrorse in the upper part; **Inf** peduncle exceeding the leaves, ±1 m, lepidote, not completely covered by the bracts, floriferous part 0.7–0.9 m, lax or sublax, cylindrical in outline, with 25–30 branches, covered with cinereous indumentum; lower peduncular **Bra** leaf-like, upper triangular, pendent, 5–6 × 2.5 cm, apex attenuate, margins serrate; primary **Bra** ovate to triangular, 5–6 × 2–2.5 cm, as long as or exceeding the stipe and shorter than the subtended branch, margins ± serrate; **Br** ellipsoid in outline, 10–18 × 3.5–4 cm, at an angle of 90° with the axis, densely 15- to 25-flowered, with a distinct stipe 2–4 cm long; lower floral **Bra** orbicular, upper ovate, 15–20 × 13 mm, acute or acuminate, reaching the middle of the sepals and longer than the pedicel, adaxially glabrous, abaxially with cinereous-lanate indumentum, margins entire; **Ped** stout, 9 mm, lanate; **Sep** tongue-shaped, with rounded and retuse apex, 24 × 9 mm, adaxially glabrous, abaxially lanate; **Pet** green,

cream or violet, 40 mm; **St** exposed; **Anth** yellow; **Sty** included.

Sometimes growing sympatrically with *P. aequatorialis*, with which it easily hybridizes (see *P. ×pichinchae*). The flower colour varies from green to cream and violet, depending on the population, probably indicating some degree of introgression from *P. aequatorialis*. The flowers are intensely visited by several species of hummingbirds, including the Giant Hummingbird of the Andes, *Patagona gigas*.

**P. tillii** Manzanares (Jewels Jungle Bromeliac. Ecuador II, Pitcairnioideae, 344–345, ill., 2005). **Type:** Ecuador, Pichincha (Manzanares 5738 [QCNE, MO, WU]). — **Distr:** Ecuador (Pichincha: W Cordillera); cloud forest, humid shrubby mountain sides, 2300–3400 m.

[2] Polycarpic, forming dense groups, 2–2.5 m tall at flowering time, stem 40 cm Ø, branched; **L** sheath fleshy, orbicular, 6 × 6 cm, glabrous, white above and chestnut-brown below, margins entire, **L** lamina 50–60 × 3.5 cm, adaxially glabrous, abaxially densely lepidote, margins serrate with brown antrorse **Sp** 10 mm long; **Inf** peduncle exceeding the leaves, 1.2 m, lepidote, not completely covered by the bracts, floriferous part 0.7 m, dense, cylindrical in outline, with 25–30 branches, brown or green-brown, densely lepidote; lower peduncular **Bra** leaf-like, the upper with an elliptic sheath, lamina triangular, pendent, 9–15 × 2.5 cm, brown, margins serrate; primary **Bra** with ovate sheath and triangular lamina, pendent or spreading, 10 × 6 cm, as long as or longer than the subtended branch but not hiding it, margins ± serrate; **Br** globose or ellipsoid in outline, 5 × 2 cm, at an angle of 90° with the main axis, densely 6- to 9-flowered, stipe nearly none, green, tomentose; floral **Bra** ovate, 35 × 18 mm, with acute or attenuate apex, hiding the sepals, adaxially glabrous, abaxially brown-tomentose, margins entire; **Ped** 4 mm; **Sep** elliptic, obtuse, 23 × 13 mm, adaxially glabrous, abaxially tomentose; **Pet** green, cream or pink, 50 mm; **St** exposed; **Anth** yellow; **Sty** included.

One of the few Ecuadorian species from the cloud forest zone. Its rosettes are usually covered by small shrubs or lichens. The majority of the

plants has pink flowers, which are pollinated by a variety of hummingbird species.

**P. tuberosa** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 483, 1896). **Type:** Bolivia ('Peru') (*Haenke* s.n. [M]). — **Lit:** Vásquez & Ibsch (2007: with ill.). **Distr:** Bolivia (Tarija, Chuquisaca, Santa Cruz); grassy-rocky slopes, 1000–1800 m. **I:** Rauh (1990: 276: Fig. 359, as *P. serranoensis* vars.).

**Incl.** *Puya hromadnikii* Rauh (1983); **incl.** *Puya serranoensis* Rauh (1983); **incl.** *Puya vallograndensis* Rauh (1983); **incl.** *Puya serranoensis* var. *brevispica* Rauh (1985); **incl.** *Puya vallograndensis* var. *simplex* Rauh (1985); **incl.** *Puya pachyphylla* R. Vásquez & Ibsch (2007).

[2] Polycarpic, forming dense groups, 30–50 cm tall at flowering time (incl. the very short erect rhizome); **L** sheath suborbicular, fleshy, forming a globose bulb 3 cm Ø, blackish-brown, **L** lamina 15–18 × 0.2–0.35 (–1.2) cm, linear, flexuose, green, adaxially glabrous, abaxially covered with pale narrow spreading scales, margins laxly serrate with antrorse and retrorse **Sp** 1–2 mm long; **Inf** peduncle erect, 10–15 cm, as long as or shorter than the leaves, white-flocculose, floriferous part 20–30 cm, simple or with a few short branches at the base, cylindrical, laxly 12- to 20-flowered, white-flocculose; lower peduncular **Bra** leaf-like, ovate with filiform lamina, pale-lepidote; primary **Bra** ovate, acuminate, 2 cm, shorter than the subtended branch, minutely serrulate; **Br** short, 2- to 5-flowered; floral **Bra** 4–7 mm, ovate, acute, red, shorter than the sepals, longer or shorter than the pedicel; **Ped** 4–7 mm, erect, white-flocculose; **Fl** secund, tubular; **Sep** lanceolate-oblong, acute, 7–9 × 6 mm, white-flocculose; **Pet** blue-violet, erect, 30 mm; **St** included; **Sty** included.

The leaves superficially resemble a bunch of grass. The plants have a basal erect rhizome that stores water and carbohydrates, to allow to survive prolonged periods without rain. *P. tuberosa* is a widespread and variable species, and several local forms that were described as independent taxa were recently synonymized (Vásquez & Ibsch 2007). Populations spanning a continuum of small plants with filiform leaves to larger plants with triangular leaves are known.

**P. venusta** Philippi (Anales Univ. Chile 91: 613, 1895). **Type** [lecto]: Chile, Región IV, Coquimbo (*Philippi* 940 [B]). — **Lit:** Zizka & al. (2013: with ill.). **Distr:** Chile (Coquimbo, Valparaíso); coastal rocks and sand, 5–250 (–750) m. **I:** Oliva-Esteve (2002: 238); Wisnev (2016: 160).

≡ *Pitcairnia venusta* (Philippi) Baker (1889); **incl.** *Pitcairnia sphaerocephala* Baker (1889); **incl.** *Puya coquimbensis* Mez (1896); **incl.** *Puya gaudichaudii* Mez (1896).

[2] Polycarpic, forming dense compact groups, 1.2–1.7 m tall at flowering time, stem to >40 cm; **L** sheath fleshy, suborbicular, **L** lamina 40–50 × 2.5–3 cm, thickly succulent, both faces appressed-lepidote and canescent, margins serrate with green antrorse and retrorse uncinata **Sp** 5–7 mm long; **Inf** peduncle far exceeding the leaves, 0.7–1 m, floriferous part 0.5–0.7 m, dense, cylindrical, simple and strobilate or compound with several spicate branches, white-tomentose; lower peduncular **Bra** leaf-like, upper triangular-ovate, 5–10 × 2.5–3 cm, acuminate, deep red-violet, margins lacinate-serrate; primary **Bra** ovate, 5–7 × 3 cm, acuminate, shorter than the subtended branch; **Br** spicate, 5–8 cm, dense, with a stipe 4–6 cm long, end part of the inflorescence cylindrical, 12 cm; floral **Bra** elliptic, 30–35 × 20–25 mm, with a rounded and acuminate apex, longer than the sepals, densely imbricate, tomentose, margins entire or at the base sparsely serrate; **Ped** stout, 7 mm, tomentose; **Sep** oblong, obtuse, 15–20 × 10 mm; **Pet** violet, 35–40 mm; **St** exposed; **Anth** yellow; **Sty** included, green.

**P. vestita** André (Enum. Bromél., 5, 1888). **Type:** Ecuador, Pichincha (*André* 3739 [K]). — **Lit:** Gilmartin (1972). **Distr:** Ecuador (Pichincha, Cotopaxi, Bolívar, Chimborazo); among shrubs and in Páramo vegetation, 2800–3900 m. **I:** Manzanares (2005: 311–312).

[2] Polycarpic, forming dense clusters, 1.5–2 m tall at flowering time, stem 25 cm Ø; **L** sheath fleshy, orbicular, 10 × 8 cm, glabrous, chestnut-brown, margins entire, **L** lamina 35 × 2.4 cm, adaxially glabrous, abaxially densely lepidote, margins serrate with bright brown antrorse **Sp** 6 mm long; **Inf** peduncle exceeding the leaves, 0.6–0.8 m, floriferous part 0.2–0.4 m, dense,



cylindrical or ellipsoid in outline, with 15–20 branches, with ferruginous indumentum; lower peduncular **Bra** leaf-like, with orbicular sheath and triangular lamina, 7–15 × 1.2 cm, lamina pendent, densely lepidote, margins serrate; primary **Bra** ovate, 7–10 × 4 cm, attenuate or long acuminate, margins ± serrulate, lower bracts exceeding the subtended branch, upper equalling or ± shorter than the subtended branch, adaxially sparsely lepidote, abaxially with ferruginous indumentum; **Br** reduced, 3–5 × 1.4 cm, densely 3- to 5-flowered, stipe nearly none; floral **Bra** ovate, 30–35 × 21 mm, with acute navicular apex, hiding the sepals, margins entire; **Ped** nearly none, 1 mm; **Sep** ovate, obtuse, 20–25 × 11 mm, adaxially glabrous, abaxially with ferruginous indumentum; **Pet** greenish, 45 mm; **St** exposed; **Anth** yellow; **Sty** included.

Related to *P. glomerifera* and *P. retrorsa*, but most clearly differing from both by the antrorse leaf margin spines (both antrorse and retrorse in *P. glomerifera*, antrorse in the distal part and retrorse in the basal part in *P. retrorsa*).

**P. weberiana** E. Morren *ex* Mez (in A. & C. de Candolle, Monogr. Phan. 9: 492, 1896). **Type:** Argentina, Salta (*Weber s.n.* in *BG Liège s.n.* [G, GH [photo]]). — **Lit:** Gómez & Grau (2009: with ill.). **Distr:** Argentina (Salta, Tucumán); among rocks, 3600–4000 m.

**Incl.** *Puya flora* Spegazzini (1896).

[2] Monocarpic and **Ros** solitary, 50 cm tall at flowering time; **L** sheath fleshy, ovate, 6 × 4 cm, **L** lamina 20 × 1–2 cm, adaxially glabrous, abaxially appressedly cinereous-lepidote, margins laxly serrate with uncinata mostly retrorse **Sp** 4 mm long; **Inf** peduncle exceeding the leaves, 20–30 cm, stout, floriferous part 20–30 cm, simple, dense, ellipsoid in outline, strobilate, compact, pink; peduncular **Bra** densely imbricate making the peduncle appear nearly as thick as the floriferous part, elliptic, pink, apex reflexed, margins serrate; floral **Bra** 45 × 15 mm, elliptic-oblong, longer than the pedicel and sepals, exceeding the flowers but reflexed, pink, margins of the lower ones ± serrulate; **Ped** obconical, stout, 8 mm; **Sep** elliptic, acute, 35 mm, lanate at the base; **Pet** blue or violet, oblanceolate, 40 mm; **St** included; **Anth** 7 mm, yellow; **Fr** subpyramidal, 25–35 mm; **Se** irregularly triangular, 3.5 mm.

Related to *P. bravoii*, from which it differs by having spiny leaf margins and a simple inflorescence.

**P. weddelliana** (Baker) Mez (in A. & C. de Candolle, Monogr. Phan. 9: 475, 1896). **Type:** Bolivia, Tarija (*Weddell* 4001 [P, GH [photo]]). — **Distr:** Bolivia (Chuquisaca, Tarija); shrubby rocky slopes, 1800–3000 m. – Fig. 10.

≡ *Pitcairnia weddelliana* Baker (1889).

**Fig. 10** *Puya weddelliana* (Bolivia, Chuquisaca, Nor Cinti, Camargo). (Copyright: S. Janke)





[1] Polycarpic, forming dense groups, 4–5 m tall at flowering time, stem prostrate, woody, simple or branched, to 1–1.5 m; **L** sheath fleshy, broad, **L** lamina 90–120 × 4–5 cm, linear-triangular, adaxially glabrous, abaxially densely grey-lepidote, margins laxly serrate with retrorse curved **Sp** 5 mm long, dark brown; **Inf** peduncle exceeding the leaves, 1–1.5 m, stout, green, soon glabrous, fertile part 1.5–2.5 m, densely branched, with 60–90 branches, cylindrical in outline, bluish, sparsely tomentose-lepidote; lower peduncular **Bra** leaf-like, upper triangular, attenuate towards the tip, reflexed, lepidote; primary **Bra** triangular-ovate, attenuate towards the tip, much shorter than the subtended branch, lepidote, bluish; **Br** shortly stipitate, 30–40 cm, spreading, densely flowered in the lower ½, sterile distally with reduced bracts; floral **Bra** 20–30 mm, lanceolate, acute, shorter than the sepals, bluish, lepidote, margins entire; **Ped** slender, 10 mm, green, ± tomentose; **Sep** oblong, broadly obtuse, 18 × 10 mm, lower part green, bluish above, first white-tomentose, becoming glabrous; **Pet** oblong, obtuse, bright blue, 40–50 mm; **St** included; **Anth** yellow; **Sty** included, longer than the stamens; **Sti** yellow.

Undoubtedly the most spectacular species of *Puya* when flowering. The inflorescence of 1–1.5 m is filled with bright blue flowers, overtopped by the sterile cinereous top of the branches.

**P. yakespala** A. Castellanos (in Descole, Gen. Sp. Pl. Argent. 3: 213, t. 55, 124d-f, 1945). **Type:** Argentina, Salta (*Reynaga* s.n. [LIL 34523]). — **Lit:** Gómez & Grau (2009: with ill.). **Dist:** Argentina (N Salta: Santa Victoria); grassy rocky slopes and ravines, 3400–4000 m. **I:** Grau & al. (2010).

[2] Polycarpic, forming dense groups, 3–4 m tall at flowering time, stem elongate; **L** sheath orbicular, fleshy, **L** lamina 40–70 × 2–3.5 cm, recurved, green, adaxially glabrous, abaxially white-lepidote, margins serrate with **Sp** 5–6 mm long; **Inf** peduncle ± upcurved at the base, 1–1.8 m, exceeding the leaves, lanate, floriferous part 0.5–0.9 × 0.2–0.3 m, simple, ellipsoid in outline, strobiliform, dense, brown-lanate becoming glabrous; lower peduncular **Bra** leaf-like, upper triangular, reflexed, with acuminate apex,

7 cm, densely imbricate making the peduncle appear nearly as thick as the flowering part; floral **Bra** 10–14 mm, longer than pedicel and sepals, elliptic, acuminate, soft and often reflexed, brown, concave, membranous, the lower part lanate, margins entire; **Ped** 2–2.5 mm, subcylindrical; **Sep** triangular, acuminate, 45 × 12 mm, lanate; **Pet** yellow, oblong, revolute, 60 × 25 mm; **St** included; **Anth** blackish; **Sty** included, green; **Fr** ellipsoid, 30–35 × 15–20 mm; **Se** alate, 3–4 × 3 mm.

A very decorative species when in flower, with a light brown inflorescence with outstanding yellow flowers. The peduncle is bent at the base and has bracts densely arranged as to give a rugged look.

## References

- Baensch, U. (1994) Blühende Bromelien. Flowering Bromeliads. Nassau (BS): Tropic Beauty Publishers.
- Duval, L. (1990) The Bromeliads. Pacifica (US): Big Bridge Press.
- Gilmartin, A. J. (1972) The *Bromeliaceae* of Ecuador. Lehre (DE): Verlag von J. Cramer.
- Givnish, T. J. [& al. 2007], Millan, K. C., Berry, P. E. & Sytsma, K. J. (2007) Phylogeny, adaptive radiation, and historical biogeography of *Bromeliaceae* inferred from *ndhF* sequence data. In: Columbus, J. T. & al. (eds.): Monocots. Comparative biology and evolution: Poales. *Aliso* 23: 3–26. <https://doi.org/10.5642/aliso.20072301.04>
- Givnish, T. J. [& al. 2011], Barfuss, M. H. J., Ee, B. van, Riina, R., Schulte, K., Horres, R., Gonsiska, P. A., Jabaily, R. S., Crayn, D. M., Smith, J. A. C., Winter, K., Brown, G. K., Evans, T. M., Holst, B. K., Luther, H., Till, W., Zizka, G., Berry, P. E. & Sytsma, K. J. (2011) Phylogeny, adaptive radiation, and historical biogeography in *Bromeliaceae*: Insights from an eight-locus plastid phylogeny. *Amer. J. Bot.* 98(5): 872–895, ills., maps. <https://doi.org/10.3732/ajb.1000059>.
- Gómez, S. & Grau, A. (2009) Las especies de *Puya* (*Bromeliaceae*) en la Argentina. *Bol. Soc. Argent. Bot.* 44(1–2): 175–208, ills., key. <http://www.biodiversitylibrary.org/part/112523#>
- Gouda, E. J. [& al. 2012+], Butcher, D. & Gouda, C. S. (2012+) Encyclopaedia of Bromeliads, Version 3.1 (2012). Utrecht (NL): University Botanic Gardens, Utrecht. <http://bromeliad.nl/encyclopedia/>
- Grau, A. [& al. 2010], Gómez Romero, S. E. & Aráoz, E. (2010) Puyas andinas. *Ci. Hoy* 20(118): 8–15, ills. <http://www.cienciahoy.org.ar/ch/In/hoy118/puyas.pdf>
- Hornung-Leoni, C. T. [& al. 2013], González-Gómez, P. L. & Troncoso, A. J. (2013) Morphology, nectar characteristics and avian pollinators in five Andean *Puya*

- species (*Bromeliaceae*). *Acta Oecol.* 51: 54–61, ills. <https://doi.org/10.1016/j.actao.2013.05.010>.
- Jabaily, R. S. & Sytsma, K. J. (2010) Phylogenetics of *Puya* (*Bromeliaceae*): Placement, major lineages, and evolution of Chilean species. *Amer. J. Bot.* 97(2): 337–356, ills., map. <https://doi.org/10.3732/ajb.0900107>.
- Jabaily, R. S. & Sytsma, K. J. (2013) Historical biogeography and life-history evolution of Andean *Puya* (*Bromeliaceae*). *Bot. J. Linn. Soc.* 171(1): 201–224, ills. <https://doi.org/10.1111/j.1095-8339.2012.01307.x>.
- Manzanares, J. M. (2005) Jewels of the jungle. *Bromeliaceae* of Ecuador. Part II. *Pitcairnioideae*. Quito (EC): Published by the author.
- Manzanares, J. M. (2011) *Bromeliaceae*. In: León-Yáñez, S. & al. (eds.): Libro rojo de las plantas endémicas del Ecuador. Ed. 2; pp. 214–245. Quito (EC): Herbario QCA, Pontificia Universidad Católica del Ecuador.
- Miller, G. A. (1994) Functional significance of inflorescence pubescence in tropical alpine species of *Puya*. In Rundell, P. W. & al. (eds.), *Tropical alpine environments: Plant form and function*; pp. 195–213. Cambridge (GB): Cambridge University Press.
- Oliva-Esteve, F. (2000) *Bromeliads*. Caracas (VE): Armitano Editores.
- Oliva-Esteve, F. (2002) *Bromeliaceae* III. Caracas (VE): Producciones Oliva Esteve.
- Oliva-Esteve, F. & Steyermark, J. (1987) *Bromeliaceae* [sic!] of Venezuela. Caracas (VE): Armitano Editores.
- Quezada, I. M. [et al. 2014], Zotz, G. & Gianoli, E. (2014) Latitudinal variation in the degree of Crassulacean Acid Metabolism in *Puya chilensis*. *Pl. Biol. (Stuttgart)* 16: 848–852, map, ill., diags. <https://doi.org/10.1111/plb.12181>.
- Rauh, W. (1966) The Bromeliads of the Peruvian Andes. *Bromeliad Soc. Bull.* 16(2): 28–39, ills. <http://journal.bsi.org/V16/2/>
- Rauh, W. (1985) *Puya graffii*, a new dwarf *Puya* from southern Venezuela. *J. Bromeliad Soc.* 35(1): 21–23, ills.
- Rauh, W. (1990) *Bromelien*. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Salazar Castillo, J. [et al. 2012], Caceres de Baldarrago, F. & Poma, I. (2012) *Puya raimondii*. La regina delle Ande. The Queen of the Andes. *Cactus & Co.* 15(4): 28–51, ills.
- Salinas, L. [et al. 2007], Arana, C. & Suni, M. (2007) El néctar de especies de *Puya* como recurso para picaflores Altoandinos de Ancash, Perú. *Revista Peruana Biol.* 14(1): 129–134, map, ills.
- Schulte, K. & Zizka, G. (2008) Multi locus plastid phylogeny of *Bromelioideae* (*Bromeliaceae*) and the taxonomic utility of petal appendages and pollen characters. *Candollea* 63(2): 209–225. [http://www.ville-ge.ch/cjb/publications\\_candollea\\_632.php](http://www.ville-ge.ch/cjb/publications_candollea_632.php)
- Schulte, K. [et al. 2009], Barfuss, M. H. & Zizka, G. (2009) Phylogeny of *Bromelioideae* (*Bromeliaceae*) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molec. Phylog. Evol.* 51(2): 327–339. <https://doi.org/10.1016/j.ympev.2009.02.003>
- Smith, L. B. & Downs, R. J. (1974) *Flora Neotropica*. Monograph No. 14 [*Bromeliaceae*]. Part 1: *Pitcairnioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/4393694>
- Subils, R. (2009) *Bromeliaceae*, Bromeliáceas. In: Kiesling, R. (ed.): *Flora de San Juan, IV*: 340–363, ills., keys. Mendoza (AR): Zeta Editores.
- Varadarajan, G. S. (1989) Genus *Puya* Molina (*Pitcairnioideae*): Relocation of several rare species and some preliminary remarks on geographic distributions and species divergence (continued). *J. Bromeliad Soc.* 39(1): 3–7, ills.
- Vásquez, R. C. & Ibisch, P. L. (2007) *Puya pachyphylla* sp. nov. (*Bromeliaceae*) and new synonyms of *Puya tuberosa* from Bolivia. *J. Bromeliad Soc.* 57(3): 102–111, ills.
- Wisnev, M. (2016) Some rarely seen *Puya* at the Huntington Botanical Gardens. *J. Bromeliad Soc.* 63(3–6): 159–179, ills.
- Zizka, G. [et al. 2002], Trumpler, K. & Zöllner, O. (2002) Revision of the genus *Ochagavia* (*Bromeliaceae*, *Bromelioideae*). *Willdenowia* 32(2): 331–350, ills., map, key. <https://www.jstor.org/stable/3997641>
- Zizka, G. [et al. 2013], Schneider, J. V., Schulte, K. & Novoa, P. (2013) Taxonomic revision of the Chilean *Puya* species (*Puyoideae*, *Bromeliaceae*), with special notes on the *Puya alpestris*-*Puya berteroniana* species complex. *Brittonia* 65(4): 387–407, ills., key. <https://doi.org/10.1007/s12228-012-9290-9>.



## Sincoraea BROMELIACEAE

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**Sincoraea** Ule (Bot. Jahrb. Syst. 42: 191, 1909).  
**Type:** *Sincoraea amoena* Ule [typification by inference; this is the only taxon included in the genus]. — **Bromelioideae** — **Lit:** Louzada & Wanderley (2010: monograph, as *Orthophytum*); Louzada & Wanderley (2017: synopsis, key).  
**Distr:** E Brazil (Bahia, Minas Gerais: mostly Serra do Espinhaço Range).

Perennial terrestrial saxicolous rosette plants, stoloniferous; **Ros** sessile or at most with a short stem covered by leaf sheaths; **L** tightly congested, (very) numerous, straight, arching or somewhat falcate, sheaths imbricate, distinct from the lamina, triangular, lepidote to glabrous, serrate, **L** lamina linear-triangular to narrowly triangular, (sub-) coriaceous to stiffly succulent, flat or canaliculate, (sparsely) lepidote on both faces or rarely adaxially glabrous, apex often a pungent spine, margins serrate with laxly to densely arranged spines; **Inf** sessile, simple or compound, inner rosette leaves and peduncular bracts becoming bright pink or red or red with a white or green base at the start of flowering and changing again to green or grey-green after anthesis; peduncular **Bra** gradually diminishing in size, outer

similar to the foliage leaves; floral **Bra** green or red, with pungent tip and serrate to serrulate margins; **Fl** sessile, hermaphrodite; **Sep** free, (sub-) erect, asymmetrical (rarely symmetrical), acute, acuminate, mucronate, with glandular trichomes (except *S. hatschbachii*); **Pet** free or forming an epigynous tube, suberect or upper parts spreading, white or greenish, 3–4.8 × longer than wide, spatulate, obtuse, with 2 callosities laterally to the filaments, appendages sacciform, lacerate or digitate; **St** included; **Fil** filiform, unequal, outer free, inner adnate to the petals; **Anth** dorsifixed, obtuse; **Ov** inferior; **Sty** long-filiform; **Sti** ± erect, 3-parted; **Fr** ovoid capsules with persistent sepals, 5–10 × 6–8 mm, greenish or white; **Se** ovate, striate, 1–2 × 0.6–1.5 mm, 30–100 per fruit.

*Sincoraea* numbers 11 species, many of them ± distinctly succulent. Until recently, the taxa here classified were treated as part of *Orthophytum* s.l. The widely circumscribed *Orthophytum* was found to be polyphyletic in several recent molecular studies (Louzada & al. 2014, Silvestro & al. 2014, Evans & al. 2015, Leme & al. 2017), where the “*amoenum* clade” (i.e. the species now segregated as *Sincoraea*) was found as sister to *Lapanthus* (not considered to include succulents), *Cryptanthus* and *Orthophytum* s.s. (see there for a fuller discussion). Recognizing the “*amoenum* clade” at generic level was first proposed in the unpublished thesis of Louzada (2012).

*Sincoraea* differs from *Orthophytum* s.s. in its acaulescent rosettes with sessile, congested, simple or compound inflorescences, and consistently

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white flowers. At flowering time, *Sincoraea* species are notable for the highly coloured (red, pink, in some species with white or green base) inner rosette leaves and peduncular bracts, and the rosette as a whole can be regarded as a highly conspicuous pseudanthium. The colouration largely disappears again after anthesis is completed.

**Succulence:** Many taxa grow in xeric habitats, often in association with cacti and other succulents. Horres & Zizka (1995) found a degree of succulence similar to that of many *bona-fide* succulents in *S. burle-marxii*. This and other succulent species have thickly fleshy, rigid leaves with considerable amounts of water storage tissue, while the other species have  $\pm$  coriaceous to leathery leaves. Succulence is very much a matter of degree, and only the most succulent taxa are covered in this handbook.

**Horticulture:** Species of *Sincoraea* are only occasionally seen in cultivation. They easily grow in collections of succulents and xerophytes, and offer a spectacular sight when flowering, but are rather uninteresting otherwise. The flowers are diurnal. Individual flowers last only a single day, but flowering of an inflorescence extends over 2–3 weeks (Herndon 2018: for the non-succulent *S. heleniceae*).

The following intergeneric hybrids have been obtained in cultivation (the respective nothogeneric

names still reflect their traditional classification as *Orthophytum*): *Sincoraea*  $\times$  *Aechmea* =  $\times$ *Orthomea*, *Sincoraea*  $\times$  *Neoglaziovia* =  $\times$ *Orthoglaziovia*, *Sincoraea*  $\times$  *Neoregelia* =  $\times$ *Neophytum*, and *Sincoraea*  $\times$  *Cryptanthus* =  $\times$ *Orthoanthus* (see separate entries for all of them in this handbook).

**S. albopicta** (Philcox) Louzada & Wanderley (J. Bromeliad Soc. 66(1): 10, ill. (p. 11), 2017).

**Type:** Brazil, Bahia (Storr 122 [CEPEC, K]). —

**Lit:** Louzada & Wanderley (2010: 3–5, 14, with ills., as *Orthophytum*). **Dist:** E Brazil (Bahia: Chapada Diamantina: Mucugé, Andaraí); rock outcrops in grassland of Campo Rupestre vegetation, 700–1500 m. – Fig. 1.

$\equiv$  *Orthophytum albopictum* Philcox (1985).

**Ros** acaulescent or with a stem to 3  $\times$  2.5–3.5 cm, offsetting with short stolons; **L** numerous, flatly spreading or slightly arched, coriaceous, sheaths broadly triangular, 0.6–3  $\times$  1.1–3.2 cm, both faces glabrous or lepidote abaxially near the tip, margins serrate, **L** lamina linear-triangular, 8–24  $\times$  0.8–2 cm, flat, green to greenish-red, basal part red at flowering time and adaxially with a white-lanate base, otherwise adaxially glabrous, abaxially densely lepidote, margins subclaxly serrate, **Sp** antrorse, 0.4–1.2 (–2) mm; **Inf** sessile, compound and head-like, many-flowered; primary **Bra** deltoid-lanceolate, 1.7–3.8  $\times$  1.6–1.7 cm, the

**Fig. 1** *Sincoraea albopicta* (Eggli 1249: Brazil; Bahia, near Mucugé). (Copyright: U. Eggli)





outer transitional to the inner rosette leaves and red with white-lanate base, the inner entirely white-lanate, all with serrate margins; floral **Bra** triangular,  $\pm 15 \times 10$  mm, mucronulate, asymmetrical, ecarinate, green, lepidote, serrate; **Fl** tubular with slightly spreading limb; **Sep** narrowly triangular,  $\pm 12\text{--}14 \times 4\text{--}5$  mm, mucronulate, asymmetrical, green, carinate, lepidote, entire; **Pet** linear-spatulate,  $\pm 18 \times 4$  mm, obtuse, white, basally with simple hairs, with 2 lacerate sacciform appendages  $\pm 6$  mm above the base, and with 2 conspicuous elongate callosities; outer **Fil** 9 mm, inner 3 mm; **Anth** 4 mm, yellow, not apiculate; **Ov** trigonous; **Sty**  $\pm 1.3$  mm; **Fr** and **Se** unknown.

**S. burle-marxii** (L. B. Smith & Read) Louzada & Wanderley (J. Bromeliad Soc. 66(1): 10, ill. (p. 11), 2017). **Type:** Brazil, Bahia (*Burle-Marx* s.n. in *Bogner* 1311 [US]). — **Lit:** Louzada & Wanderley (2010: 7–9, 14, with ills., as *Orthophytum*). **Distr:** E Brazil (Bahia): Lençóis, Morro do Chapéu; rocky outcrops in grassland, usually in full sun, 900–1400 m. **I:** Braun & Esteves Pereira (2006: 161); Roguenant & al. (2016: 609); both as *Orthophytum*; Moonen (2018). — Fig. 2.

≡ *Orthophytum burle-marxii* L. B. Smith & Read (1979); **incl.** *Orthophytum burle-marxii* var. *seabrae* Rauh (1985); **incl.** *Orthophytum roseum* Leme (2010).

**Ros** acaulescent, stoloniferous, with short stems to  $2.5 \times 4$  cm; **L** numerous, flatly spreading or arching, sheath broadly triangular or ovate-

triangular,  $1\text{--}3 \times 1\text{--}4$  cm, white-greenish, glabrous or rarely sparsely lepidote, serrate, **L** lamina linear-triangular,  $12.8\text{--}53 \times 1.5\text{--}2.5$  cm, attenuate, strongly coriaceous, red or green, cinereous, adaxially lepidote except the glabrous base, abaxially densely lepidote, margins serrate, **Sp** antrorse, 1–2 mm; **Inf** sessile, compound and head-like; outer primary **Bra** transitional to the inner rosette leaves that become red-flushed during flowering time, the inner triangular or triangular-lanceolate,  $2.2\text{--}5.5 \times 1\text{--}6$  cm, red, coriaceous, sparsely lepidote, serrate; floral **Bra** some rudimentary, otherwise triangular,  $14\text{--}48 \times 8\text{--}37$  mm, mucronulate, subcoriaceous, red, ecarinate, glabrous, serrate; **Fl** tubular with slightly spreading limb, with an epigynous tube  $\pm 2$  mm long; **Sep** narrowly triangular,  $20 \times 4\text{--}6$  mm, acuminate or mucronulate, asymmetrical, red, carinate, sparsely lepidote, entire; **Pet** linear-spatulate,  $18\text{--}25 \times 6$  mm, subacute, white, glabrous, with 2 sacciform lacerate appendages  $\pm 7$  mm above the base and conspicuous oblong callosities; outer **Fil**  $\pm 14$  mm, inner **Fil**  $\pm 0.5$  mm; **Anth**  $\pm 4.5$  mm, yellow; **Ov** trigonous, not further described; **Fr** and **Se** unknown.

Similar to the non-succulent *S. heleniceae* with hardly thickened leaves and a green-coloured zone around the inflorescence (vs. red in *S. burle-marxii*).

**S. hatschbachii** (Leme) Louzada & Wanderley (J. Bromeliad Soc. 66(1): 13, ill. (p. 12), 2017).

**Fig. 2** *Sincoraea burle-marxii* (Supthut 8935: Brazil; Bahia, near Andaraí). (Copyright: U. Eggli)





**Type:** Brazil, Bahia (*Hatschbach & Barbosa* 56,827 [MBM]). — **Lit:** Louzada & Wanderley (2010: 9–10, 14, with ills., as *Orthophytum*). **Distr:** E Brazil (Bahia: Abaíra, Rio de Contas); rock outcrops, in full sun or in the shade near streams, 1300 m.

≡ *Orthophytum hatschbachii* Leme (1995).

**Ros** subcaulescent, stem to 3–4.2 × 3 cm, stoloniferous; **L** ± 30, horizontally spreading, sheaths broadly triangular to broadly ovate, 0.5–3 × 0.8–4 cm, greenish-white, glabrous, serrate, **L** lamina linear-triangular, 6.5–33 × 0.7–1.8 cm, stiffly coriaceous, slightly canaliculate, red with greenish-white base, adaxially glabrous or lepidote, abaxially sparsely lepidote, margins strongly serrate, **Sp** straight to antrorse, (1.7–) 2–3.5 mm, ± 15 mm apart; **Inf** sessile, simple, head-like, many-flowered; outer primary **Bra** transitional to the inner rosette leaves that become red-flushed during flowering time, not further described; floral **Bra** triangular, 20–25 × 9–23 mm, symmetrical or asymmetrical, coriaceous, green, glabrous, carinate, serrate, rudimentary floral bracts absent; **Fl** narrowly tubular, with a 2.5 mm long epigynous tube; **Sep** narrowly ovate, 12 × 3 mm, asymmetrical, mucronulate, green, carinate, glabrous, entire; **Pet** linear-spatulate, 17 × 4 mm, obtuse, erect, with only the very tips spreading, white, glabrous, with 2 sacciform lacerate appendages 4 mm above the base and 2 conspicuous callosities; outer **Fil** ± 10 mm, inner **Fil** ± 2.5 mm and adnate to the petals; **Anth** 3 mm, yellow, apiculate; **Ov** trigonous; **Sty** 10 mm; **Fr** and **Se** unknown.

Similar to *S. burle-marxii* and the non-succulent *S. heleniceae*.

**S. navioides** (L. B. Smith) Louzada & Wanderley (J. Bromeliad Soc. 66(1): 14, 2017). **Type:** Brazil, Bahia (*Foster & Foster* 90 [GH, R, SP, US]). — **Lit:** Louzada & Wanderley (2010: 17–18, 25, with ills., as *Orthophytum*). **Distr:** E Brazil (Bahia: Jacobina); shaded rocks in dry forests.

≡ *Cryptanthopsis navioides* L. B. Smith (1940)

≡ *Orthophytum navioides* (L. B. Smith) L. B. Smith (1955).

**Ros** subcaulescent, stoloniferous, with a short stem ± 2 × 1.5 cm; **L** numerous, flatly spreading or arching, sheath triangular, ± 1 × 1.5 cm, white, glabrous, serrate, **L** lamina linear-triangular, 8–23 × 0.4–0.7 cm, attenuate, coriaceous, flat or slightly canaliculate, green, innermost reddish, both faces sparsely lepidote, margins serrate, **Sp** antrorse or retrorse, 1–1.5 mm; **Inf** sessile, simple and head-like, many-flowered; outer primary **Bra** transitional to the inner rosette leaves that become red-flushed during flowering time, not further described; floral **Bra** triangular, ± 20 × 10 mm, subcoriaceous, carinate, lepidote, serrate, rudimentary floral bracts absent; **Fl** narrowly tubular with spreading limb, with an epigynous tube ± 1.5 mm; **Sep** narrowly triangular, 20–30 × 5 mm, acuminate, green, with glandular trichomes, carinate, entire; **Pet** linear-spatulate, 25–30 × 4 mm, subacute, white, glabrous, with 2 sacciform lacerate appendages ± 3 mm above the base and 2 narrowly oblong callosities ± ¾ as long as the filaments; outer **Fil** ± 20 mm, free part of inner **Fil** ± 9 mm; **Anth** yellow, 2–2.3 mm; **Ov** trigonous; **Sty** 20 mm; **Sti** capitate; **Fr** and **Se** unknown.

This species is one of the most extreme xerophytes of the genus (Rauh 1990). It shows similarities with the hardly succulent *S. mucugensis*, which differs by having much shorter leaves and shorter flowers. *S. navioides* has been successfully crossed with *Aechmea* (see × *Orthomea*) and *Cryptanthus* (see × *Orthoanthus*).

## References

- Braun, P. J. & Esteves Pereira, E. (2006) Succulent and xeromorphic Bromeliads of Brazil. Part 3. *Encholirium maximum*, *Orthophytum burle-marxii* and *Dyckia goehringii*. Cact. Succ. J. (US) 78(4): 160–164, ills. [https://doi.org/10.2985/0007-9367\(2006\)78\[160:SAXBOB\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2006)78[160:SAXBOB]2.0.CO;2).
- Evans, T. M. [ & al. 2015], Jabaily, R. S., Gelli de Faria, A. P., Oliveira F. de Sousa, L. de, Wendt, T. & Brown, G. K. (2015) Phylogenetic relationships in *Bromelioideae* subfamily *Bromelioideae* based on chloroplast DNA sequence data. Syst. Bot. 40(1): 116–128. <https://doi.org/10.1600/036364415X686413>.
- Herndon, A. (2018) Flowering behavior of some *Sincoraea* species in cultivation. 1. *Sincoraea heleniceae*. J. Bromeliad Soc. 67(1): 50–60, ills.

- Horres, R. & Zizka, G. (1995) Untersuchungen zur Blattsukkulenz bei *Bromeliaceae*. Beitr. Biol. Pfl. 69(1): 43–76, ills.
- Leme, E. M. C. [ & al. 2017], Heller, S., Zizka, G. & Halbritter, H. (2017) New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (*Bromeliaceae: Bromelioideae*) based on neglected morphological traits and molecular phylogeny. Phytotaxa 318(1): 1–88, ills., maps, key. <https://doi.org/10.11646/phytotaxa.318.1.1>
- Louzada, R. B. (2012) Revisão taxonômica e filogenia de *Orthophytum* (*Bromeliaceae, Bromelioideae*). São Paulo (BR): Universidade de São Paulo, unpublished Ph.D. thesis.
- Louzada, R. B. & Wanderley, M. G. L. (2010) Revision of *Orthophytum* (*Bromeliaceae*): The species with sessile inflorescences. Phytotaxa 13: 1–26, ills., key.
- Louzada, R. B. & Wanderley, M. G. L. (2017) Re-establishment of *Sincoraea* (*Bromeliaceae*). J. Bromeliad Soc. 66(1): 6–19, ills., key.
- Louzada, R. B. [ & al. 2014], Schulte, K., Wanderley, M. G. L., Silvestro, D., Zizka, G., Barfuss, M. H. & Palma-Silva, C. (2014) Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (*Bromelioideae, Bromeliaceae*) and its implications on morphological character evolution. Molec. Phylogen. Evol. 77: 54–64. <https://doi.org/10.1016/j.ympev.2014.03.007>
- Moonen, J. (2018) *Sincoraea burle-marxii* — eine terrestrische Schönheit aus Bahia, Brasilien/a terrestrial beauty from Bahia, Brazil. Bromelie 2018(1): 4-6, ills.
- Rauh, W. (1990) Bromelien. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Roguenant, A. [ & al. 2016], Lecoufle, M. & Raynal-Roques, A. (2016) Les Broméliacées. Approche panoramique d'une grande famille "américaine". Paris (FR): Belin.
- Silvestro, D. [ & al. 2014], Zizka, G. & Schulte, K. (2014) Disentangling the effects of key innovations on the diversification of *Bromelioideae* (*Bromeliaceae*). Evolution 68(1): 163–175. <https://doi.org/10.1111/evo.12236>





## Tillandsia BROMELIACEAE

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- Tillandsia** Linné (Spec. Pl. [ed. 1], 286, 1753). **Type:** *Tillandsia utriculata* Linné. — **Tillandsioideae** — **Tillandsieae** — **Lit:** Rauh (1970: ill. synopsis); Smith & Downs (1977: 665–1069, Fl. Neotropica); Rauh (1990: ill. synopsis); Shimizu (1992: ill. synopsis); Roguenant (2001: ill. synopsis); Isley (2009: ill. synopsis); Magalhães & Mariath (2012: seed anatomy); Donadio & al. (2015: morphological phylogeny subgen. *Diaphoranthema*); Barfuss & al. (2016: phylogeny/classification *Tillandsioideae*); Granados Mendoza & al. (2017: phylogeny). **Distr:** S USA to Chile and Argentina. **Etym:** For Elias Erixi Tillandz (also Tillands or Til-Landz, later Tillander) (1640–1693), Swedish-born Finish physician and botanist at the Academy of Turku, and author of the first flora of Finland.
- Incl.** *Renalmia* Linné (1753) (*nomen rejiciendum*, Art. 56.1). **Type:** *Renalmia paniculata* Linné.
- Incl.** *Caraguata* Adanson (1763) (*nom. illeg.*, Art. 52.1). **Type:** *Tillandsia utriculata* Linné.
- Incl.** *Bonapartea* Ruiz & Pavón (1802). **Type:** *Bonapartea juncea* Ruiz & Pavón.
- Incl.** *Misandra* Dietrich (1819) (*nom. illeg.*, Art. 52.1). **Type:** *Bonapartea juncea* Ruiz & Pavón.
- Incl.** *Acanthospora* Sprengel (1825) (*nom. illeg.*, Art. 52.1). **Type:** *Bonapartea juncea* Ruiz & Pavón.
- Incl.** *Dendropogon* Rafinesque (1825). **Type:** *Renalmia usneoides* Linné.
- Incl.** *Amalia* Endlicher (1837) (*nom. inval.*, ICN Art. 36.1a). **Type:** not typified.
- Incl.** *Bonapartea* Sweet (1839) (*nom. inval.*, Art. 61.1?). **Type:** *Bonapartea juncea* Ruiz & Pavón.
- Incl.** *Strepsia* Nuttall ex Steudel (1841) (*nom. illeg.*, Art. 52.1). **Type:** *Renalmia usneoides* Linné.
- Incl.** *Allardtia* A. Dietrich (1852). **Type:** *Allardtia cyanea* A. Dietrich.
- Incl.** *Anoplophytum* Beer (1854). **Type:** *Tillandsia stricta* Solander.
- Incl.** *Diaphoranthema* Beer (1854). **Type:** *Renalmia recurvata* Linné.
- Incl.** *Platystachys* K. Koch (1854). **Type:** *Allardtia cyanea* A. Dietrich.
- Incl.** *Phytarrhiza* Visiani (1855). **Type:** *Tillandsia duratii* Visiani.
- Incl.** *Pityrophyllum* Beer (1857). **Type:** *Tillandsia erubescens* Schlechtendal.
- Incl.** *Wallisia* E. Morren (1870). **Type:** *Tillandsia hamaleana* E. Morren.
- Incl.** *Viridantha* Espejo (2002). **Type:** *Tillandsia plumosa* Baker.

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Acaulescent or sometimes caulescent herbs of very variable habit; **L** rosulate or fasciculate or distributed along the stem, polystichous or less

often distichous, entire, **L** lamina tongue-shaped to narrowly triangular or linear, leaf-scales symmetric to asymmetric and extended on one side; **Inf** usually with a distinct peduncle; floriferous **Inf** part various, usually consisting of distichously flowered spikes or sometimes reduced to a single polystichously flowered spike by the reduction of the spikes to single flowers, or rarely the whole inflorescence reduced to a single flower; floral **Bra** conspicuous to minute; **Fl** bisexual,  $\pm$  perigynous, seemingly pedicellate but in fact with an expanded receptacle looking like a pedicel; **Sep** convolute, usually symmetrical, free or equally or posteriorly joined; **Pet** free, usually naked; **St** of various lengths relative to petals and pistil; **Ov** superior, glabrous, ovules usually many, caudate; **Fr** septicidal capsules; **Se** narrowly cylindrical or fusiform, with a basal, plumose, straight, white appendage.

*Tillandsia* is the largest genus in the family, with  $\pm 690$  species (Gouda & al. 2012+). The genera *Tillandsia* and *Vriesea* are traditionally distinguished from each other by the absence (in the first) or presence (in the latter) of ligulae on the claw of the petals. This led to the transfer of numerous species from *Tillandsia* to *Vriesea*, resulting in a growing group of *Tillandsia*-like *Vrieseas*. The character has been found to be marginally useful, however, to distinguish natural groups within the family (Brown & Terry 1992, Schulte & Zizka 2008). Moreover, in at least one species (*T. incurva* Griseb.), ligulae are present in some populations, but absent from others (Gouda 1987). Recently, this group has been transferred back to *Tillandsia* (Grant 1993). According to Magalhães & Mariath (2012), the structure of the plumose seed appendages could provide a better character to separate *Tillandsia* from *Vriesea*, since seeds of the former have a double superimposed parachute-like plumose appendage derived from the exo- and mesotesta, as well as from the endotesta, while *Vriesea* seeds have a single such structure without participation of the endotesta. The derivation of the plumose appendage from the testa was probably first described by Morra & al. (2002).

In the last monograph of the family (Smith & Downs 1977), 7 subgenera were recognized.

Subgenus *Pseudo-catopsis* was subsequently elevated to genus level as *Racinaea* by Smith & Spencer (1993). Recent molecular DNA work by Barfuss & al. (2016) supports this move and shows that the traditional subgeneric classification is not fully supported. As a consequence, subgenus *Aerobia* (Mez 1896) was resurrected for 50 species that were previously placed either in subgen. *Allardtia* or subgenus *Anoplophytum*. The revised subgeneric classification is as follows:

- [1] Subgen. *Allardtia* (A. Dietrich) Baker 1888: **St** included, exceeding the claw of the petals; **Sty** slender, much longer than the ovary; **Fil** straight. — 200 species, 12 of them succulent.
- [2] Subgen. *Anoplophytum* (Beer) Baker 1887: **St** included, equalling the claw of the petals; **Sty** slender, much longer than the ovary; **Fil** strongly plicate. — 104 species, 13 of them succulent.
- [3] Subgen. *Phytarrhiza* (Visiani) Baker 1887: **Pet** blades broad, conspicuous; **St** deeply included; **Sty** short and stout; **L** lamina flat or terete. — 39 species, 7 of them succulent.
- [4] Subgen. *Diaphoranthema* (Beer) Baker 1878: **Pet** blades narrow, inconspicuous; **St** deeply included; **Sty** short and stout; **L** lamina terete, densely cinereous-lepidote. — 30 mostly tiny to small species, 22 of them succulent. Donadio & al. (2015) have recently published a phylogeny of the subgenus based on morphology.
- [5] Subgen. *Tillandsia*: **St** exerted, exceeding the petals; **Pet** erect at anthesis or nearly so, relatively firm; **L** lamina narrowly triangular in most species. — 246 species, 29 of them succulent.
- [6] Subgen. *Pseudalcantarea* Mez 1934: **St** exerted, exceeding the petals; **Pet** spreading at anthesis, rapidly becoming flaccid; **L** lamina tongue-shaped to narrowly triangular. — 5 species, none of them succulent.
- [7] Subgen. *Aerobia* Mez 1896: **St** included, often emerging from the throat of the corolla; **Sty** slender, many times longer than the ovary; **Fil** straight or plicate; **Pet** spreading at anthesis, often with distinct blade; **L** lamina narrowly triangular. — 50 species, most of



them succulent, but not treated here for space reasons.

**Succulence:** Most subgenera contain species that can be variously described as possessing succulent or semi-succulent features at least to some degree, i.e. showing considerable amounts of water-storing tissues in the leaves. Most mesophytic species have funnel-shaped rosettes with inflated leaf sheaths compounding water, and these are — though superficially appearing to have water-storage capacity — not succulent. All xerophytic species are succulent to some extent, but only 83 species are selected here because they have obviously fleshy leaves. They are all from semi-arid to arid areas, where they grow as epiphytes on cacti and small trees, or are saxicolous on rocky surfaces. In the coastal deserts of Peru and Chile, some species grow on the sand dunes in the so-called Loma vegetation belt, without any other vegetation.

**Pollination:** Many species, esp. from the largest subgen. *Tillandsia*, with tubular corolla and exerted stamens and stigma are pollinated by hummingbirds. Birds are attracted by the brightly coloured bracts (often red and yellow) and scentless flowers. Flowers are available over a longer period of time and individual flowers are open for only one or a few days. This is ideal for “trap-line” pollination by birds, where a bird flies a certain route, probably several times a day, from one plant to another. Another group of species, from subgen. *Phytarrhiza*, have open flowers with broad coloured petal blades, and are often strongly fragrant. The bracts are mostly uncoloured and do not have a role in attracting pollinators. The petals have a narrow claw that together form a narrow tube-like structure, accessible only to the long and very slender tongues of moths and butterflies.

Most species of *Tillandsia* are self-incompatible and are dependent on pollinating animals for reproduction. The flowers of monocarpic species, however, are autogamous when not pollinated. Also the small-flowering plants from subgen. *Diaphoranthema* are (partly) autogamous, which explains the pronounced variety of forms within a species and within an area. The flowers of some

species of this group are fragrant, e.g. *T. usneoides*, fragrant during the night only, and probably pollinated by small moths according to Gouda (1995).

**Horticulture:** *Tillandsia* is the subject of considerable horticultural interest. Esp. the xerophytic species are frequently seen in cultivation, no doubt in part due to the availability of synoptical literature aimed at hobby collectors, such as Rauh (1990). Several profusely illustrated accounts (e.g. Isley (1987), Isley (2009) or Shimizu (1992)) have further added to the popularity of the genus.

**T. aizoides** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 866, 1896). **Type:** Argentina, La Rioja (*Hieronymus & Niederlein* 850 [B, CORD]). — **Distr:** SW and S Bolivia (Potosí, Tarija), Argentina (widespread); epiphytic on twigs, or sometimes saxicolous, 120–2800 m.

[4] Plant small, long-caulescent, forming dense clusters or few-branched; stem to 5 cm, many from a single point; **L** densely rosulate, usually  $\pm 1$  (–2) cm  $\times$  2 mm; **L** sheaths 0.5 cm, broadly ovate, scarious, with broad nerveless margins, 4- to many-veined, glabrous except at the distal end, distinct from the lamina; **L** lamina stout, rigid, densely cinereous-lepidote, erect to somewhat divergent, sometimes slightly secund, angular-subulate, convex below, with a furrow adaxially, apex pungent; **Inf** 1-flowered, often with a reduced flower at the apex, peduncle naked except for 1 or 2 bracts below the flower or with a single bract midway, from very short to 2 cm, angled, glabrous; upper peduncular **Bra** like the floral bracts, elliptic, often carinate, sulcate and strongly veined, glabrous, acute; floral **Bra** erect, shorter than the sepals, 5.5  $\times$  3.5 mm, elliptic, membranous, at least 3-veined, ecarinate, glabrous, green, broadly rounded or subapiculate; **Sep** 7–8  $\times$  3 mm, elliptic or obovate-oblong, scarious, 5- to 7-veined, all connate for 1–2.5 mm, ecarinate, green tinged red, glabrous, broadly rounded or subapiculate; **Pet** slightly longer than the sepals, spatulate, 13  $\times$  3 mm, cream-coloured with purple-red speckles, brownish when dry, blade obscure or distinct and then suborbicular; **St** all of equal length, 6 mm, deeply included, exceeding the style; **Fil** flaccid; **Anth** basifixed, 1.4 mm; **Ov**

**Fig. 1** *Tillandsia albertiana*. (Copyright: E. J. Gouda)



4 mm, subovoid; **Sty** slender, shorter than the ovary; **Sti** capitate.

**T. albertiana** Verveorst (Bromeliad Soc. Bull. 19: 121, 128, ills., 1969). **Type:** Argentina, Salta (Verveorst 7255 [LIL, US]). — **Distr:** NE Argentina (Salta); lithophytic on rocks and cliffs, altitude not recorded. — Fig. 1.

[2] Plant short- to long-caulescent, forming dense clusters or laxly pulvinate; stem much branched, 3 mm  $\varnothing$ ; **L** distichous; **L** sheaths imbricate, making the stem appear 6 mm thick, 2–2.5  $\times$  1.4 cm, ovate, clasping the stem with overlapping margins, with broad membranous margins, veined or slightly rugose, densely appressed-lepidote abaxially and glabrous adaxially except at the distal end, green or brown, tapering into the lamina; **L** lamina linear-triangular, fleshy, at the base with extending trichomes at the margins, 5–9 (–17)  $\times$  0.4–0.8 cm, dark green flushed with red or red-striated at the base, appressed-lepidote, divergent to less often spreading, veined at the base, strongly canaliculate, convex or involute-subulate when dry, apex abruptly obtuse; **Inf** 1-flowered (with a short extended rachis), erect; peduncle  $\pm$  2 cm, concealed by the leaves; peduncular **Bra** 2, excl. lamina 1.8  $\times$  0.85 cm, the sheathing part glabrous except abaxially towards the apex, with foliaceous lamina, obtuse; floral **Bra** (excl. acumen) 17–20 (–23)  $\times$  9 mm, ovate-

oblong, clasping the flower with slightly overlapping margins, margins hyaline, veined, glabrous at the base and adaxially to subdensely appressed-lepidote abaxially, green or with reddish apical margins, rounded and fleshy-acuminate; **Fl** subsessile; **Sep** 17–24  $\times$  4–6 mm, narrowly oblong, slightly contracted in the centre, thin, with membranous margins, faintly veined, but distinctly veined when dry, free, ecarinate, green, tinged wine-red at the apex, glabrous or with a few trichomes abaxially, rounded; **Pet** claw narrow with a broad suborbicular blade or spatulate, 28–44  $\times$  to 11 mm, margins slightly crenulate, wine-red to bright red, rounded or obtuse; **St** all of equal length, 17–22 mm, included and longer than the style; **Fil** ribbon-like, flat at the base but upwards fleshy, not plicate, green towards the apex; **Anth** subbasifixed, 4 mm, linear, apex obtuse, yellow; **Ov** 5  $\times$  2.5 mm, triangular-ovoid (broadest near the base) to prismatic, gradually contracted into the style; **Sty** slender, 8–17 mm; **Sti** linear, erect, weakly conduplicate.

**T. andicola** Gillies *ex* Baker (J. Bot. 16: 239, 1878). **Type:** Argentina, Mendoza (Gillies s.n. [K, CGE, GH]). — **Distr:** Argentina (Cataramarca, Buenos Aires, San Juan, Mendoza, Río Negro); epiphytic, altitude not recorded.

[4] Plant flowering to 30 cm tall; stem to > 20 cm, branched esp. near the apex; **L** lax, weakly rosulate

or distichous, 4 (–6) cm, cinereous-lepidote with subappressed basally produced scales; **L** sheaths densely imbricate,  $\pm 5$  mm apart on the stem, making it appear 3–4 mm  $\varnothing$ , much broader than the lamina, suborbicular, occasionally with glabrous broad veinless margins, ciliate with long scales, several-veined, usually lepidote except at the extreme base or wholly glabrous in age; **L** lamina 2 mm wide, recurved, veined when dry, subulate, apex acuminate, pungent; **Inf** 1- or 2-flowered (then internode 8 mm long and rachis extended behind the terminal flower), densely lepidote; peduncle  $\pm 0$ –6 cm, bractless or with 1 bract, densely lepidote; peduncular **Bra** lanceolate, involute, lepidote, acuminate; floral **Bra** exceeding the sepals in the first flower to shorter than the sepals in the second one, to  $14 \times 7$  mm, ovate to lanceolate, clasping and closely enveloping the flower, veined, ecarinate,  $2 \times$  as long as the internodes, densely appressed-lepidote, cinereous to green, acuminate or apiculate; **Fl** subsessile; **Sep**  $10$ – $12 \times 3.5$  mm, lanceolate-oblong, with broad hyaline margins, veined, adaxial ones connate for 6 mm, the others less connate, adaxial ones with a strong midvein, green, lepidote from the middle to the apex, apiculate; **Pet** tongue-shaped,  $14 \times 3$  mm, pale white, the blade narrow, rounded; **St** deeply included, exceeding the style; **Anth** basifixed, 1.5 mm, red-orange; **Ov** 3.5 mm, ovoid, contracted into the style; **Sty** stout, 3 mm; **Sti** shortly lobed.

**T. angulosa** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 868, 1896). **Type:** Argentina, La Rioja (*Hieronymus & Niederlein* 851 [B, CORD, F [photo]]). — **Distr:** C Argentina (La Rioja, San Juan, Mendoza); epiphytic in xeric environments; 1160–1200 m.

[4] Plant small, pulvinate, stem to 3 cm, richly branched at the base; **L** weakly polystichous or somewhat distichous (to spirally distichous), to  $1.5 \times \pm 0.2$  cm, coarsely densely cinereous-lepidote; **L** sheaths suborbicular, thin, with broad nerveless margins, many-veined, densely lepidote to glabrous at the base; **L** lamina subtriangular, spreading to recurved, subulate, angled, lower  $\frac{1}{2}$  canaliculate or grooved, apex mucronate; **Inf** 1- (rarely 2-) flowered; peduncle almost none or

short and concealed by the leaves, with a single bract at the base or bractless; peduncular **Bra** ovate, involute, prominently veined, densely lepidote, acute; floral **Bra** slightly to distinctly shorter than the sepals,  $12 \times 7$  mm, ovate, clasping the flower, 5- to 9-veined, sparsely lepidote, acute; **Sep**  $11 \times 4$  mm, triangular-ovate, 7- to 9-veined, almost free or evenly shortly connate, lepidote; **Pet** elliptic,  $10$ – $13 \times 3.5$  mm, brown to yellow, obtuse; **St** included, slightly exceeding the style with part of the anthers; **Fil**  $4$ – $5 \times 0.2$  mm, whitish; **Anth** basifixed,  $\pm 3 \times$  to 0.5 mm; **Ov**  $3.5 \times 2$ – $3$  mm, obovoid-pyriform, gradually contracted into the style; **Sty** slender, 1.5 mm; **Sti** disc-shaped, shortly lobed.

**T. araujei** Mez (in Martius, Fl. Bras. 3(3): 600, t. 112, fig. 2, 1894). **Type** [lecto]: Brazil, Rio de Janeiro (*Glaziou* 16457 [B, B [photo], P]). — **Distr:** SE & S Brazil (Rio de Janeiro, São Paulo, Rio Grande do Sul), Paraguay; saxicolous or very rarely epiphytic, 0–850 m. — Fig. 2.

**Incl.** *Tillandsia araujei* var. *minima* E. Pereira & I. A. Penna (1980).

[2] Plant caulescent, flowering 15–30 cm tall; stem simple or few-branched, often curved; **L** densely polystichous along the stem, 3–7 cm; **L** sheaths short, broadly triangular, glabrous at the base, white; **L** lamina rigid, appressed-lepidote, all upwardly secund, keeled, angled-subulate, trichomes with a brown centre, apex attenuate and pungent; **Inf** simple; peduncle completely covered by the bracts or partly visible, erect or ascending, much exceeding the leaves, slender, glabrous, exposed part red; peduncular **Bra** with thick linear lepidote lamina, imbricate, elliptic or obovate, membranous, rose-coloured, **Inf** spikes sublaex, 3–5 cm, 5- to 12-flowered; floral **Bra** exceeding the sepals,  $20$ – $23 \times 10$ – $12$  mm, ovate, membranous, ecarinate, glabrous except the apex in the lower ones, dark pink-red, broadly acute or the lower ones apiculate; **Fl** sessile, polystichous, erect to slightly divergent, 30 mm; **Sep** ( $12$ –)  $15$ – $17 \times 4.5$  mm, narrowly ovate to lanceolate, with broad hyaline margins, adaxial ones highly connate for  $\pm 11$  mm, adaxial ones carinate, rose-coloured with green base, acute; **Pet** spatulate,  $20$ – $32 \times 8$  mm, white, blade tapering into the



**Fig. 2** *Tillandsia araujei*. (Copyright: E. J. Gouda)

cuneate claw, spreading, rounded or obtuse; **St** 17 mm, included; **Fil** inflated towards the apex, flaccid, lightly plicate near the apex to strongly plicate in the middle; **Anth** basifixed, 2 mm, yellow; **Ov** 3 × 2 mm, obovoid (to pyriform), abruptly contracted into the style; **Sty** slender, 16 mm, exceeding the stamens; **Sti** weakly conduplicate, erect.

There is some variation in succulence between different populations; the small, short-leaved form (var. *minima*) is more succulent than the larger ones.

**T. argentina** C. H. Wright (Bull. Misc. Inform. Kew 1907: 60, 1907). **Type:** Argentina, Córdoba (Stuckert s.n. [K, GH [photo]]). — **Distr:** S Bolivia (Chuquisaca, Tarija), N Argentina (Catamarca, Córdoba, Jujuy, Salta, Tucumán, La Rioja); saxicolous or epiphytic in dry habitats, 450–1950 m. — Fig. 3.



**Fig. 3** *Tillandsia argentina*. (Copyright: E. J. Gouda)

**Incl.** *Tillandsia unca* Baker (1887) (*nom. illeg.*, Art. 53.1).

[2] Plant distinctly short-stemmed, flowering 7–13 cm tall, rosette solitary or few-branched; **L** densely rosulate, the outer greatly reduced, 5.5–10 (–13) cm; **L** sheaths 8–11 × 8–16 mm, broadly triangular-ovate, thin, lustrous, at least the lower ½ glabrous, passing almost imperceptibly into the lamina; **L** lamina very narrowly triangular, linear, rigid, 3–6 mm wide, appressed-lepidote, divergent and often secundly curved upward, often pulvinate, canaliculate, obtusely keeled below or angular-subulate, apex abruptly acute and pungent; **Inf** always simple, shorter than to exceeding the leaves; peduncle hidden by the inner leaves and bracts, erect or ascending, shorter than the leaves, ±0–6 cm, glabrous; lowest peduncular **Bra** foliaceous, imbricate, lanceolate, chartaceous, strongly nerved, glabrous or sparsely pale-lepidote near the apex, stramineous, acuminate; **Inf** spikes



(2–) 3.5–4.5 × (0.7–) 1–1.5 cm, broadly (ob-) lanceolate, strongly complanate, (2- to) 4- to 7-flowered, rachis strongly 4-angled, nearly straight, glabrous, partly exposed; floral **Bra** imbricate, much exceeding the sepals, 19–25 × 7–10 mm, lanceolate or triangular-ovate, subcoriaceous, even or somewhat veined, sublustrous, ecarinate or carinate towards the apex, so narrow as to expose the rachis in part, glabrous throughout, rose-coloured or green, acuminate; **Fl** subsessile; **Sep** 12–18 × 4–5.5 mm, narrowly ovate or elliptic, subequal, free, adaxial ones carinate, green with reddish apex, glabrous, apiculate or broadly obtuse; **Pet** linear or subspatulate, ±30–34 × 6–7.5 mm, margins entire, bright rose-red except at the base, blade scarcely distinct, divergent to strongly recurved, obtuse or rounded-emarginate; **St** ±20 mm, included; **Fil** broadly ribbon-like, flaccid, strongly plicate near the apex, white; **Anth** basifixed, 4–5 mm, linear, cream-coloured to yellow; **Ov** 2.5 mm, subprismatic or subglobose, abruptly contracted into the style; **Sty** slender, 19–24 mm, exceeding the stamens; **Sti** spreading or recurved, conduplicate.

**T. arhiza** Mez (in A. & C. de Candolle, Monogr. Phan. 9: 855, 1896). **Type:** Paraguay, Paraguari (*Balansa* 4747 [P, GH [photo]]). — **Distr:** E Brazil (Minas Gerais), S Paraguay (Paraguari, Guairá); saxicolous, ±540 m.

**Incl.** *Tillandsia rupestris* Mez (1896) ≡ *Tillandsia arhiza* var. *rupestris* (Mez) Hassler (1919); **incl.** *Tillandsia rupestris* var. *pendens* Chodat & Vischer (1916) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Tillandsia breweri* hort. ex D. Butcher (1996) (*nom. inval.*, ICN Art. 29.1).

[3] Plant stout, caulescent; stem to 60 cm; **L** spirally arranged, 20 cm, white-tomentose-lepidote; **L** sheaths elongate, broadly elliptic, amplexicaul, glabrous inside and below the middle outside and densely lepidote upwards; **L** lamina very narrowly triangular, 7–9 mm wide, densely ferruginous or cinereous -lepidote or tomentose-lepidote, erect or divergent and recurved towards the apex, canaliculate or involute-subulate above the middle, apex filiform attenuate; **Inf** often simple or depauperate-compound, distichous; peduncle erect, exceeding the leaves, slender, glabrous;

peduncular **Bra** erect, equalling or exceeding the internodes, sublanceolate, tubular-involute, densely lepidote, acute, apiculate; primary **Bra** like the peduncular bracts, shorter than the spikes, lepidote; **Inf** spikes densely flowered, to 7.5 cm, 1 cm wide, lanceolate, (single/principal one) to linear, 6- to 12-flowered, rachis angled, slightly flexuous; floral **Bra** erect, subimbricate, from distinctly shorter than to slightly exceeding the sepals, 15 mm, narrowly elliptic, clasping the flower, chartaceous, veined, glabrous or the lowest sparsely lepidote, apiculate; **Sep** 12 × 5 mm, elliptic, coriaceous, even, subevenly short-connate for 3 mm, glabrous, acute, obtuse; **Pet** claw narrow with suborbicular blade, 23 mm long, violet; **St** deeply included, exceeding the style; **Anth** linear, apex acute; **Ov** elongate, prismatic.

**T. ariza-juliae** L. B. Smith & J. Jiménez Almonte (Phytologia 6: 433, t. 1, figs. 1–2, 1959). **Type:** Dominican Republic, La Vega (*Ariza Julia* s.n. [US, Herb. J. J. Jiménez]). — **Distr:** Dominican Republic (Santiago Rodríguez, La Vega, Santiago Rodríguez); epiphyte in pine forest or on shrubs, 200–900 m.

[5] Plant stemless, flowering 19 cm tall; **L** ±12, densely cinereous-lepidote; **L** sheaths forming an ovoid pseudobulb 3–4 cm long, orbicular, greatly inflated, green tinged with purple near the margin, abruptly contracted into the lamina; **L** lamina 3–4 × as long as the sheath, erect to convergent, 9– ± 20 cm × 2–4 mm, involute-subulate and nearly straight, narrowly canaliculate, apex attenuate; **Inf** simple or rarely branched; peduncle erect; lowest peduncular **Bra** subfoliaceous, imbricate, the uppermost broadly ovate, subchartaceous, apiculate; primary **Bra** shorter than the axillary branches; **Inf** spikes rather laxly to densely flowered, 8 cm, lanceolate, complanate, 2- to 5- (to 8-) flowered, acute, rachis slightly alate, slender; floral **Bra** imbricate at anthesis, 30 mm, ovate, subchartaceous, veined, ecarinate, >3 × as long as the internodes, densely appressed-lepidote, roseate, acute; **Fl** subsessile; **Sep** 20 mm, oblong, adaxial ones shortly connate, lepidote, apiculate; **Pet** forming an erect tube, size unknown, purple; **St** exerted.



**T. baileyi** Rose *ex* Small (Fl. Southeast. US, 246, 1903). **Type:** USA, Texas (*Bailey* "26" [226] [US]). — **Distr:** S USA (Texas); epiphytic in scattered oak forest, 0–1080 m.

[5] Plant stemless, flowering 20–40 cm tall, forming dense clusters; **L** several, to 40 cm, densely appressed-cinereous lepidote throughout; **L** sheaths forming a pseudobulb 2–5 cm long, ample, ovate, often conspicuously ciliate-lepidote, merging into the lamina; **L** lamina linear, at the base 5 mm wide, contorted or involute-subulate, apex attenuate; **Inf** simple, shorter than to as long as the leaves; peduncle nearly fully concealed by the bracts, erect or ascending, shorter than the leaves, often flexuous, internodes 2–4 mm, upwards decreasing in size, glabrous to cinereous-lepidote upwards at least near the nodes, green; peduncular **Bra** foliaceous but smaller than the leaves, suberect, few ( $\pm 4$ ), basal part (excluding lamina) slightly or not amplexicaulous,  $\pm$  as long as the internodes, upper ones  $2.3\text{--}2.7 \times 1.1$  cm, broadly ovate, abaxially densely pale-lepidote, green, shortly and weakly acuminate; **Inf** spikes, often ascending, (4–)  $8\text{--}10 \times 0.8\text{--}1.2$  cm, linear, complanate, subdensely 6- to 17-flowered; floral **Bra** erect, loosely imbricate, exceeding the sepals,  $20\text{--}23 \times 8\text{--}10$  mm, narrowly ovate-triangular, evenly incurved, closely enveloping the flowers, subchartaceous, margins membranous and with extended scales, smooth or veined, ecarinate, narrow and exposing the rachis in part,  $<2\text{--}3 \times$  as long as the internodes, appressed-cinereous-lepidote, glabrous inside except towards the apex, roseate or green, acutish or fleshy-apiculate; **Fl** with a short pedicel-like receptacle; **Sep** slightly incurved,  $15\text{--}18 \times 4.5\text{--}5$  mm, very narrowly elliptic, chartaceous, with hyaline margins, smooth or veined when dry, evenly short-connate for 1–1.5 mm, adaxial ones carinate, green, subdensely cinereous-lepidote, obtuse; **Pet** forming an erect narrow tube clasping the filaments at the apex, tongue-shaped,  $30\text{--}38 \times 6$  mm near the apex, 2.5 mm wide at the base, lower  $\frac{1}{2}$  hyaline, purple to pale lavender, triangular-acute; **St** in 2 whorls of unequal length,  $\pm 40$  mm, exserted; **Fil** thread-like in the lower  $\frac{1}{2}$  and broadened towards the apex, flat, straight; **Anth** dorsifixed just below the centre,  $4 \times 1.2$  mm before dehiscence, oblong,

base bilobed, apex obtuse, yellow; **Ov**  $4 \times 2$  mm, ellipsoid, gradually contracted into the style; **Sty** slender, 36 mm; **Sti** shortly conduplicate-spiralized.

**T. brealitoensis** L. Hromadnik (Pl. Syst. Evol. 147(3–4): 280, ill., 1984). **Type:** Argentina (*Hromadnik & Hromadnik* 7152b [WU]). — **Distr:** NE Argentina (Salta); epiphytic in bushes,  $\pm 2350$  m.

[4] Plant caulescent, few-branched; stem to 10 cm; **L** densely rosulate, erect, 1.5 cm; **L** sheaths  $5 \times 7$  mm at the base, amplexicaul, veined, lepidote to glabrous towards the base, passing almost imperceptibly into the lamina; **L** lamina narrowly triangular, 1 cm, thickly succulent, cinereous-green, densely appressed-lepidote, apex acute; **Inf** peduncle 1.5–3 cm, glabrous; peduncular **Bra** 1 only, at the base, membranous, lepidote; spikes 1- or 2-flowered; floral **Bra**  $7.6\text{--}11.6 \times 4.8\text{--}6.8$  mm, ovate to triangular, membranous, 9- to 12-veined, lepidote; **Sep**  $7.6\text{--}10 \times 2.8\text{--}3.9$  mm, membranous, 6- to 8-veined, the 2 innermost veins joining the central vein towards the tip of the sepal, evenly shortly connate for 2–3 mm, lepidote; **Pet** tongue-shaped,  $9.9\text{--}12 \times 2.4\text{--}3$  mm, violet to dark violet, rounded; **St** included; **Fil**  $3.5\text{--}4.8$  mm, 1-nerved, pale white; **Anth**  $1.5\text{--}2.1 \times 0.35\text{--}0.55$  mm, orange; **Ov**  $2.8\text{--}4 \times 1.9\text{--}2.5$  mm; **Sty** 1 mm; **Sti** conspicuous.

**T. bulbosa** Hooker (Exot. Fl. 3: t. 173, 1826). **Type:** [icono]: l.c. t. 173. — **Distr:** SE Mexico, Belize, Guatemala, N & E Honduras, Nicaragua, Costa Rica, Panama, Bahamas, Cuba, Jamaica, Dominican Republic, Puerto Rico, Leeward Islands, Trinidad & Tobago, Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Ecuador; epiphytic, 0–1210 m.

$\equiv$  *Platystachys bulbosa* (Hooker) Beer (1856); **incl.** *Tillandsia bulbosa* var. *brasiliensis* Schultes *fil.* (1830); **incl.** *Tillandsia bulbosa* var. *picta* Hooker (1847); **incl.** *Pourretia hanisiana* Morren *ex* E. Morren (1847) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Tillandsia erythraea* Lindley & Paxton (1850)  $\equiv$  *Platystachys erythraea* (Lindley & Paxton) Beer (1856); **incl.** *Tillandsia pumila* Lindley & Paxton (1850); **incl.** *Tillandsia pumila* Grisebach (1865) (*nom. illeg.*, ICN Art. 53.1).

[5] Plant stemless, flowering 10–30 cm tall, very variable in size and colour, often in clumps; **L** 8–15, mostly exceeding the inflorescence, 8–30 cm, outer leaves often reduced and sheath-like; **L** sheaths forming a small ovoid pseudobulb, ample, 1.5–3.5 cm wide, orbicular, greatly inflated, stiffly coriaceous, densely appressed-lepidote towards the apex, brownish to silvery green at the apex, often purple-red at the margins, abruptly constricted into the lamina; **L** lamina fleshy-coriaceous, 10–25 cm × 1–5 mm, pale to very dark lustrous-green, minutely appressed-lepidote, reflexed or often spreading, involute-subulate or mostly flexuous, apex attenuate, pungent; **Inf** simple or subdigitately compound with 2–5 spikes, polystichous, subdense, 7.5–23 cm, green or orange-red; peduncle completely covered by the bracts, erect, 5–15 cm; peduncular **Bra** foliaceous, exceeding the inflorescence, the upper ones often orange-red in part, with foliaceous lamina, axes short but exposed between the spreading bracts, angled, lepidote, often pale-rose; primary **Bra** like the upper peduncular bracts, the upper ones more ovate, the lower ones often exceeding the spikes with the foliaceous lamina, acuminate, clasping the spikes; **Inf** spikes short-stipitate, with a sterile bract at the base, spreading or suberect, dense, 2.5–5 × 0.7–1 cm, lanceolate, complanate, distichously 3- to 6-flowered, acute, with sterile bracts at the apex, rachis sharply angled when dry, nearly straight, lepidote, partly exposed; floral **Bra** erect, imbricate, much exceeding the sepals, 11–19 mm, ovate, somewhat incurved at the apex, subcoriaceous, (obscurely) carinate, 2–4 × as long as the internodes, densely lepidote, acute; **Fl** sessile, contiguous with each other and/or the rachis; **Sep** 10–12 mm, oblong, thin or rigid, with broad veinless margins, veined (only when dry), adaxial ones connate for up to 3 mm, adaxial ones bluntly carinate at the base, glabrous, obtuse or obscurely apiculate; **Pet** forming an erect narrow tube clasping the filaments at the apex, linear, to 40 mm, blue-violet or rarely white, acute; **St** exerted, the 3 longest ± equalling or shorter than the style; **Fil** flat or subterete towards the apex, not plicate; **Anth** dorsifixed at  $\frac{1}{3}$  from the base, 2.5 mm; **Ov** 4 mm, ovoid, tapering into the slender style; **Sti** slender, exceeding the stamens.

**T. burle-marxii** Ehlers (Bromelie 1994(2): 75, ill., 1994). **Type:** Brazil, Bahia (*Burle-Marx* s.n. [WU]). — **Distr:** NE Brazil (Bahia); ecology unknown.

[2] Plant long-caulescent, to 30 cm long and 1.5 cm Ø, forming clumps, repeatedly branched from the bottom; **L** spirally arranged, numerous, erect or bent over to the side, densely upright, 2–4 × 0.4–0.5 cm, very thick and succulent, margins with few asymmetric trichomes, both faces densely cinereous-lepidote, grey; **L** sheaths hiding the stem, 3–6 × to 5 mm, triangular, indistinctly merging into the lamina; **L** lamina erectly imbricate, slightly keeled, 1.5–3.5 cm, subulate, margins involute, outer face convex, apex triangular-acuminate; **Inf** simple, green, glabrous; peduncle partly visible, erect, decurved, exceeding the leaves, to 5 cm, slender, glabrous, light green; peduncular **Bra** few, laxly imbricate leaving the peduncle visible, 2 cm, 1.5 × as long as the internodes, elliptic, densely lepidote, acute; **Inf** spikes arching, subax, 3–4 × 1.5 cm, with 3–5 polystichously arranged flowers, rachis partly exposed; floral **Bra** exceeding the sepals, 11–15 (–19) × 7–10 mm, elliptic or suborbicular, membranous, margins hyaline, veined, ecarinate or carinate towards the (fleshy) apex, cinereously lepidote at the apex at both faces, yellow-green, cuspidate at the acute apex; **Sep** strongly incurved at the apex, 10–14 × 3–5 mm, narrowly elliptic, membranous, smooth or veined (when dry), adaxial ones highly connate for 5–9 mm and carinate, yellow-green, glabrous, acute or narrowly rounded-obtuse; **Pet** tongue-shaped, 20–23 × 5–6.5 mm, base narrowed to 3 mm, margins erose-dentate, white, the blade tip margins divergent, almost rounded or rounded-emarginate; **St** 12 mm, included; **Fil** 10–12 × 1–1.2 mm, broadly ribbon-like, the upper  $\frac{1}{2}$  slightly plicate, white; **Anth** basifixed, 2 × 0.3 mm, linear, cream-coloured; **Ov** 4–5 × 2.5 mm, ovoid, contracted into the style; **Sty** slender, to 9 × 0.4–0.5 mm; **Sti** shortly linear, hardly wider than the style, lobes erect.

**T. butzii** Mez (in Engler, A. (ed.), Pflanzenr. IV(32): 636, 1934). **Type:** Mexico, Veracruz (*Schiede* s.n. [B]). — **Distr:** SE Mexico, S Belize, Guatemala, Honduras, El Salvador, Nicaragua,

Costa Rica, W Panama; epiphytic in mostly dry open habitats, 16–2300 m.

≡ *Tillandsia variegata* Schlechtendal (1844) (*nom. illeg.*, Art. 53.1); **incl.** *Tillandsia inanis* Lindley & Paxton (1850) (*nomen rejiciendum*, Art. 56.1) ≡ *Platystachys inanis* (Lindley & Paxton) Beer (1856) (*nomen rejiciendum*, Art. 56.1).

[5] Plant stemless, flowering 20–30 cm tall; **L** few, to 50 cm, margins at first ciliate with coarse scales, wholly finely appressed-lepidote; **L** sheaths forming a pseudobulb of 2–5 cm Ø, suborbicular, inflated, green and dark brown, green with minute violet spots or wavy patterns; **L** lamina linear, 3 mm wide, often contorted and involute-subulate, apex filiform-attenuate, **Inf** digitately compound with 3–5 subequal spikes, or rarely simple; peduncle erect, slender; peduncular **Bra** leaf-like, imbricate; primary **Bra** almost leaf-like, the broadly ovate sheath much shorter than the subtended branch which is much exceeded by the linear lamina, concolorous; **Inf** spikes with 1–2 sterile bracts at the base, erect to spreading, 6–8 × 1 cm (at anthesis), linear, strongly complanate, 5- to 8-flowered, acute; floral **Bra** erect, imbricate, much exceeding the sepals, 20–28 × 9–10 mm, ovate, sometimes incurved, stiffly subcoriaceous, prominently veined, obscurely carinate towards the apex, 3–4 × as long as the internodes, densely pale appressed-lepidote, reddish with green spots or cinereous-green, acute; **Fl** subsessile, appressed to the rachis; **Sep** 12–15 × 4.5 mm, narrowly elliptic or obovate, coriaceous, adaxial ones connate for 4 mm, adaxial ones bluntly carinate, green, glabrous, narrowly obtuse; **Pet** forming an erect narrow tube clasping the filaments, with revolute apex, 30–35 × 7 mm, purple or pale violet, rounded-emarginate; **St** ±40 mm, unequal, exserted; **Fil** exposed part slightly inflated and (sub-) terete, not plicate; **Anth** dorsifixed at 1/3 from the base, 2.3 × 0.7 mm, ellipsoid, purple-blue in the upper part; **Ov** 5 mm, narrowly ovoid and broadest near the base, tapering into the style; **Sty** slender, 30 mm, exserted.

**T. caliginosa** W. Till (Pl. Syst. Evol. 147: 282–284, figs. 6a–4, 7–af, 1984). **Type:** Argentina, Jujuy (*Muhr* s.n. [HEID 30925]). — **Distr:** Bolivia, N Argentina; epiphytic, 1150–3000 m.

**Incl.** *Tillandsia myosura* Grisebach (1879) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Tillandsia crocata* var. *tristis* Rauh (1983); **incl.** *Tillandsia crocata* fa. *major* Rauh (1983) (*nom. inval.*, ICN Art. 39.1).

[4] Plant short stemmed, flowering 20–40 cm tall, branched; stem ±8 cm, 0.5 cm Ø, simple; **L** distichous, ±10; **L** sheaths densely imbricate and clasping each other and the stem, to 2 × 2.4 cm, strongly veined, glabrous and partly visible, vividly green; **L** lamina 12–18 × 0.2–0.5 cm, linear-subulate with long-attenuate apex, flexuous, horizontally spreading to reflexed, densely cinereous-lepidote, trichomes eccentric; **Inf** always simple; peduncle naked except for 1 or 2 bracts at the base, 10–16 cm, slender, straight, subdensely cinereous-lepidote; peduncular **Bra** leaf-like, remote; spikes erect, densely strongly lepidote, to 6 × 5–10 mm, complanate, 2- to 4-flowered, rachis flexuous, exposed; floral **Bra** erect, equaling or shorter than the sepals, 12–14 (–20) mm, ovate, enveloping the rachis at the base, margins with extended scales at the margins, veined esp. on the inside, ecarinate, densely cinereous-lepidote only abaxially, brownish-green, obscurely acuminate or subattenuate-acute; **Fl** with a short pedicel-like receptacle, distichous, erect and contiguous with each other and/or the rachis, fragrant; **Sep** 14 × 3.5–4 mm, obovate, 5- to 7-veined, evenly short-connate (adaxially slightly more) for 1–2 mm, adaxial one carinate, green and somewhat fleshy, flushed red upwards, then more hyaline, densely grey-scaled at least towards the apex and upper margins (with extended marginal scales) to glabrescent towards the base, acutish; **Pet** 10 (–15) mm, small, spatulate, 2 mm wide, almost blackish-brown marbled with yellow (and often with a yellow midvein), blade recurved; **St** and **Ov** with **Sty** deeply included.

**T. capillaris** Ruiz & Pavón (Fl. Peruv. 3: 42, t. 271: fig. c, 1802). **Type:** Peru (*Pavón* s.n. [BM, GH [photo], P]). — **Lit:** Till (1989); Castello & Galetto (2013). **Distr:** E Brazil (Bahia), S Ecuador (Azuay), Peru, Bolivia, N Chile, Argentina, S Uruguay; saxicolous and epiphytic, 0–4200 m.

≡ *Diaphoranthema capillaris* (Ruiz & Pavón) Beer (1856); **incl.** *Tillandsia incana* Gillies ex

Baker (1878) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Tillandsia pusilla* Gillies *ex* Baker (1878) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Tillandsia propinqua* Grisebach (1879) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Tillandsia lichenoides* Hieronymus (1885)  $\equiv$  *Tillandsia hieronymi* var. *lichenoides* (Hieronymus) A. Castellanos (1945); **incl.** *Tillandsia propinqua* var. *saxicola* Hieronymus (1885); **incl.** *Tillandsia capillaris* var. *incana* Mez (1896)  $\equiv$  *Tillandsia capillaris* fa. *incana* (Mez) L. B. Smith (1935); **incl.** *Tillandsia capillaris* var. *lanuginosa* Mez (1896); **incl.** *Tillandsia hieronymi* Mez (1896)  $\equiv$  *Tillandsia capillaris* fa. *hieronymi* (Mez) L. B. Smith (1935); **incl.** *Tillandsia capillaris* fa. *typica* L. B. Smith (1935) (*nom. inval.*, ICN Art. 24.3); **incl.** *Tillandsia permutata* A. Castellanos (1945).

[4] Very variable in size and form, flowering to 16 cm tall, forming dense clusters; stem simple or branched, many from a single point; **L** distichous, mostly 1–4 (–9) cm, rarely shorter, densely and finely punctulate-lepidote with cinereous to ferruginous scales; **L** sheaths usually elliptic, thin, several-veined, densely lepidote except where covered by the next below; **L** lamina linear, narrowly triangular, to 2 mm wide, erect to spreading or rarely contorted, straight; **Inf** 1- (rarely 2-) flowered; peduncle always naked, from almost none to 8 cm, developing almost wholly after anthesis, mostly slender, glabrous to sparsely lepidote towards the apex; floral **Bra** of the first flower exceeding or shorter than the sepals, that of the upper flower (if any) shorter than the sepals, almost orbicular, thin and soon drying, strongly 3- to 5-veined, densely lepidote to glabrous on both faces, stramineous; **Fl** subsessile or with a short pedicel-like receptacle; **Sep**  $\pm 8 \times 3$  mm, veined with strongly developed vein branches, adaxial ones for  $\pm \frac{1}{3}$  connate, ecarinate, green tinged red-purple, glabrous on both faces, obtuse or almost round; **Pet** linearly tongue-shaped to lanceolate,  $12 \times 2$  mm, cream-coloured (sometimes flushed red) or yellow or brown, blade obscure, divergent to recurved, rounded or acutish; **St** 3.5–4.5 mm, deeply included, exceeding the style; **Fil** ribbon-like, flaccid, not plicate; **Anth** basifixed,  $\pm 1$  mm, oblong-ellipsoid (to slightly tapering from base to apex), yellow; **Ov** 1.5–2  $\times$

>1 mm, obovoid (to pyriform), abruptly contracted into the style; **Sty** stout, shorter than to about as long as the ovary; **Sti** capitellate, lobes short, concave and erect.

A very variable species including many forms, some of them more succulent than others. Intra-specific taxa are no longer recognized (Till 1989, 1991), with the exception of fa. *virescens*, which is recognized as separate species, *T. virescens*. *T. virescens* is very similar, however, intermediate forms occur and separation is probably not warranted.

**T. caput-medusae** E. Morren (Belgique Hort. 30: 90, 1880). **Type:** K [Morren icono]. — **Distr:** Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, W & C Panama; epiphytic, 15–2400 m.

**Incl.** *Tillandsia langlassei* Poisson & Menet (1908).

[5] Plant stemless, flowering 15–25 (–40) cm tall; **L** often exceeding the inflorescence, densely subappressed-lepidote; **L** sheaths forming an ovoid pseudobulb, (broadly) ovate to triangular-ovate, strongly inflated, with membranous margins, adaxially densely ferruginous-lepidote with dark-centered scales, brown to dark brown inside, upwards with purple-red margins, merging into the lamina; **L** lamina linear-triangular, 10–25 cm, to 1.5 cm wide, involute-subulate or usually much contorted, apex attenuate; **Inf** simple or digitately composed of 2–6 spikes; peduncle erect, ascending, slender; peduncular **Bra** leaf-like, densely imbricate; primary **Bra** usually smaller than the floral bracts, broadly ovate, with a little lamina or without, lepidote; **Inf** spikes bearing several sterile bracts at the base, suberect to spreading, often curved, to 18 cm, linear-lanceolate, 6- to 12-flowered, acute, rachis angled, slender, nearly straight, glabrous; floral **Bra** suberect or divergent, imbricate, shorter than to slightly exceeding the sepals, 12–15 (–20)  $\times$  8–9 mm, ovate-lanceolate, incurved esp. at the apex, chartaceous, even or veined when dry, lustrous, carinate but sometimes obscurely so (not thickened), exposing most of the rachis, barely more than 2 $\times$  as long as the internodes, nearly or quite glabrous or obscurely sparsely lepidote on both faces, red or pink or sometimes green, rounded

or broadly obtuse; **Fl** subsessile; **Sep** incurved especially at the apex, 13–14 × 5 mm, oblong, thin-coriaceous to chartaceous, veined only when dry, lustrous, adaxial ones connate for 5–6.5 mm, adaxial ones sharply carinate, glabrous or very sparsely lepidote adaxially only, rounded or broadly obtuse; **Pet** forming an erect narrow tube clasping the filaments at the apex, tongue-shaped, 28–44 × 7 mm with narrow base only 2 mm wide, violet (rarely white), with cuneate claw, rounded and then abruptly obtuse; **St** unequal in length, 30 mm exerted; **Fil** 53–57 mm, thin and slender and flattened at the base and terete at the distal end; **Anth** dorsifixed just below the middle, (fresh) 6 × 1 mm, linear, base bilobed, apex apiculate; **Ov** 4 × 2 mm, ovoid, contracted into the style; **Sty** exceeding the stamens.

**T. castellanii** L. B. Smith (Contr. Gray Herb. 104: 80, t. 3, figs. 17–19, 1934). **Type:** Argentina, Córdoba (*Castellanos* s.n. in BA 1576 [GH, BA]). — **Distr:** NW & C Argentina; epiphytic, 1000–3000 m.

[4] Plant flowering to 15 cm tall, forming dense clusters; stem simple, few-branched, many from a single point; **L** dense, distichous, to 4–5 mm; **L** sheaths broadly ovate, strongly veined, densely lepidote with a ciliate margin of elongate scales; **L** lamina sublinear, 2–3 mm wide, spreading,

recurved, subulate with pungent apex, cinereous-lepidote with spreading scales; **Inf** 1- to 2-flowered; peduncle bractless, pseudo-axillary, evident, to 3 cm, slender, glabrous; floral **Bra** shorter than the sepals, (5.5–) 6.5–9.5 (–10.5) × (5.5–) 5.8–6.8 (–7) mm, ovate, strongly 9- to 11-veined, glabrous or upper part lepidote, broadly acute or short-laminate; **Fl** subsessile, not fragrant; **Sep** 7.5–8.5 (–9) × 2.9–3.3 (–3.5) mm, obovate-lanceolate, strongly 7- to 9-veined, evenly short-connate or abaxial one free, glabrous, rounded or obtuse; **Pet** ovate-lanceolate, 7–8 (–10) × 1.5–2 mm, veined, yellowish, rounded or rarely obtuse; **St** deeply included, exceeding the style; **Fil** 3–3.7 × 0.2 mm; **Anth** basifixed, 2.1–2.2 × ±0.3 mm, whitish; **Ov** obovoid (to pyriform), 3.2–3.4 mm, abruptly contracted into the style; **Sty** stout, 1.6–1.7 mm, ½ as wide as the ovary; **Sti** obscurely lobed.

**T. chiapensis** C. S. Gardner (Selbyana 2(4): 338, ill., 1978). **Type:** Mexico, Chiapas (*Gardner* 211 [SEL]). — **Distr:** SE Mexico (Chiapas); saxicolous, 600–1000 m. – Fig. 4.

[5] Plant stemless, offsetting from the base, eventually forming clumps; **L** forming a spreading rosette, numerous, 30 cm; **L** sheaths 4.5 cm wide, suborbicular, often brown-lepidote in the distal part, pale castaneous; **L** lamina narrowly

**Fig. 4** *Tillandsia chiapensis*. (Copyright: E. J. Gouda)





**Fig. 5** *Tillandsia circinnatoides*. (Copyright: E. J. Gouda)



triangular, fleshy, 2.5 cm wide at mid-blade, coarsely and densely cinereous-lepidote, curved to recurved, strongly canaliculate or the margins involute towards the base, apex attenuate, trichomes  $\pm 0.5$  mm long, suborbicular; **Inf** simple,  $\pm$  equalling or exceeding the leaves; peduncle short and concealed by the leaves and bracts; peduncular **Bra** polystichous, the lowest leaf-like, densely imbricate, tinged or wholly rose-coloured; spikes suberect or becoming decumbent after flowering, lanceolate; floral **Bra** distichous, densely imbricate,  $>2\times$  as long as the sepals,  $\pm 40 \times 26$  mm, ovate-elliptic, incurved at the apex, finely veined when dry, ecarinate or slightly so at the apex, concealing the rachis,  $3-4\times$  as long as the internodes, subdensely or densely lepidote, pink, acute or obtuse; **Fl** distichous, suberect (contiguous with the bracts in the lower part); **Sep** incurved,  $15 \times 7.5$  mm, elliptic or obovate, coriaceous esp. at the base, veined when dry, free or nearly so, adaxial ones carinate, acute or obtuse; **Pet** forming an erect narrow tube clasping the filaments, with revolute apex, narrowly tongue-shaped, 75 mm, 8.5 mm wide in the uppermost  $\frac{1}{4}$ , 3 mm wide at the base, blue-violet, obtuse; **St** in 2 whorls of unequal length, 75–80 mm, shorter than the style; **Fil** subterete towards the apex, purple; **Anth** dorsifixed at  $\frac{1}{4}$  from the base,  $3.5 \times 1$  mm, oblong-ellipsoid, apex obtuse; **Ov** narrowly ovoid, merging into the style; **Sty** slender; **Sti** conduplicate-spiral, white.

**T. circinnatoides** Matuda (Cact. Succ. J. (US) 45: 187, figs. 4, 4a, 5, 1973). **Type:** Mexico, Guerrero (*Matuda* 38432 [MEXU, US]). — **Distr:** S & E Mexico, NW Costa Rica; epiphytic on cacti, trees, and bushes in dry areas, 600–2200 m. — Fig. 5.

[5] Plant stemless, flowering 10–20 cm tall, often forming dense clusters; **L** few, the outer ones reduced and without lamina, the others 7–16 cm, appearing veined by trichomes in longitudinal rows, covered with appressed cinereous scales; **L** sheaths forming an elongate pseudobulb, large, ovate, merging into the lamina; **L** lamina narrowly triangular, erect or curved, grooved, involute-subulate; **Inf** simple; peduncle erect, 7.5 cm, concealed by the leaves; lowest peduncular **Bra** leaf-like, the upper like the floral bracts or slightly larger, densely imbricate, acuminate; spikes curved or erect, 5–10 cm, 1.4–2 cm wide, lanceolate to linear, complanate, attenuate, rachis hidden or (slightly) partly exposed; floral **Bra** densely imbricate, exceeding the sepals,  $20-30 \times 9.5$  mm, elliptic, thin, finely veined when dry, scarcely or not at all carinate towards the apex,  $3-4\times$  as long as the internodes, densely cinereous-lepidote except the base and margins and less dense on the inside, pale roseate, broadly acute or apiculate; **Fl** subsessile, contiguous with each other and/or the rachis; **Sep**  $19-25 \times 4-6$  mm, lanceolate, abaxial one chartaceous and adaxial ones with a rigid subcoriaceous keel, subfree or adaxial ones connate for up to 5 mm, adaxial ones

carinate from base to apex, lepidote with few large scales abaxially, or glabrescent; **Pet** forming an erect narrow tube clasping the filaments with revolute apex, tongue-shaped, 40–45 × 5 mm, pale blue to dark violet in the upper ½, rounded; **St** long-exserted; **Fil** twisting at the base, flat and exposed part slightly inflated and (sub-)terete, bluish in the upper ½; **Ov** ovoid, abruptly contracted into the style; **Sty** slender, exceeding the stamens; **Sti** conduplicate-spiralized, long-papillose.

**T. colganii** Ehlers (J. Bromeliad Soc. 47: 103, ill., 1997). **Type:** Bolivia, Santa Cruz (Ehlers EB951002 [WU]). — **Distr:** E Bolivia (Santa Cruz); saxicolous, 2700–3200 m.

[2] Plant short stemmed or with a rhizomatous stem, flowering 10–15 cm tall, often branched; **L** rosulate, 12–14, 3–7 cm long (outer ones reduced with short acuminate lamina), coriaceous to subsucculent, margins with asymmetric trichomes, covered with appressed cinereous scales, green-grey looking striped; **L** sheaths erect or suberect, 2–3 × 1–1.8 cm, ovate, passing almost imperceptibly into the lamina; **L** lamina narrowly triangular, 1–1.5 cm wide at the base, sometimes slightly secund or spreading or recurved, abaxially with a median keel and strongly veined, subulate or canaliculate, apex attenuate; **Inf** simple, exceeding the leaves; peduncle completely covered by bracts, erect, 0–2 cm and concealed by the leaves, stout, lepidote; lowest peduncular **Bra** almost leaf-like, imbricate, the apical ones like the floral bracts, becoming glabrous, red, attenuate or acute; spikes with a sterile bract at the base, 3–4 cm, 5–8 (–10) mm wide, lanceolate, subterete, 2- or 3-flowered, acute, rachis 4-angled, nearly straight, glabrous, hidden at anthesis, green; floral **Bra** imbricate, exceeding the sepals, 16–25 (–28) × 8–10 mm, ovate-triangular, submembranous, adaxially veined, ecarinate, glabrous or the apical 4–6 mm finely grey-lepidote, sublustrous wine-red, acute or cuspidate; **Fl** sessile, distichous, not fragrant; **Sep** 14–16 × 4.5–6 mm, narrowly elliptic, membranous, thickened along the keels, free, adaxial ones carinate, greenish with pink tips, acute; **Pet** erect and throat open, 36–40 × 5 mm, at the base 3 mm wide, margins entire, violet to

white at the base, blade spreading to recurved, obtuse; **St** just visible in the throat of the corolla; **Fil** 25–30 × 0.5 mm, flat, thin towards the base, once transversely plicate or straight; **Anth** basifixed, 4–5 mm, linear, apex acute, yellow; **Ov** 4 × 2.5 mm at the base, ovoid; **Sty** surpassing the stamens, 25–30 mm, 1 mm wide at the base, tapering to 0.7 mm at the apex; **Sti** 4 × 3 mm, exerted for 2–12 mm, narrow, spreading, papillose, yellowish.

**T. copanensis** Rauh & Rutschmann (J. Bromeliad Soc. 38: 7–9, ill., 1988). **Type:** Honduras, Copán (*Kamm* s.n. in *BG HEID* 68087 [HEID]). — **Distr:** W Honduras (Copán); saxicolous on rock cliffs and epiphytic on pine trees, elevation not recorded. — Fig. 6.

[5] Plant stemless, flowering to 80 cm tall; **L** numerous; **L** sheaths 9 × 6 cm, narrowly ovate, brown-lepidote on both faces, distinct from the lamina; **L** lamina very narrowly triangular, somewhat succulent, to 35 × ±4 cm at the base, pale green, abaxially densely white-lepidote (trichomes in rows with a green centre), recurved, canaliculate, apex attenuate and pungent; **Inf** mostly laxly 1 × branched or rarely simple, composed of up to 6 spikes, often decurved and then ascending, lax, to 30 cm (including the terminal spike), 20 (–30) cm wide; peduncle curved, shorter than the leaves, 15 mm Ø; lower peduncular **Bra** somewhat leaf-like, the upper ones like the primary bracts, imbricate, spike axes angled, 10 mm Ø, glabrous, bright carmine-red; primary **Bra** triangular, the upper ones to 9 × 3 cm, acute; spikes ±20 × 2 cm, shortly stipitate for 1.5–3 cm, with 1 or 2 sterile bracts at the base that are sharply keeled, sub-pendulous and then ascending or curved, linear-lanceolate, complanate, acute; floral **Bra** imbricate, >2 × as long as the sepals, 47–50 × 20–23 mm, elliptic, strongly convex, bluntly subcarinate towards the apex and ecarinate below, densely lepidote becoming glabrous at the base, pale green to cinereous-white at the apex, acute or obtuse; **Fl** with a stout pedicel-like receptacle, contiguous with each other and/or the rachis; **Sep** ±22 × 5–8.5 mm, oblong-lanceolate, fleshy at the base, with broad hyaline margins and apex, finely veined adaxially, evenly short-connate for

**Fig. 6** *Tillandsia copanensis*. (Copyright: E. J. Gouda)



1–2 mm, adaxial ones inconspicuously bluntly carinate, green, glabrous on both faces, obtuse; **Pet** forming an erect narrow tube clasping the filaments, with revolute apex, tongue-shaped, to  $66 \times 7.5$  mm, broadest at  $\frac{1}{4}$  from the apex, base 4 mm wide, dark violet with hyaline margins and apex, covered part white, blade rounded-emarginate; **St** in 2 whorls of unequal length, 72 and 78 mm, exserted; **Fil** exposed part slightly inflated and (sub-) terete, violet; **Anth** dorsifixed at  $\frac{1}{3}$  from the base,  $4 \times 1$  mm, elliptic in outline, apex rounded, yellowish-brown; **Ov**  $7 \times 3$  mm, attenuate from near the base, gradually contracted into the style; **Sty** slender, to 73 mm, exceeding the stamens; **Sti** 3 mm, conduplicate-spiral.

**T. cotagaitensis** L. Hromadnik (Pl. Syst. Evol. 147: 285–285, 1984). **Type:** Bolivia, Potosi (Hromadnik & Hromadnik 5093 [WU]). — **Distr:** SW Bolivia (Potosi); epiphytic on *Oreocereus* in association with *T. caliginosa*,  $\pm 3000$  m.

[4] Plant caulescent, flowering to 14 cm tall, branched; **L** densely distichous, divergent to recurving; **L** sheaths to  $1 \times 0.8$  cm, amplexicaul, scarious, with broad veinless margins, veined or lustrous, glabrous, becoming greenish; **L** lamina flexible, to  $4 \times 0.2$ – $0.3$  cm, densely tomentose-lepidote, subulate, apex subulate-acuminate; **Inf** simple; peduncle 2–3 cm, 1 mm  $\varnothing$ , densely lepidote; spike dense, 2 cm, distichously 2- to

3-flowered, rachis lepidote; floral **Bra** equalling or shorter than the sepals,  $(8.2\text{--}) 11.8 \times 5.4$ – $6.8$  mm, ovate, 11- to 12-veined, lepidote, with a very short lamina; **Fl** subsessile, fragrant; **Sep**  $8.2$ – $10.2 \times 2.4$ – $2.6$  mm, lanceolate, 5- to 7-veined, adaxial ones connate for 4–6 mm and slightly carinate, abaxial one connate for 1 mm, green, glabrescent; **Pet** tongue-shaped,  $14.2$ – $15.4 \times 2.7$ – $3.1$  mm, brown-violet to black-violet or rarely ochraceous, blade recurved, moderately broadened, tip rounded; **St** included; **Fil** 4.4–5.1 mm, white, 1-nerved; **Anth** basifixed,  $1.9$ – $2.3 \times 0.3$  mm, golden-yellow; **Ov**  $2$ – $2.3 \times 1.5$  mm, narrowly ovoid; **Sty** slender, 4–4.6 mm, included.

**T. crocata** (E. Morren) Baker (J. Bot. 25: 214, 1887). **Type:** Brazil, Rio de Janeiro (Lietze s.n. [K [icono: Morren drawing], GH [photo]]). — **Distr:** SE & S Brazil (Rio de Janeiro, Paraná, Rio Grande do Sul), NE Bolivia (La Paz), NE Argentina (Entre Ríos), SW Uruguay (Soriano); saxicolous, 875–2650 m.

≡ *Phytarrhiza crocata* E. Morren (1880).

[3] Plant short-stemmed, leafy stem part often shorter than the leaves, flowering 15–35 cm tall, forming dense clusters; stem to 20 cm, **L** distichous, 10–30 cm, densely white-tomentose-lepidote with asymmetric elongated scales; **L** sheaths broadly ovate, glabrous except for the upper  $\frac{1}{2}$

**Fig. 7** *Tillandsia curvifolia*. (Copyright: E. J. Gouda)



outside; **L** lamina linear, 2–5 mm wide, spreading and recurved, involute-subulate, apex long-attenuate; **Inf** always simple; peduncle bractless or with a single leaf-like bract at the base, erect or nearly so, 5–15 cm, slightly  $>1$  mm  $\varnothing$ , slender, retrorse-tomentose like the leaves; spike densely 2- to 6-flowered, 1–4 cm (excl. petals or capsules), lanceolate, elliptic, acute, with a reduced flower at the apex; floral **Bra** imbricate,  $\pm$  equalling the sepals, 9–10 (–20) (including blade like apex)  $\times$  6.5–7.5 mm, ovate or elliptic, 2–5 $\times$  as long as the internodes, densely tomentose-lepidote abaxially only, green, tinged purple-red, acuminate, the lowest with a thick blade-like apex; **Fl** with a  $\pm 1$  mm pedicel-like receptacle or subsessile, distichous, fragrant; **Sep** 10  $\times$  4.5 mm, elliptic or sublanceolate, thin, with veinless broad hyaline margins, faintly veined in the centre, unequally short-connate for 1–2 mm, adaxial ones obscurely carinate esp. towards the apex, lower  $\frac{1}{2}$  green and then stramineous speckled purple-red, densely appressed-lepidote abaxially on the centre ridge towards the apex, obtuse or acutish; **Pet** claw narrow with suborbicular blade or spatulate with elliptic blade, tapering into the cuneate claw, 19–20 mm, blade 6–8 mm wide, spreading, obtuse, margins slightly crenulate, bright yellow (paler towards the base), claw 1 mm wide at the base to 3 mm distally; **St** 7 mm, deeply included, much exceeding the style; **Fil** slender-attenuate

from near the base, flaccid, straight; **Anth** basifixed, 1.5 mm, apex broadly obtuse, orange-yellow; **Ov** 3  $\times$  2 mm, obovoid (pyriform), abruptly contracted into the style; **Sty** 1.5 mm; **Sti** erect, shortly lobed.

**T. curvifolia** (Ehlers & Rauh) Ehlers (Bromelie Sonderheft 6: 126–134, ill., 2009). **Type:** Mexico, Guanajuato (*Ehlers* M850201 [WU]). — **Distr:** C Mexico (Guanajuato); mostly saxicolous, sporadically epiphytic, 1650–3000 m. – Fig. 7.

$\equiv$  *Tillandsia tortilis* ssp. *curvifolia* Ehlers & Rauh (1990)  $\equiv$  *Viridantha curvifolia* (Ehlers & Rauh) Lopez-Ferrari & Espejo (2009).

[1] Plant stemless or short-stemmed, flowering 5–15 cm tall; **L** spirally arranged, 8–12, 4–16 cm, white-tomentose-lepidote; **L** sheaths 1.5  $\times$  1.2 cm, ovate, somewhat succulent, with translucent margins, densely tomentose and glabrous only at the base, conspicuously offset from the lamina; **L** lamina narrowly triangular, succulent esp. at the base, to 14 cm, 7 mm wide at the base, mostly upwardly secund or erect, silvery-white, subulate and canaliculate, margins involute, apex filiform-attenuate, adaxially densely appressed-lepidote, abaxially tomentose-lepidote, trichomes eccentric; **Inf** simple or very rarely with a smaller lateral spike, erect, shorter than or slightly exceeding the leaves; peduncle concealed within the leafy rosette or extended and hidden by the inner leaves



**Fig. 8** *Tillandsia diaguitensis*. (Copyright: E. J. Gouda)



and bracts, to 5 (–14) cm, 2 mm Ø, glabrous or sparsely lepidote; lowest peduncular **Bra** leaf-like, upper ones like the floral bracts, erect, few (3–5 only), imbricate, 3–5× as long as the internodes, with setaceous lamina to 7 cm; spikes with a sterile bract at the base, 2–3 × to 1 cm, (narrowly) ellipsoid, terete, (1- to) 2- to 5-flowered, rachis angled, stout, densely lepidote, hidden; floral **Bra** erect, densely imbricate, slightly exceeding the sepals, 10–20 × 10 mm, ovate to lanceolate, thin, margins hyaline, finely veined or distinctly veined towards the apex, 2–3× as long as the internodes, glabrous or sparsely lepidote, roseate or sometimes green, acuminate; **Fl** polystichous or subdistichous; **Sep** to 15 × 4 mm, lanceolate-oblong, membranous, with hyaline margins, free, adaxial ones distinctly carinate, glabrescent or sparsely lepidote at the apex; **Pet** for most of the length tubular-erect, tongue-shaped, 20–27 × 4 mm, green with white base, blade apex recurved, rounded; **St** all of equal length, deeply included; **Fil** to 15 mm, filiform, flat, white; **Anth** basifixed, 3–5 mm, sagittate, pale brown; **Ov** 4 × 2 mm; **Sty** slender, 6 mm; **Sti** lobes short, erect or somewhat divergent at maturity.

**T. diaguitensis** A. Castellanos (Anales Mus. Nac. Hist. Nat. Buenos Aires, ser. 3, 36: 55, t. 10, 1929). **Type:** Argentina, Jujuy (*Castillon* 7224 [BA]). — **Distr:** N Argentina (Jujuy, Formosa,

Salta, Tucumán), C Paraguay; epiphytic, ±90–2050 m. — Fig. 8.

[2] Plant long caulescent, slender; stem 60 cm, simple or few-branched, 5 mm Ø; **L** laxly polystichous along the stem, 8–10 cm, densely cinereous-lepidote (furfuraceous); **L** sheaths ±1.3 cm wide, elliptic, amplexicaul, imbricate, making the stem appear 7–10 mm thick; **L** lamina narrowly triangular, 0.6 cm wide, erect to recurved, strongly veined at least when dry, canaliculate, apex attenuate; **Inf** always simple; peduncle completely covered by the bracts, conspicuous, to 8 cm, 3 mm Ø; peduncular **Bra** imbricate, elliptic, thin, strongly veined, lepidote towards the apex, stramineous, acute; spike dense, 4–9 cm, 1.3–1.4 cm wide, lanceolate, 3- to 6-flowered, acute, rachis slender, nearly straight, glabrous, sulcate; floral **Bra** imbricate to divergent at anthesis, much exceeding the sepals, 40–50 × 10 mm, lanceolate, chartaceous, margins scarious and veinless, finely to strongly veined when dry and waxy, ecarinate, 2–3× as long as the internodes, glabrous, roseate or stramineous, narrowly acute; **Fl** subsessile, fragrant; **Sep** 26 (–32) × 4.5–6 mm (abaxial one smaller), lanceolate-oblong, with membranous margins, veined, free, adaxial ones carinate, glabrous, acute; **Pet** spatulate, 60–70 × 13 mm, margins minutely denticulate or slightly crenulate, white or bluish, claw linear, forming a tube well beyond the sepals, blade obovate,



rounded; **St** all of equal length, 38–51 mm, included and visible in the throat; **Anth** subbasifixed, 5–8 mm, linear; **Ov** 5–7 mm, tapering into the style; **Sty** slender, 37 mm, exceeding the stamens; **Sti** 3 mm, spreading, weakly conduplicate.

**T. dorisdaltoniae** Ibisch & al. (Revista Soc. Boliv. Bot. 4(1): 45, 2003). **Type:** Bolivia, Cochabamba (*Vargas* 6355 [WU]). — **Distr:** C Bolivia (Cochabamba); epiphyte, 950–1050 m.

[2] Plant short-stemmed, flowering to 20 cm tall or more, forming dense clusters; stem richly branched at the base; **L** forming a dense rosette, numerous, erect to divergent, exceeding or about equalling the inflorescence; **L** sheaths to 1.5 × 1 cm, abaxially lepidote, conspicuously offset from the lamina; **L** lamina rigid, to 10 cm, 0.6–0.7 cm wide at the base, erect or divergent, subulate, apex attenuate, acute, intensely green, sparsely lepidote, adaxially glabrescent towards the apex; **Inf** simple; peduncle erect, much shorter than the leaves, to 3 cm, slender, green; peduncular **Bra** imbricate, upper ones reduced to ovate sheaths, lepidote to glabrous on the sheath, whitish, the lower ones with leaf-like lamina; spike erect, 4–5 cm, complanate, densely ±8-flowered, rachis completely covered by the bracts at anthesis but slightly exposed when dry as the margins

of the bracts bend outwards, internodes 3.5 mm; floral **Bra** erect, distichous, densely imbricate, exceeding the sepals, 12–14 (–20) × 5–8 mm (2.5–3 mm wide in lateral view), ovate, faintly veined towards the apex esp. when dry, ecarinate, covering >½ of the flowers, glabrous, bright red, acute; **Fl** subsessile; **Sep** 11 × 3.5 mm, membranous, completely free, subaxial ones alate-carinate, whitish, glabrous, subobtusate; **Pet** suberect, tongue-shaped, 16 × 3 mm, white, blade slightly divergent, apex rounded; **St** all of equal length, 12 mm, included; **Fil** 8.5 mm, flat, slightly plicate in the upper ½; **Anth** subbasifixed, 4 mm; **Ov** 2 × 1.2 mm, ovoid; **Sty** slender, ±9 mm; **Sti** 0.5 mm, erect, papillose.

**T. ×dorotheae** Rauh *pro sp.* (Trop. subtrop. Pfl.-welt 60: 59, ill., 1987). **Type:** Argentina, Salta (*BG Heidelberg* 31306 [HEID, MO, WU]). — **Distr:** NE Argentina (Salta); saxicolous in bare lands, in crevices and almost inaccessible crags and bluffs, altitude not recorded. — Fig. 9.

[2] Plant ± caulescent, forming dense clusters; stem 5–10 cm, laxly branched at the base; **L** densely spirally arranged but sometimes showing a tendency to distichous, erect to spreading; **L** sheaths distinct, to 1.5 × 1 cm, elongate, with membranous margins, base glabrous, upper ½ densely cinereous-lepidote, whitish or

**Fig. 9** *Tillandsia* × *dorotheae*. (Copyright: E. J. Gouda)



occasionally pinkish-violet; **L** lamina very narrowly triangular, rigid, 8–10 × 0.3 cm, cinereous-green, densely lepidote, veined and distinctly rugose at the base, adaxially deeply and narrowly canaliculate but not keeled, apex abruptly obtuse; **Inf** simple, decurved, shorter than the leaves; peduncle mostly decurved, sometimes erect, short and concealed by the leaves, 4–6 cm, 2 mm Ø, terete, green; peduncular **Bra** few (3–4), the lower leaf-like, the upper 1 or 2 with shorter lamina, densely imbricate; spike decurved, subclax or subdensely flowering, to 3 × 0.8 cm, (1- to) 2- (to 4-) flowered, with a reduced flower at the apex, rachis flat on one side, slender, flexuous, glabrous; floral **Bra** erect, slightly shorter than the sepals, 20 × 5–8 mm, lanceolate, coriaceous, margins hyaline, shiny at the base, strongly veined, carinate towards the apex, lower part glabrous, scatteredly white-lepidote upwards, green to wine-red, acuminate or fleshy-apiculate; **Fl** subsessile, distichous; **Sep** 19–22 × 4 mm, lanceolate, thin, even, free, adaxial ones carinate, green and flushed red, acuminate or abruptly acute; **Pet** spatulate, 33–35 × 6–7 mm (base 2.5 mm wide) reddish or dark pink, blade obscure, recurved and often twisting, acuminate; **St** (9-) 13–17 mm, deeply included, shorter than the style; **Fil** ribbon-like, not plicate; **Anth** dorsifixed near the base, 5–6 mm, yellow; **Ov** 5 × 2.5 mm, cylindrical, abruptly contracted into the style; **Sty** slender, 15 mm; **Sti** erect, weakly conduplicate.

Considered to be the hybrid *T. argentina* × *T. albertiana*.

**T. duratii** Visiani (Nuovi Saggi Imp. Regia. Accad. Sci. Padova 5: 271, t. 29, 1840). **Type**: PAD?; [icono]: l.c. t. 29. — **Distr**: Brazil, N Peru, Bolivia, Argentina, Paraguay, NE & NW Uruguay; epiphyte or saxicolous, 80–2750 m.

≡ *Phytarrhiza duratii* (Visiani) Visiani (1854) ≡ *Anoplophytum duratii* (Visiani) Beer (1856); **incl.** *Tillandsia floribunda* Durat ex Visiani (1840) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Tillandsia circinalis* Grisebach (1874) ≡ *Phytarrhiza circinalis* (Grisebach) E. Morren ex Baker (1889); **incl.** *Tillandsia gigantea* Ruchinger (1876) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Tillandsia decomposita* Baker (1889); **incl.**

*Tillandsia weddellii* Baker (1889); **incl.** *Tillandsia revoluta* Burbidge ex Baker (1889) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Tillandsia tomentosa* N. E. Brown (1894); **incl.** *Tillandsia confusa* Hassler (1919) ≡ *Tillandsia duratii* var. *confusa* (Hassler) L. B. Smith (1968); **incl.** *Tillandsia confusa* var. *minor* Hassler (1919); **incl.** *Tillandsia confusa* var. *saxatilis* Hassler (1919) ≡ *Tillandsia duratii* var. *saxatilis* (Hassler) L. B. Smith (1968).

[3] Plant caulescent, flowering 20–100 cm tall or more; stem to 30 cm, simple, stout, curved; **L** laxly polystichous, densely cinereously lepidote with subappressed coarse scales; **L** sheaths ±2 cm, broadly ovate, distinct from the lamina; **L** lamina very narrowly triangular, rigid, thick, 15–20 (–40) × 1–2 cm, involute-subulate to often contorted towards the apex that is then twining around tree branchlets, apex pungent; **Inf** 1 × branched or 2 × branched in the lower part, 6–60 cm; peduncle erect, elongate, stout, glabrous; lowest or all peduncular **Bra** almost leaf-like, densely imbricate, elliptic, densely cinereous-lepidote, the upper apiculate; primary **Bra** erect, like the peduncular bracts, enveloping the bracteate sterile bases of the axillary branches; **Br** erect or spreading or recurving, lower **Inf** spikes long-stipitate for up to 10 cm, spikes complanate, 4.5 cm long, 1.7 cm wide, with several sterile bracts at the base, lanceolate or linear; floral **Bra** erect, slightly longer or shorter than the sepals, to 17 × 8 mm, ovate to oblong, even, ecarinate, subdensely to densely lepidote, greenish but soon stramineous, obtuse; **Fl** subsessile, fragrant; **Sep** to 14 mm, ovate, elliptic, coriaceous at the base, with membranous margins and apex, even, evenly or unequally short-connate for 2 mm, ecarinate, green or brown, glabrous, subobtuse; **Pet** 25–33 mm, claw narrow with suborbicular blade, margins slightly crenulate, usually (purple-) blue-speckled, claw linear, white, blade subrhombic to orbicular, spreading; **St** all of nearly equal length, 11 mm, deeply included but exceeding the style; **Fil** thin but not flaccid, not plicate; **Anth** basifixed, 2.5 mm, green; **Ov** 7.5 mm, bottle-shaped, ribbed; **Sty** short; **Sti** shortly lobed.

This is a very variable species growing in a range of habitats. It can grow on rock faces mixed with *T. streptocarpa*, looking very different in habit,

**Fig. 10** *Tillandsia ehlersiana*. (Copyright: E. J. Gouda)



but in other habitats intermediate forms occur. Intermediate forms between these 2 species, but also with *T. paleacea*, are common and are difficult to place under one of the 3 species, mainly because the flowers and spikes are not very different if at all from each other. The infraspecific taxa recognized by some authors are not accepted here.

**T. ehlersiana** Rauh (J. Bromeliad Soc. 34(4): 166–169, ills., 1984). **Type:** Mexico, Chiapas (*Ehlers* 83/404 [HEID]). — **Distr:** SE Mexico (Chiapas); on steep granitic rocks in deciduous forest,  $\pm 700$  m. — Fig. 10.

[5] Plant stemless, flowering to 20 cm tall, forming clumps; **L** many, exceeding the inflorescence, silver-grey; **L** sheaths forming a pseudobulb to  $8 \times 10$  cm, individual sheaths to  $7 \times 6$ – $7$  cm, suborbicular, strongly inflated, densely furfuraceously lepidote, adaxially light leather-brown, abaxially whitish, distinct from the lamina; **L** lamina narrowly triangular to linear, with asymmetric trichomes at the margins, above the sheath to 2.5 cm wide, both faces densely white-lepidote, upper part often recurved, strongly involute-subulate and canaliculate; **Inf**  $1 \times$  branched, composed of  $\pm 4$  spikes, ovoid in outline, much shorter than the leaves; peduncle short and concealed by the leaves, to 7 cm, 1 cm  $\varnothing$ , terete, appressed-lepidote; peduncular **Bra** leaf-

like, few ( $\pm 3$ ), similar to the upper rosette leaves, silver-greyish; axes compressed, 7 cm, straight; primary **Bra** erect or divergent with the branches, the basal ones with broadly ovate sheaths, somewhat leaf-like,  $2 \times 1$  cm, exceeding the spikes or inflorescence and the upper shorter than the spikes and acute, densely furfuraceously lepidote; spikes shortly stipitate for 0.5 cm, erect or divergent,  $3 \times 1.8$  cm, complanate, 2- to 3-flowered; floral **Bra** distichous, imbricate, much exceeding the sepals,  $19$ – $22$  ( $-28$ )  $\times 10$ – $13$  mm, triangular-ovate, membranous, margins even, carinate with a thick midvein, concealing the rachis, cinereously lepidote, brownish-red or roseate, acute or obscurely apiculate; **Fl** subsessile, 30–65 mm; **Sep**  $13$ – $19 \times 6$ – $7$  mm, (narrowly) elliptic, membranous, even, free or shortly connate for up to 3 mm, adaxial ones carinate (sharply so when dry), greenish-red, (very) sparsely lepidote especially on the keel, acute or broadly obtuse; **Pet** forming an erect narrow tube clasping the filaments at the apex, linearly tongue-shaped,  $(33$ – $) 42$ – $53 \times 8$  mm, upper  $\frac{1}{2}$  blue-violet, white towards the base, obtuse; **St** in 2 whorls of unequal length, 57–60 mm, exserted, shorter than or as long as the style; **Fil** subterete towards the apex, straight, upper  $\frac{1}{3}$  violet; **Anth** dorsifixed at  $\frac{1}{3}$  from the base, 2.5 mm, blackish; **Ov** 5 mm, subprismatic, gradually contracted into the slender style.

**T. erecta** Gillies *ex* Baker (J. Bot. 16: 239, 1878). **Type:** Argentina, Mendoza (Gillies s.n. [K]). — **Distr:** C Bolivia (Cochabamba), Argentina (Mendoza, La Rioja); saxicolous and epiphytic, 1300–2610 m.

**Incl.** *Tillandsia rigida* Gillies *ex* Baker (1878) (*nom. inval.*, ICN Art. 32.1c)  $\equiv$  *Tillandsia erecta* var. *rigida* (Gillies *ex* Baker) Baker (1889).

[4] Plant to 11 cm tall; stem 3–6 cm, simple or few-branched; **L** laxly polystichous, to 5 cm, densely cinereous-lepidote; **L** sheaths 0.5–1 cm, broadly ovate, glabrous; **L** lamina very narrowly triangular, rigid and succulent,  $\pm 0.4$  cm wide at the base, erect to divergent, veined or obviously grooved, involute-subulate, angled towards the acuminate apex; **Inf** 1-flowered with the rachis extended behind the flower; peduncle to 4.5 cm, elongating in fruit, slender, strongly sulcate or strongly furrowed when dry, glabrous; peduncular **Bra** 0–2,  $\pm 1.5$  cm, elliptic, glabrous; floral **Bra** equalling or shorter than the sepals, (8–) 12–13.5  $\times$  5.5–6 mm, triangular-ovate to ovate-lanceolate, not tapering at the base, distinctly 6- to 10-veined, glabrous or upper part sparsely lepidote, stramineous or brown-reddish in the lower part, acute or obtuse; **Fl** subsessile, erect, weakly fragrant; **Sep** 10–11.5  $\times$  3–4 mm, narrowly elliptic or narrowly lanceolate-triangular, 5-veined, evenly short-connate or adaxial ones somewhat more connate, glabrous or sparsely lepidote, acute or

obtuse; **Pet** broadly tongue-shaped, 9–12.5  $\times$  2.5–3 mm, dirty greenish-yellow or greenish-punctate, blade narrowly elliptic, rounded; **St** deeply included, exceeding the style; **Fil** 3–5  $\times$   $\pm 0.2$  mm, whitish; **Anth** (sub-) basifixed, 2–2.5  $\times$  0.5 mm; **Ov**  $\pm 2$  mm, obconical or subcylindrical, abruptly contracted into the style; **Sty** stout, only  $\frac{1}{5}$ – $\frac{1}{3}$  as long as the ovary; **Sti** capitellate, flat.

**T. erici** Ehlers (Bromelie 1998(1): 18–21, ills., 1998). **Type:** Bolivia, Tarija (Haugg 11,247 [WU]). — **Distr:** S Bolivia (Tarija); epiphyte, 1800–2200 m. – Fig. 11.

[2] Plant stemless, flowering 12–22 cm tall, in small clusters or solitary; **L** 12–20, forming an erect rosette to 25 cm  $\varnothing$ , almost erect, fleshy to coriaceous, strongly veined (prominently when dry), finely appressed-lepidote, reddish-brown; **L** sheaths 2.5–4  $\times$  1.4–2 cm at the base, triangular-ovate, inconspicuously offset from the lamina; **L** lamina very narrowly triangular, 6–18 cm (outer ones reduced and only 10–12 cm), 0.8–1 cm wide at the base, very finely appressed-lepidote (adaxially less), margins strongly incurved, apex acute and pungent; **Inf** simple, shorter than the leaves; peduncle completely covered by the bracts, decurved, only 3–4 cm,  $\pm 4$  mm  $\varnothing$ ; lowest peduncular **Bra** leaf-like, the upper like the floral bracts, densely imbricate, 3.5 cm, coriaceous, lower ones

**Fig. 11** *Tillandsia erici*.  
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caudate, the upper acute; spike with 1–2 sterile bracts at the base, often  $\pm$  decumbent, 4–7 cm, 0.8–2 (after flowering to 3) cm wide, lanceolate or elliptic, complanate, (1–) 3- (to 7–) flowered, acuminate; rachis 4-angled, almost straight, glabrous, green; floral **Bra** imbricate, exceeding the sepals, 18–35  $\times$  8–13 mm, narrowly ovate, rigid and coriaceous, margins broadly hyaline, veined (strongly when dry), shiny, ecarinate, concealing the rachis, glabrous, stramineous or green tinged purple, acute; **Fl** sessile or with a short bicarinate pedicel-like receptacle, distichous, not fragrant; **Sep** 18–26  $\times$  6–9 mm, elliptic or oblong, membranous, with broad hyaline margins, slightly finely veined, free or shortly connate for 1–2 mm (abaxial one less if at all), adaxial ones bluntly carinate, pale green or brown tinged purplish-red, glabrous, acute; **Pet** spatulate, throat opening, 40–60  $\times$  9–12 mm, claw 3 mm wide, margins crenate-serrate and slightly undulate, bright orange-yellow, blade spreading and recurved; **St** included or  $\pm$  equalling the petal claw; **Fil** 25 mm, ribbon-like, filiform, thin, straight, yellowish-white, upwards yellow; **Anth** basifixed, 4–5  $\times$  0.4 mm, linear, yellow; **Ov** 5  $\times$  2.2 mm, slenderly prismatic; **Sty** slender, 30 mm; **Sti** lobes 14 mm, spreading or recurved, apex somewhat papillose for  $\pm$ 4 mm, yellow.

**T. ferrisiana** L. B. Smith (Bromeliad Soc. Bull. 10: 92, ill., 1960). **Type:** Mexico, Sinaloa (*Ferris & Mexia* 5121-A [DS]). — **Distr:** Mexico (Sinaloa, Baja California); epiphytic in dry woods and scrub,  $\pm$ 630 m.

[5] Plant forming dense clusters or few-branched; stem 2–6 (–10) cm; **L** laxly spirally arranged, much exceeding the inflorescence, to 15 cm, densely cinereous-lepidote; **L** sheath  $\pm$ 1 cm, sub-orbicular to narrowly ovate, densely cinereous-lepidote but glabrous where overlapping; **L** lamina very narrowly triangular to linear, involute-subulate, apex filiform-attenuate; **Inf** simple, erect, to 3 cm; peduncle short and concealed by the leaves; peduncular **Bra** somewhat leaf-like, densely imbricate; spike dense, terete, (1- to) 2- to 3-flowered; floral **Bra** exceeding the sepals, 20 mm, ovate, thin, veined towards the apex,

ecarinate, densely cinereously-lepidote, apiculate; **Fl** subsessile, distichous,  $\pm$ 50 mm; **Sep** 12–20  $\times$  6 mm, elliptic to lanceolate, membranous, smooth, free, adaxial ones carinate, appressed-lepidote or becoming glabrous, obtuse; **Pet** erect with recurving apex margins, 50 mm, bicoloured, the base red-violet to purple, the upper 20 mm yellowish or cream-coloured (Rauh 1979); **St** and **Sty** long exserted.

**T. fresnilloensis** W. Weber & Ehlers (Feddes Repert. 94(9–10): 609–611, fig. 9, 1983). **Type:** Mexico, Zacatecas (*Ehlers* s.n. [HAL (Herb. Weber)]). — **Distr:** C Mexico (Zacatecas); ecology and altitude not recorded. – Fig. 12.

[5] Plant flowering to 22 cm tall; stem richly branched at the base; **L** forming an erect rosette, numerous, white-lepidote; **L** sheaths to 2.5  $\times$  2 cm, triangular to ovate, strongly wrinkled when dry, indistinctly merging into the lamina; **L** lamina narrowly triangular, to 9 cm, in the middle to 1 cm wide, erect and secund, strongly grooved, apex acuminate; **Inf** simple; peduncle to 12 cm with internodes 2–2.5 cm, 2 mm  $\varnothing$ , terete, smooth, with weak purplish tint; peduncular **Bra** erect, just exceeding the internodes, lanceolate, veined, sparsely appressed-lepidote to almost glabrous, stramineous, finely apiculate; spike 3- to 6-flowered, rachis strongly geniculate; floral **Bra** shorter than the sepals, 20–23  $\times$  10–12 mm, ovate or lanceolate, margins broadly hyaline, faintly veined or even, ecarinate, glabrous on both faces, green and tinged red at the base, rounded and apiculate; **Fl** with a stout pedicel-like receptacle, spreading out,  $\pm$ 40 mm; **Sep** to 25  $\times$  9 mm, narrowly obovate or lanceolate, with broad hyaline margins, finely veined adaxially, connate for 2–3 mm, ecarinate but with very fleshy midvein, green, flushed red at the apex, glabrous on both faces, rounded or obscurely apiculate; **Pet** tongue-shaped, 42  $\times$  9 mm (3 mm at the base), greenish-white or green, acute; **St** in 2 unequal series of 46 and 51 mm, exserted but shorter than the style; **Fil** fleshy throughout, slender and flattened at the base and dilated-terete at the distal end, green with paler base; **Anth** dorsifixed near the middle, 2.5 mm, apex and base both truncate, green; **Ov**



**Fig. 12** *Tillandsia fresnilloensis*. (Copyright: E. J. Gouda)



4 mm, ovoid, gradually contracted into the style; **Sty** slender, 51 mm, twisting; **Sti** shortly conduplicate-spiral and slightly dilated, green.

**T. funebris** A. Castellanos (Anales Mus. Nac. Hist. Nat. Buenos Aires, ser. 3, 37: 502, 1933). **Type:** Argentina, Tucumán (*Schreiter* 1689 [BA, B, GH, LIL]). — **Distr:** Venezuela, Bolivia, N to E & C Argentina, Paraguay; epiphytic in dry forest, 200–2100 m.

[4] Plant small, flowering rarely over 10 cm tall, forming dense clusters; stem 2–5 cm, few- to richly branched at the base but otherwise simple; **L** laxly polystichous, to 5 cm; **L** sheaths making the stem appear stout, 0.5–0.8 cm, suborbicular to reniform, densely imbricate, subcoriaceous, with broad veinless margins, many-veined, lepidote and glabrous below, distinct from the lamina; **L** lamina narrowly triangular, densely cinereous-lepidote with small nearly symmetrical subappressed scales, divergent to reflexed, often distinctly keeled below,  $\pm$  contorted, triangular-subulate, strongly angled but not at all sulcate-striate, with a furrow above that does not reach the attenuate apex; **Inf** simple, 1- or 2-flowered, glabrous; peduncle distinct, nearly naked, erect or curved, much

exceeding the leaves, to 6 cm, 0.5 mm  $\varnothing$ , slender, glabrous; peduncular **Bra** 1–2 just below the flowers, 1.3 (–1.7) cm, oblong-lanceolate, subcoriaceous, even or many-veined, glabrous, acute; spike rachis like the peduncle and nearly as thick, swollen at the nodes; floral **Bra** slightly shorter or longer than the sepals, 9–15  $\times$  4.5–5 mm, like the upper peduncular bract but more ovate or elliptic, progressively smaller upwards, even, ecarinate, subacute; **Fl** subsessile, erect; **Sep** 9.5–10  $\times$   $\pm$  3 mm, narrowly elliptic, even or finely veined (many-veined), evenly shortly connate for <1–2 mm, adaxial ones with a strong midvein but ecarinate, acute; **Pet** spatulate, to 14  $\times$  3 mm, yellowish or coffee-brown when fresh and dark orange-brown when dry, blade distinct, subrhombic, spreading or near the tip margins recurved to helicoid, obtuse; **St** slightly unequal in length, 6–7 mm, deeply included; **Fil** slightly shorter than the style; **Anth** basifixed, 1.5–2 mm, linear, apex acute; **Ov** 2.5 mm, ellipsoid or shortly cylindrical, obtusely angled, contracted into the thick style; **Sty** short, 2 mm; **Sti** broadly capitate.

**T. gilliesii** Baker (J. Bot. 16: 240, 1878). **Type:** Argentina, Mendoza (*Gillies* s.n. [K, CGE, GH]).

— **Distr:** S Peru (Arequipa), Bolivia, Chile, Argentina; epiphytic, 310–3200 m.

**Incl.** *Tillandsia compressa* Gillies ex Baker (1878) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Tillandsia andicola* Wittmack (1887) (*nom. illeg.*, ICN Art. 53.1).

[4] Plant caulescent, flowering 4–6 cm tall, forming dense clusters; stem to 8 cm; **L** very densely arranged, distichous, 2–8 cm, densely cinereous-lepidote; **L** sheaths densely imbricate making the stem appear 5–7 mm Ø, broadly oblong, margins not overlapping behind the stem except at the extreme base, many-veined, glabrous where covered or lepidote upwards, passing gradually into the lamina; **L** lamina narrowly triangular, arching-recurved and often somewhat contorted, subulate and narrowly triangular, canaliculate above and much compressed laterally, apex acuminate and pungent; **Inf** peduncle distinct to almost absent, bractless or with 1 lanceolate involute bract at the very base, 5–13 cm, appressed-lepidote; **Inf** proper mostly 2-flowered, to 3.8 cm, densely cinereous-lepidote; spike rachis flexuous or straight, lepidote; floral **Bra** erect, equalling or exceeding the sepals, (11–) 14–16 (–18.5) × (7–) 9–10.5 mm, the uppermost sometimes slightly shorter, ovate-lanceolate to broadly triangular, thin, many-veined ( $\pm 15$  veins), distinctly so at the apex, ecarinate, slightly to 2× as long as the internodes, lepidote, acute or obtuse; **Fl** subsessile, erect, subdensely arranged; **Sep** (11.5–) 12.5–14.5 × 4–6 mm, ovate-lanceolate or narrowly ovate-triangular, thin, many-veined ( $\pm 10$  veins), evenly shortly connate, adaxial ones carinate, lepidote towards the apex or glabrous, apiculate or obtuse; **Pet** tongue-shaped, 12–15 × 3–4 mm, pale yellow, blade narrow, broadly rounded; **St** deeply included, exceeding the style; **Fil** 5–6 ×  $\pm 0.3$  mm, whitish; **Anth** subbasifixed, 2.5–4 × to 0.9 mm; **Ov** 3.5–5.5 × 2.5–3.5 mm, subglobose or obovoid (pear-shaped), abruptly contracted into the style; **Sty** stout, if at all slightly tapering, shorter than the ovary,  $\pm 1.5$  mm; **Sti** erect, slightly wider than the style, flat-capitate.

**T. glabrior** (L. B. Smith) López-Ferrari & al. (Selbyana 25(1): 60, 2004). **Type:** Mexico, Oaxaca (*Foster & Van Hyning* 2937 [US]). —



**Fig. 13** *Tillandsia glabrior*. (Copyright: E. J. Gouda)

**Distr:** S Mexico (Oaxaca); saxicolous on canyon walls, 910–1220 m. – Fig. 13.

≡ *Tillandsia pueblensis* var. *glabrior* L. B. Smith (1958) ≡ *Tillandsia schiedeana* ssp. *glabrior* (L. B. Smith) Gardner (1984).

[5] Plant caulescent, flowering to 35 cm tall; **L** spirally arranged, exceeding the peduncle and much shorter than the inflorescence, densely appressed-lepidote; **L** sheaths 1.5 × 1 cm, broadly ovate, sulcate towards the base, moderately contracted into the lamina; **L** lamina narrowly triangular, distinctly fleshy-succulent, whitish-cinereous-green, upwards secund, arcuate-recurved, to 11 cm and to 0.7 cm wide above the sheath, subulate and canaliculate; **Inf** simple; peduncle completely covered by its bracts, suberect, terete, 6–8.5 cm, 2 mm Ø; lower peduncular **Bra** somewhat leaf-like and laminate, erect, lamina gradually reduced in size distally, imbricate, longer than the internodes, densely enveloping the peduncle, appressed-lepidote; spike to 7 × 0.7 cm, lanceolate, subterete,  $\pm 5$ -flowered, acute, rachis partly exposed when dry; floral **Bra** erect, laxly imbricate, much exceeding the sepals, to 30 × 10 mm, lanceolate, veined, ecarinate, concealing the rachis or so narrow as to partially expose the rachis,  $\pm 3 \times$

as long as the internodes, scatteredly appressed-lepidote to subglabrous; **Fl** distichous; **Sep** to  $18 \times 6$  mm, ovate-lanceolate, adaxial ones connate for 8 mm, carinate, glabrous; **Pet** forming an erect narrow tube clasping the filaments at the apex, size not recorded, (rose-)red or partly yellow towards the apex; **St** exerted; **Anth** dorsifixed near the middle; **Ov** not described; **Sty** just exceeding the stamens; **Sti** lobes slightly divergent, green.

**T. guerreroensis** Rauh (Trop. subtrop. Pfl.-welt 60: 65–67, ill., 1987). **Type:** Mexico, Guerrero (*Koide* s.n. in *HEID* 66721 [HEID]). — **Distr:** S Mexico (Guerrero); saxicolous,  $\pm 1000$  m.

[1] Plant stemless or with a short rhizome, flowering to 15 cm tall; **Ros**  $12 \times 18$  cm; **L** numerous; **L** sheaths distinct,  $2 \times 1.5$  cm, broadly ovate, both faces densely leather-brown-lepidote; **L** lamina very narrowly triangular, to  $8 \times$  basally 0.8 cm, spreading to strongly recurved, fleshy, with extending trichomes at the margins, strongly canaliculate, both faces densely cinereous-lepidote, margins  $\pm$  involute, apex attenuate and abruptly pungent; **Inf** simple or rarely digitate with 2 spikes; peduncle erect, very short, largely concealed by the leaves and bracts, mostly  $< 5$  cm; lowest peduncular **Bra** somewhat leaf-like, the upper like the floral bracts, erect, densely imbricate; spikes decumbent, to  $7 \times 1.5$  cm, lanceolate, complanate with convex sides, 5- to 6-flowered, acuminate;

floral **Bra** suberect and contiguous with each other, densely imbricate, much exceeding the sepals,  $25 \times 12$  mm, ovate, margins membranous, veined esp. when dry, ecarinate, concealing the rachis, abaxially subdensely lepidote masking the colour in part, rose-red, with pale green edges, broadly rounded; **Fl** distichous, erect appearing at the upper side of the curving spike; **Sep**  $15 \times 5$  mm, membranous, free, adaxial ones sharply carinate, whitish with reddish midvein, glabrous, acuminate; **Pet** forming an erect narrow tube clasping the filaments at the apex, the tips spreading, tongue-shaped, to  $30 \times 8$  mm, deep dark violet; **St** exerted; **Ov** not described; **Sty** shorter than the stamens.

**T. hasei** Ehlers & L. Hromadnik (Bromelie 1996(3): 76, ill., 1996). **Type:** Bolivia, Chuquisaca (*Hase & al.* s.n. [EB 951501, WU]). — **Distr:** S Bolivia (Chuquisaca); on rocks in a river bed,  $\pm 3100$  m. — Fig. 14.

[2] Plant strongly rooted on rocks, short-stemmed, flowering rosette  $6\text{--}10 \times 2\text{--}2.5$  cm, forming large mats; **L**  $10\text{--}20$ , densely rosulate, erect or spreading, the outer ones reduced and to 6 cm, robust, very thick or stiffly succulent, margins with asymmetric trichomes, densely cinereous-lepidote, grey; **L** sheaths  $1\text{--}2 \times$  basally 0.7–1.2 cm, elliptic to triangular, lepidote with fine grey scales on both faces but adaxial base glabrous for 1–2 mm, slightly

**Fig. 14** *Tillandsia hasei*.  
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distinct from the lamina; **L** lamina very narrowly triangular, 2–4 cm, base 0.4–0.5 cm wide, strongly secund, densely lepidote on both faces with large grey scales, strongly veined particularly abaxially, adaxially keeled, margins involute, subulate, apex attenuate or long-caudate; **Inf** always simple; peduncle erect or decurved, very short and concealed by the leaves, 1–2 cm,  $\pm 2$  mm  $\varnothing$ , terete, glabrous; lowest peduncular **Bra** somewhat leaf-like and 2 cm, the upper shorter and like the floral bracts, densely imbricate, lepidote; spike 2–2.5 cm, 3–6 mm wide, linear-lanceolate, complanate, distichously 1- to 3-flowered, acute, with 1 sterile bract at the apex, rachis 4-angled, sinuous or almost straight, glabrous, exposed; floral **Bra** imbricate, exceeding the sepals for 5–8 mm, 15–23  $\times$  5–7 mm at the base, triangular, coriaceous, strongly veined, towards the base glabrous but lepidote in the upper  $\frac{1}{3}$  and esp. at the tip with large grey scales, red, cuspidate; **Sep** 13–15  $\times$  3 mm, lanceolate, very thinly coriaceous, veined, free, adaxial ones strongly carinate, light green with a red tip, glabrous, acuminate; **Pet** erect, linear without a distinct blade, 25–29  $\times$  2.5 mm, shiny carmine-red, white at the base, blade tip margins recurving or helicoid, rounded; **St** 15 mm, included; **Fil** thin, ribbon-like, plicate in the middle, white; **Anth** basifixed, 3.5–4  $\times$  0.4 mm, linear, olive-green; **Ov** 2  $\times$  1 mm,

ellipsoid; **Sty** 15 mm; **Sti** lobes 0.8 mm, inconspicuous, spreading.

**T. hegeri** Ehlers (Bromelie 1994(2): 33, ill., 1994). **Type:** Bolivia, Tarija (*Heger* s.n. [WU]). — **Distr:** S Bolivia (Chuquisaca, Tarija); saxicolous, 2700–2720 m. — Fig. 15.

[1] Plant stemless or very short-stemmed, flowering 10–14 cm tall; **Ros** broad, basally offsetting; **L**  $\pm 12$ , erect to becoming spreading horizontally, to 12 cm, very thick-leathery or succulent, margins with asymmetrical trichomes, densely cinereous-lepidote, somewhat reddish-grey; **L** sheaths 3–4  $\times$  2–2.3 cm, ovate, passing gradually into the lamina; **L** lamina narrowly triangular, canaliculate or subulate towards the apex, with a central keel, outer face very strongly veined, apex attenuate; **Inf** simple, terminal, exceeding the leaves; peduncle very short and concealed by the leaves; lowest peduncular **Bra** somewhat leaf-like and similar to the rosette leaves, densely imbricate, 1–1.5 cm, upper ones similar to the floral bracts, ovate, coriaceous, lepidote to glabrous, wine-red, acute; spike with 1 sterile bract at the base, 6  $\times$  2 cm, elliptic,  $\pm 10$ -flowered, acuminate, rachis almost straight, glabrous; floral **Bra** imbricate, exceeding the sepals, 14–16 mm wide, ovate, thinly coriaceous, veined on the inner face, shiny, often slightly waxy, carinate towards the

**Fig. 15** *Tillandsia hegeri*.  
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apex, concealing the rachis at anthesis, glabrous on the outer face, dark wine-red, acute or cuspidate; **Fl** sessile, distichous, not fragrant; **Sep** 20–24 mm, elliptic, thinly coriaceous, evenly shortly connate for 2 mm, adaxial ones strongly carinate, red with strong thicker green centre, glabrous, acute; **Pet** forming an erect narrow tube clasping the filaments at the apex and the tips spreading with opening throat, almost tongue-shaped, 36–39 × 7 mm, base 4 mm wide, margins finely serrulate, blue-violet, white towards the base, blade slightly if at all divergent, obtuse; **St** included; **Fil** 20–25 × 1.2 mm in the basal 1/3, ribbon-like, almost straight, wavy at the base, white; **Ov** ovoid; **Sty** as long as the petal tube, narrowing towards the tip; **Sti** 4 mm, lobes strongly spreading, papillose, yellowish.

**T. helmutii** L. Hromadnik (Bromelie 1990(3): 63, ill., 1990). **Type:** Bolivia, Chuquisaca (Hromadnik 13,009 [WU]). — **Distr:** S Bolivia (Chuquisaca); saxicolous on vertical cliffs, 1700–1800 m. – Fig. 16.

[1] Plant short-stemmed, flowering 50 cm tall; **Ros** solitary or few-branched; **L** densely rosulate, the upper ones erect and those below spreading, 20–30 cm, becoming stiff, margins fimbriate; **L** sheaths ±2 × 4 cm, broadly triangular, thickly leathery, with membranous lobes at the margins, finely veined, lower 1 cm of the adaxial face glabrous, upper 1/2 and abaxially densely appressed-lepidote with radial trichomes, greenish-yellow; **L** lamina narrowly triangular, thick, succulent, 1.7–2.5 cm wide at the base, densely lepidote with prominent dorsiventral silvery scales, smooth and upper 1/2 strongly grooved to finely veined, apex apiculate; **Inf** simple or 1 × branched and subdigitate, exceeding the leaves; peduncle not wholly hidden by its bracts, erect, ± equalling the leaves, 5 mm Ø, smooth towards the base, internodes 2–3 cm, glabrous, green; lowest peduncular **Bra** somewhat leaf-like, 4.5–6 cm, narrowly ovate, the top ones convex, thickly leathery, veined, densely lepidote, green, apiculate; primary **Bra** like the peduncular bracts or narrowly ovate with distinct tip, 4–4.5 × 1.5 cm, thickly leathery, veined, apiculate, abaxially densely appressed-lepidote, adaxially glabrous except at



**Fig. 16** *Tillandsia helmutii*. (Copyright: E. J. Gouda)

the tip, greenish to pale pinkish-orange; spikes up to 5, almost sessile, erect, 8 × 1.9 cm, strongly complanate, long acuminate, rachis straight, sparsely lepidote with scattered punctulate scales, partly exposed, with cavities, green, internodes 0.7 cm; floral **Bra** densely imbricate, 25–40 × 12–15 mm, narrowly or triangularly ovate, convex, fleshy-coriaceous, margins membranous, strongly veined when dry, obscurely carinate towards the apex and bicarinate at the base, lower ones lepidote, upper ones glabrous, green or pale pink-orange, apiculate; **Fl** densely distichous, 55 mm, not fragrant; **Sep** 20–30 × 9.5 mm, ovate, fleshy in the lower 1/2 to membranous upwards, veined, evenly short-connate or at least the adaxial ones connate for 1 mm and bluntly carinate, green, glabrous, slightly acuminate or attenuately acute; **Pet** forming an erect narrow tube clasping the filaments at the apex, tongue-shaped, 41–47 × 5–6 mm, margins slightly undulate at the apex, white and tinged pale violet on the blade, blade



indistinct, divergent to spreading, obtuse; **St** 28–32 mm, included; **Fil** thin and ribbon-like, flaccid, straight, basally white, near the tip pale violet; **Anth** basifixed, 3.5–4 mm, linear, pale yellow; **Ov** 6–7 × 2 mm, shortly cylindrical or slenderly ovoid, merging into the style; **Sty** slender, 23 mm, exceeding the stamens and emerging from the corolla throat; **Sti** spreading or erect, linear, papillose, lobes white.

**T. hirta** W. Till & H. Hromadnik (Pl. Syst. Evol. 147: 285–286, 1984). **Type:** Bolivia, Cochabamba (*Hromadnik & Hromadnik* 5001 [WU]). — **Distr:** S Peru (Arequipa), Bolivia, NE Argentina; epiphytic on trees, bushes or cacti, 1800–3700 m.

[4] Plant short-stemmed, flowering 10–20 cm tall, few-branched; **L** distichous, 2–6 cm, densely silvery-white tomentose-lepidote; **L** sheaths 0.8 × 0.6 cm, ovate, clasping the stem, membranous, veined, densely tomentose but glabrous towards the base; **L** lamina 1–5 × 0.2–0.3 cm, ± recurved with the tips spreading and bending outwards, subulate, apex acuminate; **Inf** simple; peduncle naked or rarely with 1 bract just below the flower, 1–6 cm, 1 mm Ø, subglabrous, spike 1–2.5 cm, 1- to 3-flowered; floral **Bra** erect, equalling or exceeding the sepals, 7–15 × 5 mm, ovate, lanceolate, veined, ecarinate, densely lepidote, acute; **Fl** subsessile, distichous; **Sep** 10–12 mm, lanceolate, thin, veined, evenly shortly connate, densely lepidote; **Pet** erect, forming a tube, 30–40 mm, yellowish, blade narrow; **St** included; **Fil** 1-veined, (3.2–) 3.8 (–4.9) mm, white; **Anth** basifixed, (1.4–) 1.7 (–2.1) × ±0.3 mm, orange; **Ov** (3.8–) 4.3 (–5.2) × (1.8–) 2.2 (–2.7) mm; **Sty** much shorter than the ovary; **Sti** inconspicuous.

**T. intermedia** Mez (Bull. Herb. Boissier, sér. 2, 3: 141, 1903). **Type:** Mexico, Guerrero (*Langlássé* 370 [G, F, GH, US]). — **Distr:** Mexico (Guerrero, Jalisco, Sinaloa, Colima, Yucatán); epiphytic, 0–290 m.

**Incl.** *Tillandsia paucifolia* var. *schubertii* F. Ebel & Röth (1988).

[5] Plant flowering to 40 cm tall or much longer when growing from shoots from the inflorescence; **L** to 35 cm; **L** sheaths forming an elongate pseudobulb, 2.5 cm wide, inflated, densely

cinereous-lepidote, merging gradually into the lamina; **L** lamina linear, rigid, covered with dense pale appressed lepidote trichomes for most part, erect or irregularly curved, involute-subulate or more canaliculate at the base, apex subpungent; **Inf** simple or 1 × branched, composed of up to 4 almost equal-sized spikes; peduncle shorter than or much exceeding the leaves, slender; peduncular **Bra** somewhat leaf-like with conspicuous decurved involute lamina, shorter than the internodes; primary **Bra** like the upper peduncular bracts but with a shorter lamina, decurved, densely lepidote abaxially; spikes subsessile, strictly erect, sublax, 4–10 × 1.2 cm, elliptic, 3- to 12-flowered, acute, rachis lepidote, partly exposed, green-brown; floral **Bra** distichous, becoming further apart but laxly imbricate, slightly exceeding the sepals, 18–20 × 8 mm, triangular-ovate, convex, coriaceous, distinctly veined, ecarinate (but bi-angled at the base), so narrow as to partly expose the rachis, abaxially densely to sparsely lepidote with small appressed scales, green and tinged reddish at the apex and margins or roseate, narrowly rounded; **Fl** with a short pedicel-like receptacle, distichous, suberect, densely arranged, 50 mm; **Sep** elliptic, thinly coriaceous, even or prominently veined near the apex, adaxial ones connate for up to 3 mm, adaxial ones carinate at the base, green and tinged red, glabrous, broadly acute; **Pet** forming an erect narrow tube clasping the filaments at the apex, tongue-shaped, 38 × 5.5 mm, basally 2 mm wide, purple, blade tip margins recurving, acutish or obtuse; **St** 47 mm, exerted; **Fil** exposed part slightly inflated and (sub-)terete; **Anth** dorsifixed at ¼ from the base, 3 mm, apex obtuse, brownish; **Ov** 5 × 2.5 mm, ovoid, gradually contracted into the style; **Sty** slender, exceeding or ± equaling the stamens.

**T. ionantha** Planchon (Fl. Serres Jard. Eur. 10: 101, t. 1006, 1855). **Type:** [icon]: l.c. t. 1006. — **Distr:** SE & S Mexico, Guatemala, C & S Honduras, NW El Salvador, W & C Nicaragua, NW & W Costa Rica, W Panama, S Peru; epiphyte, 0–3050 m. – Fig. 17.

**Incl.** *Tillandsia erubescens* H. Wendland (1854) (*nom. illeg.*, ICN Art. 53.1) ≡

**Fig. 17** *Tillandsia ionantha*. (Copyright: E. J. Gouda)



*Pityrophyllum erubescens* (H. Wendland) Beer (1856); **incl.** *Pourretia stricta* hort. ex Beer (1856); **incl.** *Tillandsia quesneliana* hort. ex Beer (1856); **incl.** *Tillandsia scopus* Hooker fil. (1871) (*nom. inval.*, ICN Art. 32.1c); **incl.** *Tillandsia rubentifolia* Poisson & Menet (1908); **incl.** *Tillandsia ionantha* var. *zebrina* B. T. Foster (1982).

[5] Plant stemless or rarely shortly caulescent, usually forming dense clusters; stem stout and fleshy; **L** rarely >6 cm, densely cinereous-lepidote with spreading scales; **L** sheath  $\pm\frac{1}{2}$  as long as the lamina, elliptic; **L** lamina narrowly triangular, 5 mm wide at the base, green or the inner ones (or all) becoming deep red at anthesis, densely cinereous-lepidote to tomentose-lepidote, divergent esp. upwards, subulate and canaliculate except the attenuate apex; **Inf** appearing to be a simple abbreviated spike with polystichous flowers, but actually a reduced compound panicle; peduncle nearly none, axes abortive; primary **Bra** narrowly ovate,  $\pm 23 \times 5$  mm, equalling or exceeding the sepals, membranous, acute, lepidote towards the apex; spikes reduced to a single flower each; floral **Bra** like the primary bracts but shorter than to slightly exceeding the sepals,  $13\text{--}20 \times 4\text{--}8$  mm, triangular-ovate, faintly veined, obtuse; **Fl** sessile, erect; **Sep**  $16\text{--}18 \times 4\text{--}5$  mm, lanceolate to oblong-lanceolate, membranous, with broad hyaline margins, evenly short-connate for 1 mm, or free, adaxial ones carinate, glabrous, acutish; **Pet**

forming an erect narrow tube clasping the filaments at the apex, tongue-shaped,  $40\text{--}48 \times 7$  mm, base 3 mm wide, violet, claw linear-cuneate, blade tip margins recurving, subacute or rounded; **St** in 2 whorls of unequal length,  $45\text{--}56$  mm, long-exserted; **Fil** exposed part slightly inflated and (sub-)terete, straight, exposed part violet; **Anth** dorsifixed at  $\frac{1}{3}$  from the base, apex obtuse or rounded, yellow; **Ov**  $6 \times 2\text{--}2.5$  mm, narrowly ovoid, tapering into the style; **Sty** slender,  $42\text{--}52$  mm, exceeding the stamens, dilatated in the upper part; **Sti** spreading, white.

A very variable species with several published varieties and forms. The most different and succulent is var. *vanhyningii* M. B. Foster that grows on steep rock surfaces and has a more cinereous appearance.

**T. kirschnekii** Rauh & W. Till ex Rauh (Trop. subtrop. Pfl.-welt 43: 13–14, ill., 1983). **Type:** Peru, Apurímac (*Kirschnek* s.n. in *BG Heidelberg* 39,770 [HEID]). — **Distr:** S Peru (Apurímac); rock walls,  $\pm 2500$  m. — Fig. 18.

[3] Plant long caulescent, richly branching from the base forming big cushions; leafy stem part to 15 cm,  $3\text{--}5$  mm  $\varnothing$ ; **L** densely rosulate, numerous, erect; **L** sheaths  $\pm 1 \times 1.5$  cm, very broadly ovate, tightly clasping the stem, membranous, glabrous in the lower  $\frac{2}{3}$  to densely cinereous-lepidote abaxially in the uncovered upper part; **L** lamina narrowly triangular,



**Fig. 18** *Tillandsia kirschnekii*. (Copyright: E. J. Gouda)

succulent, 2–3.5 (–4) × 0.4 cm, cinereous-green, densely lepidote on both faces with brown-centred trichomes, suberect or slightly divergent and then curved inwards, angled subulate and shallowly canaliculate in the lower ½ and with a furrow in the centre, apex acute or filiform-attenuate; **Inf** simple, short to much exceeding the leaves; peduncle completely covered by its bracts, erect, 1–3 cm, mostly short and concealed by the leaves, glabrous; lowest peduncular **Bra** somewhat leaf-like, the upper like the floral bracts, few (2–4), imbricate, cinereous-lepidote, the upper ones only acute without lamina; spikes 1–3 × 1 cm, elliptic to lanceolate, strongly complanate, (1- to) 3- to 5-flowered, apex irregular with sterile bracts, rachis alate-excavated, slightly flexuous, partly exposed or hidden, green, internodes 2–5 mm; floral **Bra** imbricate, slightly exceeding the sepals, 10–16.5 × 4–7 mm, narrowly ovate or elliptic, closely enveloping the flowers, chartaceous, margins scarious and

veinless, strongly veined when dry, ecarinate, so narrow as to expose the rachis in part, ±3× as long as the internodes, abaxially lepidote but sparsely so towards the base, green, obtuse or obtuse-apiculate; **Fl** with a short pedicel-like receptacle, distichous, contiguous with each other and/or the rachis, densely arranged; **Sep** 9–14 × 5–5.5 mm, obovate, slightly asymmetrical, membranous, with broad hyaline margins, finely veined (strongly so when dry), evenly shortly connate (obscure when fresh), adaxial ones carinate, green and rose or tinged purplish towards apex and margins, glabrous on both faces, obtuse or acutish; **Pet** claw narrow with suborbicular (to subdeltoid) blade, 22–25 × 12–15 mm, blue-violet with white claw, blade abruptly broadened, spreading, broadly rounded; **St** 7 mm, deeply included, exceeding the style; **Fil** flat, lanceolate, tapering from near the base, thin; **Anth** basifixed (?), 1.5 mm, yellow; **Ov** 3 × 2 mm, pyriform or ellipsoid, abruptly contracted into the style; **Sty** stout, 1 mm; **Sti** capitate.

**T. klausii** R. Ehlers (J. Bromeliad Soc. 38(6): 257–260, ills., 1988). **Type:** Mexico, Chiapas (Ehlers & Ehlers EM851801 [WU, HAL, WU]). — **Distr:** SE Mexico (Chiapas); saxicolous on steep rocks. — Fig. 19.

[5] Plant stemless, flowering 15 cm tall, forming clumps; **L** forming a subbulbous or a spreading rosette, few to many, to 17 cm, succulent and soft or brittle, green to rose or red in bright sun; **L** sheaths suberect, to 4 × 3.5 cm, broadly ovate, ± inflated, densely cinereous-lepidote on both faces, both faces (pale) brown or abaxially green (in cultivation), conspicuously offset from the lamina; **L** lamina narrowly triangular to linear, to 13 × 2 cm wide, densely cinereous-lepidote with spreading scales on both faces, spreading to recurved, trichomes with elongated wings, margins involute-subulate and nearly touching each other when dehydrated; **Inf** simple, erect, ± equalling to much exceeding the leaves; peduncle erect, short and concealed by the leaves, 1–5 cm, 7 mm Ø; peduncular **Bra** similar to the floral bracts but smaller, erect, few, densely imbricate, to 3.5 cm, elliptic, densely lepidote, green-rose, shortly acuminate; spike (3–) 5–9 × to 2.2 cm, elliptic or lanceolate, complanate, 2- to



**Fig. 19** *Tillandsia klausii*. (Copyright: E. J. Gouda)

4- (to 7-) flowered; floral **Bra** erect,  $\pm$  imbricate,  $>2\times$  as long as the sepals,  $35\text{--}45 \times 15\text{--}20$  mm, narrowly ovate, faintly veined, ecarinate, mostly concealing the rachis,  $2\text{--}3\times$  as long as the internodes, densely lepidote except towards the base, pink or roseate, acute; **Fl** with a short pedicel-like receptacle, not fragrant; **Sep**  $22\text{--}24 \times 4\text{--}5$  mm, lanceolate to narrowly oblong, subcoriaceous, with broad hyaline margins, veined, connate for  $\pm 1$  mm, fleshy, adaxial ones carinate at the base (sharply so when dry), green at the base but centre part red, glabrous, acutish; **Pet** erect, forming a tube, tongue-shaped,  $50\text{--}70 \times 9\text{--}10$  mm, basally 4 mm wide and white, upper  $\frac{1}{2}$  blue-violet, blade tip margins recurving, rounded; **St**  $70\text{--}75$  mm, exerted; **Fil** flat, thicker towards the apex but still complanate, thin and flaccid at the base, sometimes slightly twisted, white at the base and violet upwards; **Anth** dorsifixed at  $\frac{1}{3}$  from the base,  $3\text{--}4 \times 1$  mm, pale brown; **Ov**  $7 \times 2.5$  mm, cone-shaped with flat sides, contracted into the

style; **Sty** slender, more robust in the upper  $\frac{1}{3}$ ,  $\pm 70$  mm, exceeding the anthers for 8 mm; **Sti**  $3 \times 2$  mm,  $\pm$  spreading, papillose, white.

**T. kuehhasii** W. Till (Bromelie 1995(2): 33, ill., 1995). **Type:** Bolivia, Chuquisaca/Potosí (*Kühhas & Kirschnek* s.n. [WU]). — **Distr:** S Bolivia (Chuquisaca, Potosí); saxicolous, 3600 m.

[4] Plant forming dense clusters; stem to 25 cm but usually only terminal 10 cm with living leaves, branched at several nodes along the stem; **L** densely distichous, distally straight, flexible, white; **L** sheaths  $\pm 1.5$  cm, broadly ovate, amplexicaul, densely lepidote, merging gradually into the lamina; **L** lamina subulate, (2.5–)  $5\text{--}7.5$  cm, 2 mm wide at the base, densely cinereous-lepidote, suberect or irregularly spreading, upper face with a furrow; **Inf** 1-flowered, erect,  $\pm 5$  cm, shorter than to as long as the leaves; peduncle with a single bract at the base, partly visible, very short or slightly elongate,  $2\text{--}3.5$  cm, elongating after flowering, 1 mm  $\varnothing$ , grooved when dry, sparsely lepidote to almost glabrous towards the base; peduncular **Bra** involute around the peduncle with overlapping margins, cinereous-lepidote, with leaf-like lamina; floral **Bra** shorter than the sepals,  $13 \times 10$  mm, broadly ovate to ovate-oblong, distinctly 10- to 12-veined, abaxially densely lepidote only, cinereous-green or tinged brown towards the margins, rounded and apiculate or caudate with a 2 mm long apiculus; **Sep** (10–)  $13.5\text{--}16 \times 3.5$  mm, lanceolate, veined, adaxial ones connate for  $5\text{--}7$  mm, adaxial ones bluntly if at all carinate or narrowly convex, green or tinged brown-red at the apex, abaxially sparsely to subdensely appressed-lepidote towards the apex, apiculate or obtuse; **Pet** tongue-shaped,  $15\text{--}25 \times 4$  mm, yellow tinged brown to chestnut-brown with yellow claw, apical part recurved to recoiled; **St**  $\pm 10$  mm, deeply included, much exceeding the pistil; **Fil** flat, attenuate from near the base, straight; **Anth** basifixed, slightly  $< 2$  mm, narrowly oblong, yellow; **Ov** 2.5 mm, obconical, abruptly contracted into the style; **Sty** stout,  $\pm$  as long as the ovary; **Sti** erect, short and capitellate.

**T. latifolia** Meyen (Reise um die Erde 2: 45, 1835). **Type:** Peru, Arequipa (*Meyen* s.n. [B]).





**Fig. 20** *Tillandsia latifolia*. (Copyright: E. J. Gouda)

— **Lit:** Rauh & Bismarck (1996). **Distr:** C Venezuela (Aragua), Ecuador (widespread), Peru (widespread); terrestrial or epiphyte, 0–3500 m. — Fig. 20.

≡ *Platystachys latifolia* (Meyen) K. Koch (1874); **incl.** *Tillandsia kunthiana* Gaudichaud (1842) ≡ *Platystachys kunthiana* (Gaudichaud) Beer (1856); **incl.** *Tillandsia grisea* Baker (1887); **incl.** *Tillandsia oxysepala* Baker (1888); **incl.** *Tillandsia lanata* Mez (1905); **incl.** *Tillandsia murorum* Mez (1913).

[1] Usually caulescent, flowering to 60 cm high; stem often branched, prostrate; **L** to 20 (to 30 and more) cm, covered with appressed cinereous scales; **L** sheath slightly distinct from the lamina; **L** lamina narrowly triangular, to 3 cm wide at the base, usually spreading to recurved, canaliculate, apex acute or long attenuate; **Inf** 1 × branched or rarely simple, dense or lax, sometimes viviparous; peduncle (almost) completely covered by the bracts, shorter than or exceeding

the leaves but always distinct, from short to ±40 cm, 3.5 mm Ø, stout, glabrous; lowest peduncular **Bra** leaf-like, slender with spreading to recurved blades, imbricate, the upper more lanceolate, cinereous-lepidote; primary **Bra** like the upper peduncular bracts, suberect, shorter than the spikes, apiculate or acute; spikes subsessile, erect or mostly spreading sideways (from between the bract and axis), 1 cm wide, lanceolate, complanate, 6- to 12-flowered; floral **Bra** densely imbricate, slightly shorter than to exceeding the sepals, 10–13 (–23) mm, broadly ovate, ± incurved, strongly convex, stiffly subcoriaceous, even or nearly so, upper ½ finely or obscurely carinate, subdensely cinereous-lepidote with large trichomes or generally becoming glabrous with age, base often green to wholly red, tip acute or finely apiculate; **Fl** subsessile; **Sep** incurved, 10.5–12 (–20) × 3.5–4 mm, narrowly ovate or lanceolate, nearly even, adaxial ones connate for 5.5–8 mm, adaxial ones sharply carinate from base to apex, green and with red upper ½ or apex, sparsely lepidote or glabrescent, acutish or obtuse; **Pet** erect, (ob-)lanceolate, 18–19 (–27) × 3–4 mm, blades to 7 mm longer than the sepals (according to Mez), upper ½ (deep) pink, blade narrow, suberect or slightly divergent, narrowly rounded to obtuse or acutish; **St** 13 mm, included, exceeding the style; **Fil** broadly ribbon-like, flaccid, plicate in the upper ¼; **Anth** dorsifixed near the base or at ½ from the base, 3.5 mm, linear, obtuse, yellow; **Ov** obovoid (to pyriform), 3 mm, gradually contracted into the style; **Sty** slender, 8 mm, attenuate from the base upwards; **Sti** erect, shortly conduplicate with papillae only near the apex, pink at the base.

Very variable in habitus, esp. as to leaf size and succulence. The variety from the Peruvian desert forming adventitious shoots has short fleshy leaves. The status of the published varieties and the relationships with closely similar species have not yet been fully investigated.

Plants depicted on Mochica pottery from the Río Moche area near Trujillo dating from 600 BCE to 1000 CE are likely this species and/or *T. purpurea*, making them the earliest-figured species of the genus (Rauh & Bismarck 1996).



**T. lepidosepala** L. B. Smith (Proc. Amer. Acad. Arts 70: 155, t. 2, figs. 2–3, 1935). **Type:** Mexico, Michoacán (*Pringle* 5323 [GH]). — **Distr:** Mexico (Aguascalientes, Guanajuato, Michoacán); saxicolous and epiphytic, dry slopes, 1460–2500 m.

≡ *Viridantha longisepala* (L. B. Smith) Espejo (2002).

[1] Plant stemless or short-stemmed, flowering to 15 cm tall; **Ros** 18 cm Ø, irregular and open, often in groups or forming clumps; **L** laxly arranged, few to many, spreading, to 16 cm, fairly succulent, densely cinereous-lepidote; **L** sheath 1–1.5 × to 1.5 cm, ovate or suborbicular, somewhat inflated, lepidote but glabrous towards the base; **L** lamina narrowly triangular, to 15 cm, 0.7 cm wide at the base, silvery cinereous-lepidote, spreading to recurved, slightly canaliculate, apex acuminate; **Inf** simple or more rarely with a small second lateral spike, shorter than the leaves; peduncle short and concealed by the leaves, slender; peduncular **Bra** leaf-like, the lower roughly as long as the inflorescence, the upper like the floral bracts, erect, densely imbricate, much exceeding the internodes; spikes 3–5 × (1–) 1.2–1.8 (–2) cm, complanate with ± flat sides, 2- to 5-flowered; floral **Bra** densely imbricate, exceeding the sepals, 19–21 (–35) × 6–9 mm, narrowly or triangular-ovate, almost membranous, finely veined when dry, ecarinate, 3–4× as long as the internodes, densely lepidote, cinereous to dark green at the base, shortly fleshy-acuminate; **Fl** sessile, densely distichous; **Sep** 12–15 (–20) × 4–5.5 mm, widest just above the base, lanceolate or narrowly ovate, with broad hyaline margins, strongly veined when dry, free or unequally short-connate for up to 1.5 mm, adaxial ones carinate, green, subsparingly lepidote on both faces, attenuately acute or obscurely apiculate; **Pet** erect with slightly divergent apex, linearly tongue-shaped, 20–25 × 2.5–3.5 mm, basally only 2.5 mm wide, green, narrowly rounded; **St** 15 mm, included, longer than the style; **Fil** 15–18 mm, thread-like, thin, straight, white; **Anth** dorsifixed near the base, 2–3 mm, linear, apex obtuse, olive-green; **Ov** 4–5 × 3.5 mm, ellipsoid, gradually contracted into the style; **Sty** slender, incl. stigma 8–10 mm;

**Sti** shortly conduplicate, small, erect or the green lobes somewhat divergent, papillose at the apex only.

**T. lithophila** L. Hromadnik (Bromelie 5: 48–51, ill., 2005). **Type:** Peru, La Libertad (*Hromadnik & Hromadnik* 23,115 [USM, WU]). — **Distr:** NW Peru (La Libertad); saxicolous on steep rocks, ±2200 m.

[1] Plant with very short stem, flowering to 20 cm tall, growing in groups; **L** forming a narrow tuft-like rosette, polystichous, erect, 6–12 cm; **L** sheath 1.5 cm wide at the base, triangular, subamplexicaul, appressed-lepidote, indistinctly merging into the lamina; **L** lamina narrowly triangular to linear, rigid and somewhat succulent, 0.7 cm wide at the base, silvery and densely lepidote, secund-arcuate, involute-subulate, apex attenuate and subpungent; **Inf** 1× branched or rarely simple, composed of up to 4 spikes, 5.5 × 1.5 cm; peduncle erect or decurved, much exceeding the leaves, to 12 cm, 1–2 mm Ø, densely white-lepidote; peduncular **Bra** densely imbricate, longer than the internodes, to 2.5 cm, coriaceous, veined, abaxially densely lepidote, adaxially glabrous, purplish-red, with an awl-like tip, keeled; primary **Bra** like the upper peduncular bracts, 1.5–1.7 cm, caudate-acuminate; spikes short-stipitate, stipe 2–3 cm, bearing 2–3 small sterile bracts at the base, erect to somewhat divergent, 3–3.5 cm, 6–9 mm wide, lanceolate, strongly complanate, 4- to 7-flowered, rachis lepidote, exposed, internodes 3–4 mm; floral **Bra** distichous, densely imbricate, 13 × 6 mm, triangular to ovate, coriaceous, veined, ecarinate, adaxially glabrous, abaxially densely lepidote, purplish-roseate, white-caudate; **Fl** sessile, to 20 mm; **Sep** 12 × 2 mm, lanceolate, chartaceous, 3-veined, connate for 3 mm, adaxial ones alate-carinate, rose, abaxially lepidote only along the midvein; **Pet** tongue-shaped, to 18 × 2 mm, white, with a blue band above the sepals (changing to pale violet immediately after flowering), blade tip margins divergent, obtuse; **St** 15 mm, included and visible in the throat, as long as the style; **Fil** filiform, straight, white; **Anth** dark brown; **Ov** 3 × 1 mm; **Sti** lobes suberect and very thin.

**T. loliacea** Martius ex Schultes *fil.* (in Roemer & Schultes, Syst. Veg. 7(2): 1204, 1830). **Type:** Brazil, Bahia (Martius s.n. [M, GH [photo]]). — **Lit:** Till (1989). **Distr:** Brazil, Bolivia, Argentina, Paraguay, Uruguay; saxicolous and epiphytic in semi-arid habitats, 0–2400 m.

**Incl.** *Tillandsia undulata* Baker (1887); **incl.** *Tillandsia quadriflora* Baker (1889); **incl.** *Tillandsia atrichoides* S. Moore (1895).

[4] Plant with a rhizomatous stem, flowering to 17 cm tall but usually much less, stem rarely >4 cm, most of it leafless, simple or few-branched; **L** densely rosulate, mostly 2–3 (–4) cm, densely cinereous-lepidote; **L** sheath  $\pm 0.3$  cm, only slightly broader than the lamina, subcoriaceous, with broad hyaline margins, veined, glabrous, whitish; **L** lamina very narrowly triangular, rigid, 0.3–0.5 cm wide, densely cinereous-lepidote with  $\pm$  spreading scales, erect to suberect or arching-secund, subulate, apex long-attenuate but not filiform; **Inf** simple or very rarely forked; peduncle (nearly) completely covered by its bracts, curved, mostly much exceeding the leaves, to 10 cm but often much less,  $\pm 1$  mm  $\varnothing$ , straight, lepidote near the nodes, dark green; peduncular **Bra** like the floral bracts, many,  $\pm$  equalling the internodes, elliptic or obovate, tubularly amplexicaul, chartaceous, veined, densely lepidote, acutish; spikes to 4 cm, linear, sinuous, very much like those of *Lolium*, to 16-flowered but often with very few flowers or reduced to a single flower at the apex, rachis excavated next to the flowers,  $\pm$  flexuous, lepidote with large scales; floral **Bra** not at all imbricate, shorter than the sepals, 3–6 (–8)  $\times$  3.5–4 mm, (broadly) ovate, closely enveloping the flowers, thin, margins hyaline, veined, ecarinate, small and exposing most of the rachis, just exceeding the internodes, only abaxially subdensely lepidote with large green centered scales, cinereous-green, acute or apiculate; **Fl** with a short pedicel-like receptacle, distichous, erect, appressed to the rachis except the upper part of the sepals and petals caused by the flexuous rachis; **Sep** 5.5–6 (–9)  $\times$  3.5–4 mm, (oblong) lanceolate, faintly 7-veined, evenly short-connate for >1 mm, green or spotted brown-red, glabrous, acutish or obtuse; **Pet** 10 mm, claw sublinear, yellow, blade narrow, spreading or recurved, obtuse or narrowly rounded;

**St** 4 mm, deeply included, exceeding the style with much of the anthers; **Fil** filamentous, thin; **Anth** basifixed,  $\pm 1.5$  mm, yellow; **Ov** shortly cylindrical, obovoid or pyriform, abruptly contracted into the style; **Sty** stout, shorter than the ovary.

**T. lydiae** Ehlers (Bromelie 2000(2): 55–59, ills., 2000). **Type:** Mexico, Guerrero (*Köhres & Köhres* s.n. [MEXU, WU]). — **Distr:** S Mexico (Guerrero); epiphytic, 350–1000 m.

[5] Plant flowering 20–30 cm tall; **Ros** 3–4 cm  $\varnothing$ ; **L** 5–8, forming a bulbous rosette, 25–30 cm, the outer greatly reduced, very thick and succulent, stiffly leathery, margins very strongly grooved, densely appressed-lepidote, silver-grey but lustrous; **L** sheaths erect, 6–10  $\times$  3–4 cm, narrowly ovate, firmly pressed together, inflated, appressed-lepidote, glabrous towards the base, inside brown, outside dark green, conspicuously offset from the lamina; **L** lamina narrowly triangular, 10–20 cm, 2–2.5 cm wide at the base, red-brown, with striking longitudinal brown-red stripes, almost erect or slightly divergent, in dry conditions appearing grooved or strongly veined, subulate, margins involute, apex acuminate tapering to a sharp tip; **Inf** 1  $\times$  branched or simple, composed of (1–) 2–5 spikes; peduncle with a single bract similar to the inner leaves, short and concealed by the leaves, 4 mm  $\varnothing$ , sparsely lepidote; primary **Bra** with a basal flat part like the floral bracts, 1–1.8 cm, but with an acute short lamina, densely grey-lepidote; spikes short-stipitate, stipe 2–4 cm, with 2–3 (bi-) carinate sterile bracts at the base, spreading at an angle of 45–90°, 5–12 cm, 8–10 (–12) mm wide, lanceolate, complanate, 3- to 11-flowered, rachis with internodes 8–10 mm; floral **Bra** 3–5 mm shorter than the sepals, 13–15  $\times$  6–8 mm, ovate, veined, towards the apex keeled, densely appressed-lepidote, pink, acute; **Fl** distichous, contiguous with each other and/or the rachis; **Sep** 20–22  $\times$  6–7 mm, elliptic, with membranous margins, subfree, ecarinate or adaxial ones slightly carinate at the base, raspberry-red except the base, glabrous, acute; **Pet** erect, forming a tube, spatulate, 35  $\times$  6 mm (base 4 mm wide), pale violet with white base, blade tip margins divergent; **St** in 2 whorls of unequal length, exserted; **Fil**

**Fig. 21** *Tillandsia mauryana*. (Copyright: E. J. Gouda)



34–36 mm, broadened towards the apex and 0.8 mm wide, the upper portion pale lilac tapering to the white base; **Anth** dorsifixed at  $\frac{1}{3}$  from the base,  $3 \times 0.75$  mm (5 mm before dehiscence), linear or somewhat sagittate, dark yellow; **Ov**  $4 \times 2$  mm, cone-shaped; **Sty** slender, to 35 mm; **Sti**  $1.5 \times 1-2$  mm, narrow, small, erect, lobes green.

**T. mauryana** L. B. Smith (Contr. Gray Herb. 117: 31, t. 2, figs. 32–33, 1937). **Type:** Mexico, Hidalgo (*Maury* 5747 [GH, F]). — **Distr:** C Mexico (Hidalgo); saxicolous, 1200–2000 m. — Fig. 21.

≡ *Viridantha mauryana* (L. B. Smith) Espejo (2002).

[1] Plants often vertically on steep rockwalls, stemless or short-stemmed, flowering 5–15 cm tall; **Ros** 4–11  $\times$  5–14 cm, usually in groups; **L** densely rosulate, to 30, 5–10 (–12) cm, thick-fleshy, densely cinereous-lepidote, silver-grey; **L** sheath  $1.5-2 \times 0.8-1.2$  cm at the base, triangular, grey to brown-lepidote, glabrous for the lower 2 mm, both faces light brown, inconspicuously offset from the lamina; **L** lamina narrowly triangular, 4–10  $\times$  0.5–1 cm wide at the base, densely cinereous-lepidote, spreading or reflexed, flat, apex attenuate; **Inf** composed of 3–9 spikes, longer or shorter than the leaves; peduncle short and concealed by the leaves, 1–2 (–3.5) cm, with a

collar of bladeless acute bracts below the inflorescence; lowest peduncular **Bra** leaf-like, the upper like the primary bracts, erect or bent outward, densely imbricate, (2–) 5–8 cm, narrow-triangular; primary **Bra** like the floral bracts, lanceolate,  $2.5-3 \times 1-1.5$  cm, shorter than the spikes, membranous, acuminate, densely lepidote; spikes with 1 or 2 sterile bracts at the base, erect or divergent, to  $30 \times 10$  (–15) mm, complanate and with slightly convex sides, 3- to 8-flowered, rachis hardly visible at anthesis; floral **Bra** densely imbricate, slightly exceeding the sepals, 13–20 (–25)  $\times$  10–15 mm, (triangular-) ovate, thin, faintly veined, finely to sharply carinate esp. at the apex, adaxially glabrous, abaxially cinereously lepidote with large grey spreading scales, roseate, acuminate; **Fl** subsessile, distichous, densely arranged; **Sep** 12–15 (–17)  $\times$  4–5 mm, narrowly ovate, membranous, evenly short-connate for 1 mm or subfree, alate, adaxial ones carinate, sparsely to subdensely lepidote, acute; **Pet** almost erect, linear, 14–24  $\times$  3–4 mm (base 2–2.5 mm wide), dark emerald-green and yellow-green at the base, blade suberect or slightly divergent, rounded or obtuse; **St** all of equal length, 18–20 mm, included; **Fil** 12–14 mm, ribbon-like, thin and flaccid, white; **Anth** subbasifixed,  $2.5-3 \times 0.4$  mm, linear, base bilobed, apex apiculate, yellow-olive to light brown; **Ov** 3  $\times$  2 mm, ovoid, tapering into the

**Fig. 22** *Tillandsia mitlaensis*. (Copyright: E. J. Gouda)



style; **Sty** 11 mm, reaching or surpassing the anthers; **Sti** erect, slightly wider than the style, linear, lobes green.

**T. mitlaensis** W. Weber & Ehlers (Feddes Repert. 94: 617–618, ill., 1983). **Type:** Mexico, Oaxaca (Ehlers s.n. [Herb. Weber 283]). — **Distr:** S Mexico (Oaxaca); saxicolous,  $\pm 1800$  m. — Fig. 22.

[5] Plant flowering  $\pm 16$  cm tall; **L** suberect, the outer ones reduced, densely coarsely white-tomentose-lepidote; **L** sheath to  $3 \times 2$  cm, ovate, indistinctly merging into the lamina; **L** lamina narrowly triangular,  $\pm$  to strongly secund, finely veined, 7–9 cm, stout, canaliculate, apex subulate, subobtusate or acute, not pungent; **Inf** simple; peduncle suberect, short and concealed by to  $\pm$  equalling the leaves, stout; peduncular **Bra** with short somewhat leaf-like blades, erect or slightly bent upwards, densely imbricate, enveloping the peduncle, densely lepidote; spike 7–12  $\times$  1.6–1.8 cm, lanceolate, subterete to distinctly complanate,  $\pm 5$ -flowered, attenuately acute; floral **Bra** suberect, densely imbricate, much exceeding the sepals, 32–35 (–44)  $\times$  16 mm, ovate-lanceolate, submembranous, margins hyaline, strongly veined, ecarinate, densely concealing the rachis, on both faces (sub-) densely lepidote, reddish, obtuse or obscurely acuminate; **Fl** with a short pedicel-like receptacle, distichous; **Sep** 23–24  $\times$  5 mm, lanceolate,

membranous, with broad hyaline margins, veined, adaxial ones connate for 4–5 mm, abaxial one subfree, adaxial ones distinctly bluntly carinate, whitish-green, glabrous or abaxially sparsely lepidote with large trichomes, acute; **Pet** forming an erect narrow tube clasping the filaments at the apex, 50  $\times$  7.5 mm, pale to dark violet, whitish below, blade tip margins recurved, rounded-emarginate; **St** in 2 whorls of unequal length,  $\pm$  exserted; **Fil** 50–54 mm, slender and flattened at the base and dilated-terete at the distal end, white below, exserted part violet; **Anth** dorsifixed at  $\frac{1}{3}$  from the base, 2 mm, elliptic, brownish-green; **Ov** 5 mm, ovoid, contracted into the style; **Sty**  $\pm 55$  mm, slender, slightly dilated upwards; **Sti** conduplicate-spiral, unequal, 2.5 mm, whitish-green.

**T. mollis** H. Hromadnik & W. Till (Pl. Syst. Evol. 142: 123–128, ill., 1983). **Type:** Bolivia, Tarija (Hromadnik 9088 [WU, B, NY, W, Herb. W. Till]). — **Distr:** S Bolivia (Tarija); saxicolous on S-facing cliffs, 1770–2700 m.

[4] Plant flowering (9–) 16–24 (–26) cm tall and 3.5 – 4 cm wide, forming dense clusters  $\pm 40$ –50 cm  $\varnothing$ ; stem simple or few-branched, internodes (0.7–) 0.8–1 cm; **L** distichous, spreading, (2–) 3–5 (–6) cm, soft, flexible; **L** sheath amplexicaul, completely covering the stem and making it firm, 0.9–1.1  $\times$  0.8–1.1 cm, broadly obovate, with translucent margins near the

middle, margins connate to each other in the lower  $\frac{1}{2}$ ,  $\pm 9$ - to 10-veined, adaxially glabrous, abaxially densely lepidote with eccentric spreading scales, pale stramineous; **L** lamina subulate-terete, 1.9–4  $\times$  0.3–0.5 cm wide at the base, silvery-white, densely lepidote, trichomes eccentric and spreading, apex subacuminate, abruptly flattened and obtuse; **Inf** 1-flowered, rachis thread-like extended above the flower but hidden between the bract; peduncle nearly none or very short, to 0.8 cm, soon laterally displaced after anthesis, densely lepidote; peduncular **Bra** 1, placed approximately beneath the floral bract, 1.2–1.3 cm, densely lepidote, short-caudate; floral **Bra**  $\pm$  equalling the sepals, 6–9  $\times$  2–5.5 mm, suborbicular, 9-veined, ecarinate, shortly laminate or obtuse-apiculate; **Fl** sessile, distinctly terminal; **Sep** (5–) 6–7.5  $\times$  2.5–3.5 mm, (narrowly) ovate, thin-membranous, with overlapping broad hyaline margins, (3- to) 4- to 5-veined, the outer veins joined to the midvein near the apex, subfree, ecarinate, abaxially densely lepidote except the bottom  $\frac{1}{3}$ , adaxially glabrous, rounded; **Pet** tongue-shaped, 10–15  $\times$  2–2.5 mm, base 2 mm wide, dirty yellow-brown or olive-green, blade recurved, rounded-emarginate; **St** all of equal length; **Fil** 7  $\times$  0.5 mm, flat and attenuate, flaccid, straight or rarely plicate, white; **Anth** basifixed, 1.8–2.5  $\times$  0.5 mm, apex obtuse, greenish-yellow; **Ov** 1.5–2  $\times$  1.5 mm, ovoid to shortly cylindrical, abruptly contracted into the style; **Sty** 3 mm,  $\pm 0.4$  mm  $\varnothing$ ; **Sti** short, lobes crested, capitellate, not wider than the style.

**T. myosura** Grisebach *ex* Baker (J. Bot. 16: 240, 1878). **Type:** Argentina, Córdoba (*Lorentz* 122 [BM, B, G, MO, NY, P]). — **Distr:** S Peru (Arequipa), Bolivia, Argentina, Uruguay; epiphytic in dry habitats, 700–3200 m.

$\equiv$  *Tillandsia nappii* Lorentz & Niederlein (1881) (*nom. illeg.*, ICN Art. 52.1); **incl.** *Tillandsia mandonii* E. Morren *ex* Mez (1896).

[4] Plant flowering to 30 cm high or sometimes more, forming dense clusters; stem to 6 (–10) cm, simple, few-branched or richly branched at the base; **L** subdensely distichous, 5–17 cm, stiff; **L** sheaths densely imbricate and margins overlapping behind the stem for most of their length,

making the stem to appear stout (5–8 mm  $\varnothing$ ), 1–1.5 cm, suborbicular to reniform, normally with the upper  $\frac{1}{2}$  densely lepidote like the lamina or sometimes glabrous except a fringe of narrow marginal scales, distinct from the lamina; **L** lamina narrowly triangular or linear, 0.3–0.5 cm wide, densely cinereous-lepidote with small basally produced subappressed to reflexed pruinose scales, strongly recurved, becoming strongly sulcate when dry,  $\pm$  contorted, subulate, with a furrow, apex acuminate and pungent; **Inf** simple; peduncle bractless or with 1 bract well removed from the flowers, erect, 4–20 cm, lepidote or glabrous; peduncular **Bra** lanceolate, involute, lepidote; spikes lax, to 8 cm but often much shorter, linear, (1- to) 2- to 5- (to 8-) flowered, rachis slender, flexuous in the few-flowered specimens or usually geniculate in the larger ones,  $\pm$  lepidote; floral **Bra** slightly or not at all imbricate, the lower ones exceeding or equalling or the upper ones often distinctly shorter than the sepals, (13–) 17.5–30  $\times$  9–9.5 mm, broadly ovate or ovate-lanceolate, clasping the flower, chartaceous, many-veined, not concealing the rachis except by their extreme base, rarely  $>2\times$  as long as the internodes (but much less esp. in the many-flowered specimens), cinereously lepidote, acuminate with a short tip; **Fl** subsessile, closely appressed to the rachis, fragrant; **Sep** 11–13.5  $\times$  5–5.8 mm, oblong-lanceolate, thin, many-veined, evenly short-connate, adaxial ones bluntly carinate, usually sparsely lepidote or glabrescent, rounded or obtuse; **Pet** linear to tongue-shaped,  $\pm 13$  (–30)  $\times$  3 mm, at the base slightly narrowing, pale yellow; **St** deeply included, exceeding the style; **Fil** to 5.5 mm; **Anth** (sub-)basifixed,  $\pm 3.5$   $\times$  0.5 mm; **Ov**  $\pm 4$   $\times$  2 mm, subcylindrical, tapering into the style; **Sty**  $\pm$  as long as or shorter than the ovary; **Sti** almost flat and disc-shaped (gemmate).

**T. neglecta** E. Pereira (Bradea 1: 78, t. 2, 1971). **Type:** Brazil, Rio de Janeiro (*Sucre* s.n. [HB]). — **Distr:** SE Brazil (Rio de Janeiro); saxicolous on granitic rock walls. – Fig. 23.

[2] Plant caulescent, flowering to 20 cm tall, often forming dense clusters; stem few-branched at the base, curved; **L** rosulate, somewhat curved,





**Fig. 23** *Tillandsia neglecta*. (Copyright: E. J. Gouda)

4–7 cm, stiff and fleshy-coriaceous, subappressed-lepidote on both faces, green or tinged reddish or silver-grey at the base because of spreading trichomes; **L** sheaths 1.5 cm wide, whitish; **L** lamina narrowly triangular, not or slightly secund, subulate towards the apex, apex abruptly acute and pungent; **Inf** simple, mostly much exceeding the leaves; peduncle completely covered by its bracts or partly visible, erect, equalling or exceeding the leaves, glabrous, green; peduncular **Bra** erect, laxly imbricate, much (3–4× longer than) to slightly exceeding the internodes, ovate-oblong, sparsely pale-lepidote at the margins and apex, long-acuminate; spike 3–4 cm, corymbiform, 6- to 10-flowered; floral **Bra** equalling to much exceeding the sepals, 17 × 9.5 mm, ovate or elliptic, margins narrowly hyaline, darker veined, subglabrous or lepidote towards the apex (esp. the lower ones), green to reddish esp. at the margins, acutish or obscurely acuminate; **Fl** sessile,

polystichous, suberect or divergent, densely arranged, 22–30 mm; **Sep** 15–16 × 3 mm, lanceolate, with broad hyaline margins, connate for 2–2.5 mm, ecarinate, glabrous, narrowly acute; **Pet** spatulate or tongue-shaped with long cuneate base, 22–30 × 5 mm (base 1.5 mm wide), blue, blade slightly divergent, rounded-emarginate; **St** 11–16 mm, included, visible in the throat but shorter than the style; **Fil** slender and narrow at the distal end or ribbon-like, towards the middle slightly plicate, 17.5 mm long; **Anth** basifixed, 2 × 0.5 mm, linear, base bilobed, apex obtuse; **Ov** 3–4 × 1.5 mm, trigonous or ellipsoid, the top  $\frac{1}{3}$  sterile, tapering into the style; **Sty** ± 14 mm, slender; **Sti** erect, linear, unequal.

**T. paleacea** C. Presl (Reliq. Haenk. 1: 125, 1827). **Type:** Chile (*Haenke* s.n. [PR, GH [photo]]). — **Distr:** C Colombia (Cauca, Huila, Tolima), Peru (widespread), NE Bolivia (La Paz), N Chile, S Paraguay; on rocks and desert sands, or on trees in dry areas, 0–3900 m. – Fig. 24.

**Incl.** *Tillandsia fusca* Baker (1878); **incl.** *Tillandsia scalarifolia* Baker (1887); **incl.** *Tillandsia chilensis* Baker (1889); **incl.** *Tillandsia schenckiana* Wittmack (1889); **incl.** *Tillandsia favillosa* Mez (1906).

[3] Plant variable in habit, caulescent, flowering 10–70 cm tall, often much branched; stem 10–35 cm, appearing stout because of the densely imbricate leaf sheaths, brittle; **L** laxly spirally arranged, densely tomentose-lepidote, silvery-grey often becoming fuscous with age; **L** sheaths large, broadly ovate, elliptic, glabrous, the upper  $\frac{1}{2}$  clearly visible, outside lepidote; **L** lamina narrowly triangular, to 12 cm, 4–6 mm wide, abruptly spreading, usually slightly flexuous, for most part canaliculate to subulate in the upper part, apex attenuate; **Inf** simple; peduncle mostly completely covered by its bracts, erect, shorter than to much exceeding the leaves, to 15 cm or sometimes much more, slender, glabrous or nearly so; lowest peduncular **Bra** somewhat leaf-like with short lamina, soon erect, laxly imbricate, exceeding or about equalling the internodes, narrowly elliptic, tightly enveloping the peduncle, lepidote, apiculate; spike dense, to 5 cm, linear-lanceolate, complanate, (1- to) 2-



**Fig. 24** *Tillandsia paleacea*. (Copyright: E. J. Gouda)

5- (to 12-) flowered, acute, rachis angled, straight or flexuous, glabrous, partly exposed; floral **Bra** distichous, slightly shorter than or slightly exceeding the sepals, 13–16 × 6 mm, ovate or elliptic, finely veined, ecarinate, so narrow as to expose the rachis in part, ±2–3× as long as the internodes, soon glabrous or in the upper part subdensely lepidote, green, sometimes tinged reddish; **Fl** with a short pedicel-like receptacle; **Sep** 10–17 × 5 mm, elliptic or obovate-lanceolate, with hyaline margins, free, ecarinate but slightly fleshy at the base, tinged reddish-purple, glabrous; **Pet** claw narrow with suborbicular blade, 20–23 × 10 mm, margins slightly undulate, blade blue to violet or rose, claw white, corolla sometimes with a white eye; **St** 6–8 mm, deeply included; **Anth** basifixed, 1.5 mm; **Ov** subcylindrical, 2.5–3.5 mm, abruptly contracted into the style; **Sty** stout, 1.5 mm (incl. stigma); **Sti** disc-shaped, gemmate.

**T. paraensis** Mez (in Martius, Fl. Bras. 3(3): 586, t. 109, 1894). **Type:** Brazil, Pará (*Sieber* 68 [BR, GH [photo]]). — **Distr:** SE & S Colombia (Vaupés, Amazonas), E & S Venezuela (Bolívar, Amazonas), Guyana (Cuyuni-Mazaruni, Potaro-Siparuni, Upper Takutu-Upper Essequibo), E & S Suriname (Brokopondo, Sipaliwini), French Guiana (Saül, Régina, Maripasoula), Brazil (Amazonas, Mato Grosso, Rio Grande do Norte, Rondônia, Roraima, Pará, Rio de Janeiro, Bahia, Pernambuco), NE Ecuador, Peru, NE Bolivia; epiphytic in forest, 20–1120 m.

**Incl.** *Vriesea sanctae-crucis* S. Moore (1895) ≡ *Tillandsia sanctae-crucis* (S. Moore) Mez (1896); **incl.** *Tillandsia juruana* Ule (1907).

[5] Plant stemless, flowering 12–40 cm tall; **L** 10–25, forming a narrowly utriculate rosette, often exceeding the inflorescence or at least the peduncle, 10–35 cm, the outer greatly reduced and sheath-like, very densely subappressed-lepidote throughout; **L** sheaths forming an elongate pseudobulb, 3–7 × 1.7–3 cm, ovate, inflated-convex, stiff-coriaceous, with membranous margins, slightly distinct from and merging into the concolorous lamina; **L** lamina very narrowly triangular, succulent (fleshy) and coriaceous, 6–25 (–33) × 1.4–2 cm, suberect or curved, often finely keeled on both faces, often the margins involute towards the apex when dry, apex attenuate and abruptly pungent; **Inf** simple (or rarely compound of 2 spikes), 10–30 (–40) cm; peduncle completely covered by its bracts or partly visible, often curved, short and concealed by the leaves or elongate, 8–19 cm, 2–3.5 mm Ø, sparsely lepidote or subglabrous; lowest peduncular **Bra** leaf-like, erect, densely imbricate to remote, ovate, chartaceous, (densely) appressed-lepidote or floccose at least at the apex, the upper ones more apiculate; spikes mostly curved, 6–15 (–20) cm, 1–1.5 cm wide, linear (-lanceolate), complanate, subdensely distichously 4- to 15-flowered, acute, rarely with >1 sterile bract at the apex, rachis sharply angled when dry, ± flexuous, sparsely lepidote or glabrate, only partly hidden at anthesis but often wholly exposed when dry; floral **Bra** scarcely imbricate (if at all), equalling to much exceeding the sepals, 23–39 mm, (broadly) elliptic, clasping the flower,

scarcely incurved, subchartaceous, even or veined, ecarinate, so narrow as to expose the rachis in part,  $<2-4\times$  as long as the internodes, densely lepidote or subglabrous, often yellow-green or tinged with red or wholly reddish, obtuse or the lower ones minutely apiculate; **Fl** subsessile, erect or suberect; **Sep** slightly incurved at the apex, 15–23 mm, ovate-oblong, thin-coriaceous, veined only when dry, free, sparsely or minutely lepidote, rounded, then obtuse or subacute; **Pet** erect with slightly divergent apex and forming a tube, linear-lanceolate, 33–65 mm, rose to pink, attenuate and obtuse; **St** unequal in length, 40–45 mm, exerted or  $\pm$  equalling the petals, shorter than or equalling the pistil; **Fil** flat or subterete towards the apex, straight; **Anth** dorsifixed just below the middle; **Ov** slenderly ovoid, gradually contracted into the slender style.

**T. paucifolia** Baker (Gard. Chron., ser. nov. 10: 748, 1878). **Type:** K, GH [photo]. — **Distr:** SE USA (Florida), SE Mexico, N & E Guatemala, C & S Honduras, E El Salvador, Nicaragua, NW & W Costa Rica, Bahamas, Cuba, Jamaica, Haiti, Dominican Republic, N Colombia, C & NE Venezuela; epiphytic in low forest and scrub.

**Incl.** *Tillandsia yucatanana* Baker (1887).

[5] Plant stemless, flowering 10–45 cm tall, with few offsets; outer **L** reduced, without lamina, other leaves densely appressedly cinereous-lepidote; **L** sheaths forming an elongate pseudo-bulb 5–15 cm long, large, broadly ovate, merging gradually into the lamina; **L** lamina thick, to 20 cm but often much shorter even in large plants, 3–7 mm wide at the base, curved, involute-subulate, the lower often contorted, apex attenuate and abruptly pungent; **Inf** simple, digitate (or slightly spaced), composed of (1–) 3–6 spikes; peduncle erect, very short and concealed by the leaves; peduncular **Bra** leaf-like with spreading lamina, erect, imbricate; primary **Bra** like the peduncular bracts, leaf-like, at least the lower ones much exceeding the spikes with their lamina, rose; spikes suberect or divergent and often curved, to 12 cm but normally much smaller, linear-lanceolate, complanate, 2- to 10-flowered, acute; floral **Bra** erect, imbricate, exceeding or slightly shorter than the sepals, 20–21 (–30)  $\times$

11 mm, elliptic or ovate, subchartaceous, margins hyaline, veined when dry, the apex scarcely or not at all carinate, concealing the rachis (alive), 3–4  $\times$  as long as the internodes, appressed-lepidote, acute or obtuse; **Fl** sessile, distichous; **Sep** 18–20  $\times$  5 mm, lanceolate-oblong or narrowly obovate, subchartaceous, finely veined when dry, unequally short-connate (adaxial ones more) for 2–4 mm, adaxial ones carinate in the lower  $\frac{2}{3}$ , glabrous or abaxially sparsely lepidote at the base centre, rounded, then obtuse (or subacute); **Pet** forming an erect narrow tube clasping the filaments at the apex, linearly tongue-shaped, to 43  $\times$  7 mm, basally narrowed to 3 mm, violet, blade tip margins recurving, rounded; **St** in 2 whorls of unequal length,  $\pm 45$  mm, exerted; **Fil** exposed part slightly inflated and (sub-)terete, violet in the upper part; **Anth** dorsifixed near the middle, 2.5  $\times$  1 mm, elliptic, apex obtuse, dark brown; **Ov** 6  $\times$  2.5 mm, narrowly ovoid, contracted into the style; **Sty** 54 mm, exceeding the stamens; **Sti** dilated, spreading, white.

**T. pedicellata** (Mez) A. Castellanos (Lilloa 11: 144, 1945). **Type:** Argentina, Córdoba (*Hieronymus* 795 p.p. [B, BM, CORD, GH]). — **Distr:** Cuba (Camagüey), S Brazil (Paraná), Bolivia (Chuquisaca, Cochabamba, La Paz, Potosí, Santa Cruz, Tarija), Argentina (Buenos Aires, Catamarca, Córdoba, Jujuy, Mendoza, Salta, San Juan, San Luis, La Pampa, Rio Negro, Tucumán); epiphytic, 60–3660 m. — Fig. 25.

$\equiv$  *Tillandsia coarctata* var. *pedicellata* Mez (1896) (*nom. inval.*, ICN Art. 35.1); **incl.** *Tillandsia coarctata* Gillies ex Baker (1878) (*nom. inval.*, ICN Art. 32.1c).

[4] Plant small, flowering to  $\pm 6$  cm tall, forming dense clusters; **L** rosulate, densely imbricate, to 8  $\times$   $\pm 1$  mm; **L** sheaths suborbicular, with broad veinless margins, 3- to 4-veined, glabrous; **L** lamina lanceolate in outline, densely lepidote with green-centred trichomes, fleshy, subulate, apex apiculate or obtuse; **Inf** peduncle at flowering time very short (0.3 cm) or almost missing to elongate at fruiting time, glabrous; floral **Bra** (5.5–) 6.5–7  $\times$  (2.6–) 3–3.3 mm, ovate to broadly triangular, 1- to 3-veined, glabrous or sparsely lepidote towards the apex with large

**Fig. 25** *Tillandsia pedicellata*. (Copyright: E. J. Gouda)



trichomes, apiculate; **Fl** erect, slightly zygomorphic with 2 petals spreading, sometimes barely exceeding the leaves, weakly fragrant; **Sep** 5.8–7 × 1.3–2 mm, lanceolate, 3- (to 5-) veined, outer vein much shorter than the midvein, equally subfree or adaxial ones connate for  $\pm\frac{1}{2}$  their length or all connate for up to 3 mm, glabrous, apiculate or obtuse; **Pet** tongue-shaped, often widest at  $\pm$  the middle, 8–9 × 1.3–1.8 mm, (4- to) 5- to 6-veined, pale yellow to dark violet or brown, broadly rounded; **St** all of equal length, 3.5 mm, deeply included; **Fil** 2.7–3 × 0.15 mm, thread-like, 1-veined, whitish; **Anth** basifixed, 1–1.5 × 0.25–0.3 mm; **Ov** 1.5 mm, cylindrical or subglobose, abruptly contracted into the style; **Sty**  $\pm\frac{1}{3}$  as wide as the ovary,  $\frac{1}{3}$  as long as the ovary; **Sti** disc-shaped, gemmate.

**T. peiranoi** A. Castellanos (Lilloa 2: 14, t. 2, 1938). **Type:** Argentina, Salta (*Peirano* s.n. [LIL, BA, GH [photo]]). — **Distr:** NE Argentina (Salta); saxicolous, 1200 m.

[3] Plant caulescent, flowering 20 cm tall but normally much smaller, few-branched; stem to 10 cm; **L** subdensely spirally arranged, 2–5 cm, cinereously-lepidote with subappressed scales; **L** sheaths large but obscure, broadly ovate, with broad thin margins, many-veined, merging into the lamina; **L** lamina narrowly triangular or triangular, rigid and fleshy, 0.5 cm wide, suberect to

recurved, veined, with subulate apex, strongly canaliculate except at the attenuate and pungent apex; **Inf** simple or 1 × branched with 1–2 small suberect branches, composed of 1–3 (–5) spikes; peduncle completely covered by its bracts, erect, very slender, glabrous; peduncular **Bra** laxly imbricate, lanceolate, thin, veined, lepidote, acuminate; primary **Bra** like the floral bracts, much shorter than the spikes; spikes to 6 cm, linear (at least the terminal one),  $\pm$ 6-flowered, rachis slender, flexuous or suberect, glabrous; floral **Bra** erect, slightly shorter than the sepals, 12 mm, elliptic or ovate, closely enveloping the flowers, thin, veined, ecarinate, so narrow as to expose the rachis in part and sometimes part of the sepals, slightly  $<2\times$  as long as the internodes, glabrous, green or purple-brown or soon dry and stramineous; **Fl** distichous, suberect or divergent caused by the flexuous rachis, always partly contiguous with the rachis; **Sep** 10–12 × 3 mm, elliptic, thin, centrally (3- to 5-) veined with broad veinless margins, free, adaxial ones carinate, tinged reddish-purple, glabrous, sharply acute; **Pet** claw narrow with suborbicular blade, 16 × to  $>7$  mm, pale blue to nearly white, blade recurved. **St** deeply included, exceeding the style; **Anth** 2.5 mm, linear.

**T. porongoensis** L. Hromadnik & P. Schneider (Haussknechtia 4: 39–41, 1988). **Type:** Argentina,



La Rioja (*Hromadnik & Hromadnik* s.n. [WU]). — **Distr:** NW Argentina (La Rioja); epiphytic,  $\pm 850$  m.

[4] Plant caulescent, stem arched, hardly branched; **L** few, forming a spreading open rosette, laxly rosulate, to 15 cm, stiff and succulent, densely cinereous-lepidote, silver-white; **L** sheaths  $1.2\text{--}1.5 \times 1.5\text{--}2$  cm, triangular to ovate, clasping the stem and concealing it, adaxially smooth, glabrous towards the base to densely lepidote in the upper  $\frac{1}{2}$ , cherry-red up to  $\frac{1}{2}$  the length, abaxial face paler with spots, distinct from the lamina; **L** lamina very narrowly triangular, near the sheath with extending trichomes at the margins, to  $12 \times 0.8\text{--}1$  cm wide at the base, spreading to recurved into a semicircle, margins strongly involute, canaliculate and subulate from  $\pm$  the middle to the apex, apex acute and pungent with a sharp point; **Inf** simple; peduncle completely covered by its bracts, 4.5–5 cm, 1.5 mm  $\varnothing$ , glabrous; peduncular **Bra**  $\pm$  equalling the internodes,  $3.2 \times 0.9$  cm, the upper ones completely enveloping the peduncle, with only the tip flaring slightly, distinctly veined, silvery cinereous-lepidote, stramineous, the lower ones with leaf-like blade and more apiculate; spike 4–4.5 cm, 7–9 mm wide, lanceolate, complanate, 4- to 8-flowered, rachis 4-angled, geniculate, glabrous, hidden or partly exposed, internodes 4 mm; floral **Bra**  $\pm$

imbricate, exceeding or much shorter than the sepals, upper ones very short, (10–) 16–20  $\times$  10 mm, coriaceous, veined, ecarinate, concealing the rachis or so narrow as to expose the rachis in part, adaxially glabrous, the lower ones densely lepidote or the upper ones lepidote at the margins with large trichomes, tinted reddish-brown, apiculate; **Fl** distichous, erect; **Sep** 12–14  $\times$  4 mm, narrowly ovate, coriaceous, soon straw-like, veined, evenly shortly connate, adaxial ones slightly carinate, reddish-brown, adaxially glabrous, abaxially glabrous in the lower  $\frac{1}{2}$  and densely grey-scaled in the upper  $\frac{1}{2}$ , apiculate; **Pet** 20  $\times$  5 mm, 2–3 mm wide at the base, yellowish-brown, blade ovate, recurved, rounded; **St** deeply included; **Fil** 10  $\times$  0.3 mm, ribbon like, straight, white; **Anth** 1.5 mm; **Ov** 4  $\times$  2.5 mm, slenderly ovoid; **Sty** stout, somewhat thinner than the ovary, 8 mm including the stigma.

**T. praschekii** Ehlers & K. Willinger (*Bromelie* 1989(2): 36, ill., 1989). **Type:** Cuba, Pinar del Río (*Prášek* 32/83 [WU]). — **Distr:** Cuba (Pinar del Río); on rocks, 200–300 m. – Fig. 26.

[5] Plant stemless, flowering 8–10 cm tall, growing in large groups; **L** to 15, forming an almost bulbous rosette, succulent; **L** sheaths  $1.5 \times 1.5$  cm, suborbicular to elliptic, inflated, with small asymmetrical trichomes on the margins,

**Fig. 26** *Tillandsia praschekii*. (Copyright: E. J. Gouda)





densely furfuraceous-lepidote, outer face dark green and brownish at the base, inner face brown, abruptly contracted into the lamina; **L** lamina narrowly triangular, to 7 cm, 6 mm wide near the base, cinereous-green, densely and furfuraceously lepidote with small spreading scales, divergent to strongly recurved, the edges grooved, canaliculate, apex attenuate and then abruptly acute; **Inf** 1× branched, appearing simple but composed of 10 polystichously arranged hidden spikes, erect or almost upright, dense, capitate, to 4 × 3 cm, the uppermost 2–5 spikes at the apex of the inflorescence remaining undeveloped; peduncle completely covered by its bracts, short and concealed by the leaves, ±2 cm, 5 mm Ø; peduncular **Bra** leaf-like; primary **Bra** spreading to recurving, like the peduncular bracts, blade narrowly triangular, the lower ones 4 cm long, upper ones shorter, much exceeding and wholly hiding the spikes, subsucculent, densely furfuraceous-lepidote, leaf-like and almost forming an involucre, green to pink; spikes shortly stipitate, with sterile bracts at the base, erect and appressed to the axis, excluding the petals 2 cm, 8–10 mm wide, complanate, 1- to 3-flowered (upper spikes 1-flowered), with a reduced flower at the apex; floral **Bra** 3–4 mm shorter than the sepals, 7–9 × 7 mm at the base, broadly triangular, rigid and coriaceous, margins hyaline, strongly veined, alate-carinate, inside sparsely lepidote, outside furfuraceously lepidote, green with red hooked tip; **Fl** with a short pedicel-like receptacle; **Sep** 12 × 5 mm, elliptic, rigid, with hyaline margins, evenly shortly connate for 1 mm, adaxial ones carinate, at the base green, otherwise wine-red, sparsely lepidote with large trichomes, acuminate; **Pet** erect and forming a tube, tongue-shaped, 36 × 6 mm (base 3 mm wide), violet-blue with white base, blade tip margins divergent; **St** in 2 whorls of unequal length, to 45 mm, exerted for 10 mm; **Fil** slender and flattened at the base and dilated and becoming terete at the distal end, violet with white base; **Anth** dorsifixed near the middle or at ½ from the base, 2 × 0.75 mm, elliptic, brown; **Ov** 5 × 3 mm, narrowly ovoid, angled; **Sty** slender, exceeding the anthers; **Sti** 2 × 2 mm, erect or lobes spreading, papillose, white.

**T. pruinosa** Swartz (Fl. Ind. Occid. 1: 594, 1797). **Type:** Jamaica (Swartz s.n. [S]). — **Distr:** SE USA (Florida), SE Mexico, C & S Belize, N Guatemala, Honduras, Nicaragua, Costa Rica, Cuba, Jamaica, Dominican Republic, Puerto Rico, Colombia, Venezuela, Guyana, Suriname, Brazil, Ecuador; epiphytic, 0–1400 m.

≡ *Platystachys pruinosa* (Swartz) Beer (1856); **incl.** *Tillandsia breviscapa* A. Richard (1850).

[5] Plant stemless, flowering 8–12 (–23) cm tall; **L** ±10–20, 7–25 cm, white-tomentose-lepidote (often ferruginous when dry); **L** sheaths forming an ovoid pseudobulb, 2–4.8 × 2–4.3 cm, suborbicular or elliptic, much inflated-convex, papyraceous, with broad membranous purple-red margins, densely ferruginous-lepidote to somewhat ferruginously tomentose-lepidote at the base, inner face pale brown to deep purple, abruptly contracted into the lamina; **L** lamina fleshy-coriaceous and flexible, 5–21 cm, 2–5 mm wide, secund or suberect, often slightly flexuous, very densely white- to somewhat ferruginous-lepidote to tomentose-lepidote, involute-subulate, apex filiform-attenuate; **Inf** simple or rarely digitately compound of 2–4 spikes, 5 (–15) cm, densely tomentose-lepidote; peduncle densely covered by its bracts and concealed within the leafy rosette, erect, 5–8 cm, 2–3 mm Ø; peduncular **Bra** leaf-like, suberect, with densely imbricate sheaths, the upper ones more oblong, acute; axes of the inflorescence hidden, very short; primary **Bra** like the upper peduncular bracts, subspreading with the spikes, exceeding the spikes with the leaf-like lamina, shorter than the axillary branches; spikes shortly stipitate (<1 cm), with a sterile bract (prophyllate) or with few sterile bracts at the base and apex, suberect or divergent when compound, dense, 4–6.5 cm, 1.8–4.5 cm wide, (broadly) elliptic, slightly complanate, 3- to 6- (to 15-) flowered, acute, rachis angled, nearly straight, densely tomentose-lepidote, hidden; floral **Bra** suberect, densely imbricate, nearly 2× as long as the sepals, 20–29 mm, elliptic, thin-coriaceous, even, obscurely carinate towards the apex, 4–5× as long as the internodes, pale silvery green tinged with or wholly dull roseate-red, acutish or obtuse and obscurely apiculate; **Fl** sessile, distichous, contiguous with each other and/or the rachis; **Sep**

13–19 mm, elliptic, very thin-coriaceous, with broad membranous margins, even, abaxial one subfree, adaxial ones about  $\frac{1}{2}$  connate for  $\pm 6$  mm, adaxial ones bluntly carinate at the base, sparsely appressed-lepidote on both faces or glabrescent, rounded, then obscurely acuminate; **Pet** erect and forming a tube, tongue-shaped, 30 mm, violet, blade tip margins recurved, obtuse or acute; **St** in 2 whorls of unequal length, long-exserted, the shorter equalling and the longer exceeding the style; **Fil** slender and flattened at the base and dilated and becoming terete at the distal end, violet; **Anth** dorsifixed at  $\frac{1}{3}$  from the base,  $>3$  mm; **Ov** ovoid (?), contracted into the style; **Sty** slender; **Sti** conduplicate-spiralized, linear.

**T. pseudobaileyi** C. S. Gardner (Selbyana 7 (2–4): 363, ill., 1984). **Type:** Mexico, Chiapas (Gardner 1118 [SEL]). — **Distr:** S Mexico, C & SE Guatemala, SW & S Honduras, El Salvador, W & C Nicaragua; epiphytic on trees of open seasonally dry forests, 100–1500 m.

[5] Plant stemless, flowering to 30 cm tall, with few offsets; **L** 10–12, the outer greatly reduced, the others 20–35 cm; **L** sheaths forming an ovoid pseudobulb, 4–5  $\times$  5–6 cm, orbicular, much inflated, stiff-coriaceous, with reddish margins, veined esp. in the upper  $\frac{1}{2}$ , adaxially red-brown-lepidote and abaxially appressed-lepidote, brownish towards the base; **L** lamina narrowly triangular or linear, succulent and rigid, 1–1.5 cm wide, minutely appressed-lepidote, with striking longitudinal brown-red stripes (veins) in bright light, curved or divergent, distinctly veined (fresh and dry), the margins involute and often contorted; **Inf** compound, composed of 2–5 spikes; peduncle erect, short and concealed by the leaves or slightly elongate, to 15 cm, blood-red; peduncular **Bra** leaf-like, laxly imbricate, involute, the sheath blood-red, the lamina green or reddish; primary **Bra** lanceolate, the lowest  $\pm\frac{1}{2}$  as long as the spikes, acuminate and pungent, blood-red; spikes with a sterile bract, bicarinate at the base, spreading at 40–45°, linear-lanceolate, complanate, 4- to 6-flowered; floral **Bra** slightly exceeding the sepals, 17–20  $\times$  9–11 mm, ovate, convex, rigid, scarcely or not at all carinate at the apex, the adaxial face glabrous with a few trichomes near

the apex, abaxially appressed-lepidote, cinereous, tinged red or with reddish margins; **Fl** suberect, contiguous with the rachis and each other; **Sep** 14–16  $\times$  5–6 mm, elliptic, thin or rigid, evenly shortly connate or free, adaxial ones slightly to moderately carinate, green with red edges, adaxially glabrous and abaxially appressed-lepidote; **Pet** erect and forming a tube, spatulate, 29–32  $\times$  6–8 mm, margins slightly undulate, lavender, blade tip margins recurving; **St** in 2 whorls of unequal length, exserted, the longest just exceeding the style; **Fil** 36–43 mm, broadened towards the apex, upper part lavender; **Anth** dorsifixed at  $\frac{1}{3}$  from the base or near the middle, 2–3 mm, black; **Ov** not described; **Sty** 29–34 mm; **Sti** lobes erect or spreading, dilated, slightly papillose, green.

Material separated as this species was treated as part of *T. baileyi* by Smith & Downs (1977).

**T. pueblensis** L. B. Smith (Contr. Gray Herb. 104: 81, t. 3, figs. 1–2, 1934). **Type:** Mexico, Puebla (*Purpus* 5856 [GH, BM, F, MO, NY, UC, US]). — **Distr:** E & S Mexico (Puebla, Oaxaca); saxicolous,  $\pm 1680$  m. — Fig. 27.

[5] Plant stemless or short-stemmed or with a rhizomatous stem, flowering 16–24 cm tall, stem sometimes few-branched; **L**  $\pm 15$ , densely rosulate, erect or curved in the upper part, the outer ones reduced to pointed sheaths, the inner to 16 cm, densely tomentose-lepidote, silver-grey; **L** sheaths scarcely distinct from the lamina; **L** lamina narrowly triangular, brittle and fleshy,  $\pm 1$  cm wide at the base, involute-subulate or strongly convex, apex acute or subpungent; **Inf** simple; peduncle completely covered by its bracts, erect, short and concealed by to  $\pm$  equalling the leaves; lowest peduncular **Bra** somewhat leaf-like and long-laminate, the upper ones lanceolate, membranous, cinereous-lepidote, grey-green, acute; spikes erect, densely flowered, 8–9  $\times$  1 cm, linear-lanceolate in outline, slightly complanate, typically 4- (to 7-) flowered; floral **Bra** erect, imbricate, much exceeding the sepals, 25–33  $\times$  10 mm, oblong-lanceolate, convex, membranous, margins hyaline, even or finely veined when dry, ecarinate, concealing the rachis (alive),  $\pm 3 \times$  as long as the internodes, the base glabrous and subdensely lepidote towards the apex and margins, bright roseate or more

**Fig. 27** *Tillandsia pueblensis*. (Copyright: E. J. Gouda)



often wine-red with green margins, narrowly rounded or obtuse; **Fl** subsessile, distichous; **Sep** 20–21 × 5.5 mm, narrowly obovate, chartaceous, with broad hyaline margins, veined at least when dry, adaxial ones connate or subfree, connate for up to (if at all) 6 mm, adaxial ones carinate, broadly obtuse or narrowly rounded; **Pet** forming an erect narrow tube clasping the filaments at the apex, tongue-shaped with long-cuneate base, 40–50 × 8.5 mm (base 3 mm), violet, blade tip margins recurved, rounded and then obtuse; **St** in 2 whorls of unequal length, ±60 mm, exserted; **Fil** slender and flattened at the base and dilated, becoming terete at the distal end; **Anth** dorsifixed near the middle, 2.5 × 1 mm, apex obtuse; **Ov** 5.5 × 2.5 mm, ovoid, tapering into the style; **Sty** slender, 62 mm, exceeding the stamens; **Sti** spreading, dilated.

**T. rectangula** Baker (J. Bot. 16: 238, 1878). **Type:** Argentina, Córdoba (Lorentz 127 p.p. [K, G, WU]). — **Distr:** C & S Bolivia (Cochabamba, Tarija), Argentina (Catamarca, Córdoba, La Rioja, San Luis, Santiago del Estero); epiphytic, 500–2720 m.

**Incl.** *Tillandsia propinqua* var. *rectangula* Grisebach (1879).

[4] Plant small, caulescent, forming a globose mass, stems many from a single point, richly branched at the base; **L** loosely polystichous, rarely

>2 cm; **L** sheaths densely imbricate making the stem appear stout, ±0.6 cm, suborbicular, scariosus, with broad veinless margins, several-veined, glabrous except for the extreme apex, distinct from the lamina; **L** lamina narrowly triangular, 0.2 cm wide, densely cinereous-lepidote, divergent or spreading from the stem at ±90°, with a central keel, with small nearly symmetrical sub-appressed trichomes, subulate and strongly angled, with a furrow not reaching the apex, apex attenuate and pungent; **Inf** 1-flowered; peduncle naked for most of its length, erect to ascending, apparently always terminal, almost none or elongate to 2 (–4) cm, slender, strongly angled, glabrous; peduncular **Bra** usually 2, one at the extreme base of the peduncle, mostly hidden by the leaves, the other just below the flower, lanceolate, subcoriaceous, several-veined, even, glabrous or occasionally pale-appressed-lepidote, acute or obtuse; floral **Bra** much shorter than the sepals, 8 × 4 mm, like the upper peduncular bract but smaller, hyaline, glabrous, pale green, obtuse; **Fl** subsessile; **Sep** 9–10 × 4 mm, narrowly elliptic, membranous, with broad hyaline margins, even, evenly short-connate or slightly longer connate posteriorly for up to 2 mm, pale green, glabrous or sparsely lepidote, acute, obtuse; **Pet** tongue-shaped, 13 × 3 mm, yellow to ochre-brown, blade spreading or recurved at anthesis, obtuse; **St** 6 mm, deeply included, exceeding the

style with most of the anthers; **Anth** dorsifixed near the base, >1 mm, linear, apex obtuse; **Ov** subprismatic,  $\pm 2.5$  mm, contracted into the style; **Sty** slender, shorter than the ovary; **Sti** capitate.

**T. reducta** L. B. Smith (Phytologia 5: 399, t. 1, figs. 11–12, 1956). **Type:** Peru, Cajamarca (*Ferreyra* 3216 [US, USM]). — **Distr:** NE Peru (Cajamarca); only on rocks in higher regions, 2500–2600 m; only known from the type.

[1] Plant caulescent, forming dense clusters, stem >8 cm, 0.5 cm  $\varnothing$  but appearing stout (0.8 cm  $\varnothing$ ) because of the densely imbricate leaf sheaths; **L** persistent, densely tomentose-lepidote with fine linear spreading trichomes; **L** sheath 1.2–2  $\times$  1.2–1.8 cm, broadly ovate, thin at the base and margins; **L** lamina very narrowly triangular, fleshy, spreading or slightly recurved, 4–5 (–8) cm, subulate but adaxially flat or with a weak furrow; **Inf** depauperately compound, subdigitate, composed of 3–5 spikes, dense, ellipsoid, fertile part 2–3  $\times$  1 cm; peduncle completely covered by its bracts, erect, 2–10 cm, 2 mm  $\varnothing$ , slender, lepidote at least near the nodes and in the upper part; lowest peduncular **Bra** almost leaflike with short lamina, the upper like the primary bracts, erect and with tightly inrolled margins, imbricate, sheath rose, axes of the inflorescence hidden and very short; primary **Bra** dense, suberect, ovate, to 2.2 cm, nearly as long as the spikes and covering them, thin, strongly veined and carinate, acuminate, abaxially lepidote; spikes with 1 (–2) sterile bracts at the base, (1- to) 2- to 3-flowered (topmost spike to 5-flowered), with a reduced flower at the apex, rachis stout and short, densely lepidote, internodes 2 mm; floral **Bra** suberect,  $\pm$  equalling the sepals, 11–13  $\times$  7–8 mm, ovate or triangular-ovate, incurved, closely enveloping the flowers, chartaceous, veined, scarcely or not at all carinate, so narrow as to expose the rachis in part, sparsely lepidote with few coarse white subappressed trichomes, roseate, acute or apiculate; **Fl** subsessile, distichous; **Sep** 9–11  $\times$  5 mm, oblong, thin, somewhat veined, evenly shortly connate or subfree, adaxial ones carinate (faintly when fresh), rose in the upper part, glabrous, sometimes with a few trichomes at the base, broadly acute; **Pet** barely exceeding the stamens, tongue-

shaped, 15–21  $\times$  3–4 mm (base 1.5 mm), centre violet, apical part white (often turning purple after anthesis), blade slightly divergent and then recurved, rounded-emarginate; **St** 15–17 mm; **Fil** narrowly ribbon-like, straight; **Anth** dorsifixed near the base, 3–3.5  $\times$  0.7 mm, lanceolate, grey-brown; **Ov** 3–4  $\times$  1.5 mm, narrowly ovoid or subglobose, contracted into the style; **Sty** slender, 8–9 mm, slightly longer or shorter than the stamens; **Sti** spreading, shortly lobed.

**T. reichenbachii** Baker (Handb. Bromel., 166, 1889). **Type:** K [icono, Reichenbach drawing]. — **Distr:** SE Brazil (Rio de Janeiro), Bolivia (Santa Cruz, Tarija, Cochabamba, La Paz, Chuquisaca), N Argentina, Paraguay; epiphytic in woods, 100–2500 m.

$\equiv$  *Tillandsia duratii* ssp. *reichenbachii* (Baker) Halda (2005); **incl.** *Tillandsia tucumanensis* Mez (1896); **incl.** *Tillandsia herzogii* Wittmack (1916); **incl.** *Tillandsia euosma* Spegazzini (1917).

[3] Plant caulescent, flowering to >20 cm tall, stem 2–5 cm, stout, curved; **L** laxly spirally arranged, to 14 cm; **L** sheaths suborbicular or very broadly elliptic, lustrous, glabrous except for the lepidote apex, very distinct from the lamina; **L** lamina very narrowly triangular, thick, to 8 cm, 0.8 cm wide, cinereous-lepidote, spreading to reflexed and often recurved at the apex, strongly canaliculate (involute-subulate when dry), slightly flexuous; **Inf** subdigitate or sometimes simple, composed of 2–8 spikes, to 7  $\times$  3–4.5 cm; peduncle completely covered by its bracts, erect,  $\pm 15$  cm, 2.5 mm  $\varnothing$ , slender; lowest peduncular **Bra** somewhat leaf-like but soon with much reduced lamina, imbricate, sublanceolate, enveloping the peduncle, veined, lepidote, subacute; primary **Bra** like the upper peduncular bracts, much shorter than the stipe of the axillary branches, obtuse; spikes long-stipitate, stipe to 3 cm and densely bracteate, first often erect and then suddenly divergent, densely flowered, 3 cm, 0.9–1 cm wide, linear, complanate, 5- to 7-flowered; floral **Bra** much shorter than the sepals, 10–11  $\times$  5 mm, elliptic, clasping the flower, subchartaceous, veined when dry, ecarinate, exposing most of the rachis, 3 $\times$  as long as the internodes, subglabrous or sparsely lepidote, green tinged with

reddish-brown, obtuse or acutish; **Fl** subsessile, slightly divergent or contiguous with each other and/or the rachis; **Sep** 12–12.5 × 6 mm, elliptic or obovate, thin-coriaceous, with broad hyaline margins, even, adaxial ones or all evenly shortly connate for 1–2 mm, ecarinate, green tinged with reddish-brown, glabrous, rounded or obtuse; **Pet** with narrow claw and suborbicular blade, 23 × 13 mm (base 2.5 mm wide), white or the blade often pale blue, margins crenate-serrate, blade spreading at right angle; **St** ± of equal length, 8 mm, deeply included; **Fil** ribbon-like, straight; **Anth** basifixed, 1.5 mm, greenish; **Ov** ±2.5 mm; **Sty** stout, ± as long as the ovary, shorter than the stamens; **Sti** disc-shaped, gemmate.

**T. retorta** Grisebach ex Baker (J. Bot. 16: 238, 1878). **Type:** Argentina, Córdoba (Lorentz 125 [BM, B, GOET, M, P]). — **Distr:** N and C Argentina (widespread to Mendoza and La Pampa in the S); epiphytic, 600–1460 m.

**Incl.** *Tillandsia caespitosa* Gillies ex Baker (1878); **incl.** *Tillandsia nappii* var. *darwinii* Lorentz & Niederlein (1881) (*incorrect name*, ICN Art. 11.4).

[4] Plant flowering usually 7.5 or rarely to 15 cm tall, forming a globose mass, stem 2–8 cm, many from a single point, usually much branched; **L** distichous, 3–5 (–7) cm, densely cinereous-lepidote; **L** sheaths imbricate, suborbicular, making the stem appear 3–5 mm thick, with broad veinless margins, veined, normally glabrous with a ciliate margin of elongate scales or occasionally in the upper part lepidote like the lamina; **L** lamina barely over 2 mm wide, recurved, then often towards the apex spreading again, veined when dry, subulate, apex acuminate and pungent; **Inf** 1- or 2-flowered, densely cinereous-lepidote; peduncle bractless, from almost none to much surpassing the leaves but usually quite short, slender, densely lepidote, reduced rachis extended from the base of the terminal flower; floral **Bra** erect, equalling or exceeding the sepals, 10–12 (–15) × 7 mm, triangular-ovate, veined, slightly >2× as long as the internodes, densely lepidote, acute, acuminate; **Fl** subsessile, erect; **Sep** 10–10.5 × 3 mm, lanceolate-oblong or narrowly obovate, thin, with broad hyaline margins, finely

veined, adaxial ones connate for 3 mm, abaxial one almost free, adaxial ones carinate, sparsely lepidote, acute or obtuse; **Pet** erect with slightly divergent apex, tongue-shaped, 12.5 × 3.3 mm (base 1.3 mm wide), yellow, blade distinct, narrowly elliptic, rounded-emarginate, subtruncate; **St** 7 mm, deeply included, exceeding the style by ½ of the anthers; **Fil** ribbon-like and tapering from base to apex, straight; **Anth** basifixed, 2 mm, linear; **Ov** 3.5 × 5 mm, ovoid, abruptly contracted into the style; **Sty** stout, 2.5 mm; **Sti** erect, shortly lobed.

**T. schatzlii** Rauh (Trop. subtrop. Pfl.-welt 27: 8, 1979). **Type:** Mexico, Oaxaca (*Rutschmann* s.n. in *BG Heidelberg* 46304 [HEID, US]). — **Distr:** S Mexico (Oaxaca); steep rock walls; altitude not recorded.

[5] Plant stemless or sometimes with a rhizomatous stem; flowering **Ros** 25 × 12 cm; **L** ±10, forming a small funnel-shaped rosette, densely appressed-lepidote with trichomes with a green centre, outer leaves reduced and deltoid; **L** sheaths 4 × 3 cm, broadly ovate, wrinkled, light brownish to violet inside, inconspicuous from and merging into the lamina; **L** lamina narrowly triangular, slightly succulent, to 20 cm, 2 mm wide at the base, divergent and often the upper ½ spreading, apex attenuate and subpungent; **Inf** simple, often subpendulous or erect; peduncle completely covered by its bracts, erect or curved, shorter than the leaves, 5 mm Ø; lower peduncular **Bra** with short leaf-like blade but soon bladeless, raspberry-red or rose but colour masked by the trichomes; spikes to 16 × 2 cm, lanceolate, slightly complanate, 8- to 10-flowered; floral **Bra** imbricate, much exceeding the sepals, 47–60 × 20 mm, (narrowly) ovate, margins with extended scales, finely veined when dry, ecarinate, densely lepidote, raspberry-red or rosy yellow-green towards the base; **Fl** to 80 mm (incl. stamens and style); **Sep** 21.5–27 (–29) × 6–7 mm, narrowly obovate, finely veined when dry, adaxial ones connate for 3–4 mm, adaxial ones bluntly carinate at the base, green, sparsely lepidote with large trichomes, obtuse or acute; **Pet** forming an erect narrow tube clasping the filaments at the apex, narrowly tongue-shaped with long cuneate



base, 65–80 × 9 mm (base 2.5 mm wide), dark violet fading to the white base, blade tip margins recurving; **St** in 2 whorls of unequal length, 70–85 mm, exserted, shorter than the style; **Fil** slender and flattened at the base and dilated becoming terete at the distal end, violet in the upper part; **Anth** dorsifixed, 3 mm, apex obtuse; **Ov** 5 × 2.5 mm, ovoid, tapering or gradually contracted into the style; **Sty** slender, exceeding the petal tube.

**T. schiedeana** Steudel (Nomencl. Bot. ed. 2, 2: 688, 1841). **Type:** Mexico, Veracruz (*Schiede & Deppe* 1004 [B, BM, HAL]). — **Distr:** USA (Missouri), Mexico, Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Cuba, Jamaica, Haiti, Dominican Republic, N & C Colombia, Venezuela, NW Peru; epiphytic, 0–2250 m.

≡ *Tillandsia vestita* Schlechtendal & Chamisso (1831) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Tillandsia flavescens* Martens & Galeotti (1843); **incl.** *Tillandsia caerulea* Grisebach (1865) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Tillandsia grisebachii* Baker (1887); **incl.** *Tillandsia eggersii* Baker (1889).

[5] Plant caulescent, flowering usually ±20 (–40) cm tall, forming a globose mass, stem 5–20 cm, simple or few-branched; **L** polystichously few-ranked, varying greatly in density, to 25 cm, densely cinereous-lepidote or sometimes ferruginous-lepidote; **L** sheaths large, suborbicular, densely imbricate; **L** lamina very narrowly triangular, divergent to spreading at a right angle from the stem, adaxially often with 1 or few grooves, subulate (involute when dry) and angled, shallowly canaliculate, slightly flexuous, apex filiform-attenuate; **Inf** always simple; peduncle completely covered by its bracts, erect, shorter than the leaves and ± as long as the spike; lowest peduncular **Bra** leaf-like, imbricate, nearly all with leaf-like lamina; spikes ±7 cm, 0.7 cm wide, lanceolate, distichously arranged, rachis slender, glabrous; floral **Bra** densely imbricate, much exceeding the sepals, 27 × 9 mm, chartaceous and with coriaceous base, veined near the apex, sublustrous, ecarinate, concealing the rachis, 3–4 × as long as the internodes, glabrous or the lower ones sparsely lepidote, red or sometimes

yellow, obtuse; **Fl** sessile, distichous, 45–55 mm; **Sep** 14 (–20) × 3 mm, lanceolate, thin-coriaceous, even, evenly short-connate for 1 mm, adaxial ones bluntly carinate, yellow, glabrous, rounded or obtuse; **Pet** forming an erect narrow tube clasping the filaments at the apex, 44 × 8 mm, lemon-yellow, blade tip margins recurved; **St** in 2 whorls of unequal length, exserted; **Fil** slender and flattened at the base and dilated becoming terete at the distal end, green; **Anth** dorsifixed near the middle, apex apiculate, brownish; **Ov** ellipsoid; **Sty** shorter than or equalling the shorter stamens; **Sti** spreading, green.

**T. seleriana** Mez (Bull. Herb. Boissier, sér. 2, 3: 84, 1903). **Type:** Mexico, sine loco (*Seler* 3439 [B]). — **Distr:** SE Mexico (Jalisco, Michoacán, Chiapas, Nayarit, Oaxaca, Veracruz), Guatemala, C & SW Honduras (Francisco Morazán, Lempira), NW El Salvador (Santa Ana), N & W Nicaragua (Estelí, Nueva Segovia); epiphytic in pine and oak woods, 270–2100 m. — Fig. 28.

[5] Plant stemless, flowering 20–25 cm tall; **L** much shorter than to exceeding the inflorescence, outer ones reduced and sheath-like, densely cinereous-lepidote or ferruginous-lepidote; **L** sheaths forming an ovoid pseudobulb 7–12 cm, broadly ovate or suborbicular, whitish-cinereous-green, merging into the lamina; **L** lamina linear to triangular, fleshy, 1 cm wide at the base, green (masked by the trichomes but less so than on the sheaths), erect or curved or secund, involute-subulate, apex attenuate; **Inf** 1 × branched, subdigitate or nearly so, composed of 3–6 spikes, dense, 6–10 cm; peduncle often partly visible, erect, short and concealed by the leaves or rarely elongate; peduncular **Bra** leaf-like, lamina shorter than or exceeding the inflorescence, erect, densely imbricate except the upper ones, with rose-coloured sheath; primary **Bra** broadly ovate or elliptic, the lower ones slightly shorter and the upper ones much shorter than the axillary branches, shortly laminate or apiculate, densely lepidote, rose-red; spikes sessile, 4 cm, broadly elliptic, strongly complanate, 4- to 8-flowered, rachis straight, densely lepidote, exposed; floral **Bra** exceeding the sepals except in the top flower and so narrow as to expose part of



**Fig. 28** *Tillandsia seleriana*. (Copyright: E. J. Gouda)

the sepals, 20–28 × 9 mm, narrowly elliptic, incurved at the apex, coriaceous, margins with extended scales at the margins, slightly if at all carinate, not concealing the rachis, 4× as long as the internodes, densely cinereous-lepidote with coarse spreading scales, acute; **Fl** sessile, densely distichous, contiguous with each other; **Sep** 15.5–17 × 4 mm, narrowly elliptic, prominently veined, adaxial ones connate for 4–6 mm, adaxial ones distinctly carinate, green or red, glabrous, acute, obtuse; **Pet** forming an erect narrow tube clasping the filaments at the apex, constricted above the ovary, linear-oblong, 35–37 × 6 mm (3 mm at the base), violet for most of the length, blade tip margins recurved, narrowly rounded; **St** in 2 whorls of unequal length, 44–46 mm, exserted; **Fil** slender and flattened at the base and dilated becoming terete at the distal end; **Anth** dorsifixed near the middle, black; **Ov** ovoid, 6 mm; **Sty** slender, 44 mm, exceeding the stamens; **Sti** spreading, dilated, white.

**T. subulifera** Mez (Repert. Spec. Nov. Regni Veg. 16: 74, 1919). **Type:** Trinidad (*Broadway* 4200 [B, B [photo]]). — **Distr:** NE Nicaragua (Atlántico Norte), W Costa Rica (Puntarenas), C Panama (Panamá), Trinidad & Tobago (Couva-Tabaquite-Talparo (Chaguanas)), NW Colombia (Antioquia), Venezuela (Miranda, Sucre, Táchira); epiphytic in forests and plantations, 5–980 m.

[5] Plant stemless, flowering 15–19 cm tall; **L** few, erect, the outer greatly reduced, the inner to 18 cm, appressed-lepidote, with distinct or faint white cross-bands; **L** sheaths forming a cylindrical pseudobulb, inflated, about ½ as long as the lamina, concolorous with the lamina; **L** lamina linear, fleshy, coriaceous, 5 mm wide at the base, strongly angled, subulate and shallowly canaliculate, apex obtuse or abruptly acute; **Inf** simple; peduncle erect, shorter than and largely concealed by the leaves, slender; peduncular **Bra** erect, imbricate, many-veined, densely lepidote; spikes erect or curved downwards, 5–12 cm, ±1.5 cm wide, oblong-lanceolate or linear in outline, complanate, 4- to 12-flowered, without sterile bracts at the apex or base, rachis slender, flexuous to geniculate (when dry), appressed-lepidote, exposed, mostly not or only partly covered by the floral bracts; floral **Bra** erect, much shorter than the sepals, 20–25 × 15 mm, elliptic, incurved, margins hyaline, prominently veined, ± carinate towards the apex, appressed-lepidote, (yellowish-) green or roseate, broadly acute; **Fl** with a short pedicel-like receptacle, distichous, suberect; **Sep** slightly incurved at the apex excluding the apiculus, 22–25 × 8 mm, narrowly elliptic or narrowly obovate, finely veined (prominently when dry), free, ecarinate, rose, cinerous-appressed-lepidote, apiculate or narrowly obtuse; **Pet** forming a tube slightly widening towards the apex, linear-oblong, 32–34 × 7 mm (at the base 5 mm), rose, upper part yellow, often with rose margins and apex, narrowly rounded; **St** ± 32 mm, included and visible in the throat; **Fil** terete, slightly coiled halfway, rose towards the distal end; **Anth** dorsifixed near the middle, 3 × 1.8 mm, oblong, base bilobed, apex obtuse and apiculate; **Ov** 5.5 × 3 mm, ovoid, tapering form near the base, slightly contracted into the style; **Sty** slender, to 27 mm; **Sti** weakly conduplicate, spreading.

**Fig. 29** *Tillandsia tectorum*. (Copyright: E. J. Gouda)



**T. tectorum** E. Morren (Belgique Hort. 27: 328, t. 18, 1877). **Type:** Peru (*Wallis* s.n. [BR]). — **Lit:** Hromadnik (2005: synopsis *T. tectorum*-complex). **Distr:** N & S Ecuador (Azuay, El Oro, Loja, Pichincha), Peru (Amazonas, Cajamarca, Huánuco, La Libertad, Ancash, Lima); saxicolous, and cultivated on roofs, 680–3400 m. — Fig. 29.

**Incl.** *Tillandsia argentea* K. Koch (1867) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Pourretia nivosa* hort. ex E. Morren (1877) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Tillandsia saxicola* Mez (1906).

[1] Plant short-stemmed to long caulescent, flowering 30–100 cm tall; **L** densely rosulate, 12–25 cm, white-tomentose-lepidote; **L** sheaths 1.2–3 cm wide at the base, triangular-ovate, clasping the stem, fleshy in the upper part, densely lepidote except the inner base, distinct from the lamina; **L** lamina very narrowly triangular, fleshy and 0.8–1.5 cm wide at the base, silvery-white, divergent to spreading, apex filiform-attenuate, trichomes eccentric, with elongated wings; **Inf** compound, densely digitate with  $\pm 4$ –6 spikes, 5–10  $\times$  (2.5–) 5–8 cm; peduncle erect, much exceeding the leaves, 10–40 cm  $\times$  5 mm  $\varnothing$ , slender, densely lepidote; lowest peduncular **Bra** somewhat leaf-like with setaceous lamina, sheaths imbricate, 1.5–2.5  $\times$  0.8–1.2 cm, broadly ovate, membranous, veined, adaxially scatteredly

lepidote and abaxially densely lepidote; primary **Bra** like the upper peduncular bracts, much shorter than the spikes; spikes sessile, erect or somewhat spreading, 3–4.5  $\times$  1–1.2 cm, lanceolate, strongly complanate, (3- to) 5- to 10-flowered; floral **Bra** densely imbricate,  $\pm$  equalling to exceeding the sepals, 10–17  $\times$  7–11 mm, ovate, thin, veined, carinate at least at the apex, lepidote to subglabrous, red, green or roseate, acutish or apiculate; **Fl** subsessile, 20 mm; **Sep** 9–15  $\times$  3–4 mm, ovate-lanceolate, thin, with broad hyaline margins, free, adaxial ones carinate, green and flushed red in the upper  $\frac{1}{2}$ , abaxially sparsely lepidote along the midvein or glabrous; **Pet** erect and forming a tube, tongue-shaped, 15–25  $\times$  3–4 mm, white with a blue band in the middle section, paler blue to whitish towards the apex, becoming pink after anthesis, blade divergent, obtuse; **St** all of equal length, 12–17 mm, included but visible in the throat; **Fil** narrowly ribbon-like, flaccid, straight or plicate, white; **Anth** subbasifixed or dorsifixed at  $\frac{1}{4}$  from the base, 2–3 mm, linear, black or brown; **Ov** 2.5–3  $\times$  2 mm, ovoid; **Sty** slender, 5–15 mm, longer than the stamens; **Sti** with short somewhat spreading lobes.

**T. tenebra** L. Hromadnik & W. Till (Bromelie 1991(2): 32, ill., 1991). **Type:** Argentina, La Rioja

**Fig. 30** *Tillandsia tenebra*. (Copyright: E. J. Gouda)



(*Hromadnik & Hromadnik* 7275 [WU, WU]). — **Distr:** Argentina (Catamarca, La Rioja, Buenos Aires, San Luis); saxicolous, 800–1900 m. — Fig. 30.

**Incl.** *Tillandsia myosura* var. *saxicola* Hieronymus ex A. Castellanos (1945) (*nom. inval.*, ICN Art. 36.1c).

[4] Plant short-stemmed, flowering 4–6 cm tall, few-branched or forming clumps; **L** densely distichous, appearing to be equitant; **L** sheaths densely imbricate, 1–1.2 × 1.4 cm, upper part densely cinereous-lepidote like the lamina; **L** lamina succulent, rigid, 4–6 × 0.4–0.5 cm, recurved or spreading, adaxially grooved in the lower ½, subulate and laterally compressed, apex subulately acuminate and pungent, densely cinereous-lepidote, with extending trichomes at the margins, trichomes suborbicular; **Inf** simple; peduncle bractless or with 1–2 bracts at the base, erect, very short to elongate, lustrous, glabrous or lepidote near the first flower, often dark brown; peduncular **Bra** 2–4.5 cm, tightly enveloping the peduncle, fleshy, short-caudate; spike 1- to 2- (to 3-) flowered, rachis straight, lepidote, barely visible, internodes 0.25–0.4 (–0.65) cm; floral **Bra** much shorter than the sepals, (7–) 10–12 (–15) × 6–7 (–8) mm, broadly ovate or rarely triangular, margins hyaline, distinctly 14- to 16-veined, the lower one densely appressed-lepidote

and the upper sparsely lepidote esp. at the base, cinereous or brown-red, apiculate; **Fl** subsessile, distichous, strongly fragrant; **Sep** (8–) 9.5–11 × (3–) 3.5–4.5 mm, elliptic, thin-coriaceous at the base, 8- to 10-veined (distinctly so at the apex), unequally short-connate for 1–3 mm, adaxial ones with a strong midvein and slightly carinate near the apex, brown to red in the upper part, glabrescent or sparsely appressed-lepidote at the apex, rounded or apiculate; **Pet** spatulate, 12–14 (–15) × 3.5–4.2 mm (base 1.5 mm wide), fleshy, with a thick midvein or with ridges, dark brown-violet, blade broadest near the apex, tapering into the cuneate claw, recurved, rounded; **St** all of equal length, 7 mm, deeply included; **Fil** 4–5.5 mm, ribbon-like and tapering from near the base to the apex; **Anth** basifixed, 1.5 × 0.5 mm, yellow; **Ov** 3.4–4 (–6) × 2–2.5 (–3) mm, angular-obconical, abruptly contracted into the style; **Sty** stout, 1.1–1.5 mm, 0.5–0.8 mm Ø, almost conical; **Sti** capitate.

**T. tortilis** Klotzsch ex Baker (J. Bot. 25: 237, 1887). **Type** [lecto]: Mexico, San Luis Potosí (*Parry & Palmer* 872 [BM, E, GH, K, MO, P, US]). — **Lit:** Till (1986). **Distr:** C & E Mexico, Jamaica; epiphytic or saxicolous, 1830–2440 m.

≡ *Viridantha tortilis* (Klotzsch ex Baker) Espejo (2002); **incl.** *Platystachys ehrenbergii*



Beer (1856) (*nom. inval.*, ICN Art. 36.1); **incl.** *Platystachys tortilis* Beer (1856) (*nom. inval.*, ICN Art. 36.1); **incl.** *Tillandsia ehrenbergii* Klotzsch ex Beer (1856) (*nom. inval.*, ICN Art. 38.1); **incl.** *Tillandsia tortilis* Klotzsch ex Beer (1856) (*nom. inval.*, ICN Art. 38.1); **incl.** *Platystachys ehrenbergii* K. Koch (1874) (*nom. inval.*, Art.?)  $\equiv$  *Tillandsia ehrenbergii* (K. Koch) Klotzsch ex Mez (1896); **incl.** *Tillandsia ehrenbergiana* Baker (1889).

[1] Plant short stemmed to distinctly caulescent, flowering 10–20 cm tall, forming dense clusters; stem 3–5 cm, simple or branched; **L**  $\pm$ 15, densely rosulate, to 17 cm, densely tomentose-lepidote or villous, with fine silver-grey scales; **L** sheaths  $2 \times 1.2$  cm, elliptic, the lower part membranous, strongly veined, densely tomentose except at the base, distinct from the lamina; **L** lamina 6–15  $\times$  0.5–1 cm, mostly spreading to reflexed, with a distinct midvein adaxially, with involute margins, subulate towards the long-attenuate apex, trichomes with elongated wings; **Inf** always simple; peduncle erect or ascending, much shorter than to just exceeding the leaves, 4–8 cm, 1–2 mm  $\varnothing$ , strongly sulcate, glabrous; lowest peduncular **Bra** leaf-like, imbricate, much exceeding the internodes, lanceolate, involute, thin, strongly veined, lepidote, the upper roseate, acuminate; spike 3–4  $\times$  1–1.6 cm, elliptic, strongly complanate, 3- to 10-flowered, rachis slender, nearly straight; floral **Bra** densely imbricate, much exceeding the sepals, 20–26  $\times$  8–12 mm, lanceolate, membranous, veined at least when dry, upper  $\frac{1}{2}$  distinctly carinate, concealing the rachis, 3–4  $\times$  as long as the internodes, abaxially cinereously lepidote, roseate, acute or acuminate; **Fl** subsessile, distichous, suberect, dense; **Sep** (16–) 17–20  $\times$  3–5 mm, lanceolate, membranous, strongly veined, subfree, adaxial ones carinate, rose but green in the lower  $\frac{1}{2}$ , lepidote, acuminate; **Pet** erect with slightly divergent apex, linearly tongue-shaped, 25–38 (–40)  $\times$  4 mm, green, lower  $\frac{1}{2}$  white, rounded; **St** 24–31 mm, included (reported as exerted by Mez); **Fil** white; **Anth** basifixed, 4 mm; **Ov**  $\pm$ 4.5 mm, ellipsoid; **Sty** slender, 11–20 mm, shorter or  $\pm$  equalling the stamens; **Sti** erect to spreading at maturity, green.

**T. violaceiflora** L. Hromadnik (Bromelie 2012 (2): 49, ills. (pp. 48, 50), 2012). **Type:** Argentina, Salta (Hromadnik 7176 [MCNS, WU]). — **Distr:** NE Argentina (Salta: Quebrada de las Conchas); rocky cliffs,  $\pm$ 1500 m.

[5] Plant saxicolous, nearly stemless forming a short,  $\pm$ 3 mm thick rhizome, flowering **Ros** only 10–12  $\times$  6–10 cm, growing in groups; **L** 4.5–9 cm, stiff; **L** sheaths 0.6–1  $\times$  1.2–2 cm, trapezoid, amplexicaul, adaxially veined, glabrous, abaxially the upper  $\frac{1}{2}$  lepidote like the lamina, pale brownish, slightly distinct from the lamina; **L** lamina narrowly triangular, fleshy, rigid, 0.7–1 cm wide at the base, divergent and the longer ones upwardly secund, finely veined, strongly canaliculate and subulate at the somewhat pungent apex, cinereous-lepidote; **Inf** simple, erect or somewhat decurved, 6–8 cm, equalling or exceeding the leaves; peduncle completely covered by its bracts, short and concealed by the leaves, 3–4 cm, 2 mm  $\varnothing$ , glabrous, white; peduncular **Bra** 2–3  $\times$  0.7 cm, oblong, membranous, strongly veined, glabrous or sparsely pale-lepidote on the lamina, the basal ones pale green, greenish-white or whitish, acuminate; spike 4  $\times$  1.2 cm, lanceolate, strongly complanate, densely 3- to 5-flowered, rachis 4-angled, slender, glabrous, partly exposed, green, internodes 5 mm; floral **Bra** exceeding the sepals, 30  $\times$  12 mm, lanceolate, subcoriaceous, smooth but rapidly veined after anthesis, glabrous, greenish to ruby-red, apiculate; **Fl** sessile, distichous, erect and densely appressed to the rachis, 40 mm, not fragrant; **Sep** 15–18  $\times$  4 mm, lanceolate, the adaxial pair nearly free, adaxial ones carinate, keels red; **Pet** forming a narrow tube exceeding the floral bracts, then spreading, spatulate, 40  $\times$  to 5 mm (base 2 mm wide), violet, the lower  $\frac{1}{3}$  white, obtuse, abaxially weakly carinate; **St** 25 mm, included; **Fil** ribbon-like, straight, white; **Anth** subbasifixed, 3 mm; **Ov** 5  $\times$  2 mm, ellipsoid; **Sty** slender, 25 mm, exceeding the stamens; **Sti** reaching the throat of the corolla, the narrow lobes spreading, white.

**T. virescens** Ruiz & Pavón (Fl. Peruv. 3: 43, t. 270: fig. b, 1802). **Type:** Peru, Huánuco (Ruiz & Pavón s.n. [MA?/BM?, F]). — **Lit:** Till (1989);



Maruska (2012); Castello & Galetto (2013). **Distr:** SE Brazil (Rio de Janeiro), Peru, Bolivia, N & C Chile, N to NC Argentina, C Paraguay; saxicolous or epiphytic in dry habitats, 3–4000 m.

≡ *Diaphoranthema virescens* (Ruiz & Pavón) Beer (1856) ≡ *Tillandsia capillaris* fa. *virescens* (Ruiz & Pavón) L. B. Smith (1935); **incl.** *Tillandsia propinqua* Gay (1853); **incl.** *Tillandsia recurvata* Grisebach (1874) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Tillandsia cordobensis* Hieronymus (1885) ≡ *Tillandsia capillaris* fa. *cordobensis* (Hieronymus) L. B. Smith (1935); **incl.** *Tillandsia stolpii* Philippi (1895); **incl.** *Tillandsia dependens* Hieronymus ex Mez (1896); **incl.** *Tillandsia dependens* var. *percordobensis* Mez (1896) ≡ *Tillandsia dependens* fa. *percordobensis* (Mez) A. Castellanos (1933); **incl.** *Tillandsia dependens* var. *perusneoides* Mez (1896) (*nom. inval.*, ICN Art. 26.1?) ≡ *Tillandsia dependens* fa. *perusneoides* (Mez) A. Castellanos (1933) (*nom. inval.*, ICN Art. 26.1?); **incl.** *Tillandsia williamsii* Rusby (1910); **incl.** *Tillandsia dependens* var. *sanzinii* Hicken (1914) ≡ *Tillandsia virescens* var. *sanzinii* (Hicken) A. Castellanos (1945); **incl.** *Tillandsia tomasii* Halda (2005).

[4] Plant small but very variable in both size and form, flowering 2–16 cm tall, densely clump-forming; stems many from a single point, simple or branched; **L** distichous, mostly 1–4 (–9) cm (rarely <1 cm), cinereous- or ferruginous-lepidote; **L** sheaths usually elliptic, thin, several-veined, densely lepidote except where overlapping; **L** lamina linear or very narrowly triangular, ± succulent, to 2 mm wide, erect to spreading or recurved; **Inf** normally 1- or rarely 2-flowered; peduncle always naked, almost none or elongate (mostly after anthesis) to 8 cm, mostly slender after anthesis, glabrous or slightly lepidote near the flower; floral **Bra** usually equalling or exceeding the sepals, 5–7 × 3.5–4.5 mm, deltoid to oblong, closely enveloping the flower, thin, strongly 3- to 6-veined, ecarinate, densely lepidote at least at the very tip to glabrous, bluntly apiculate; **Fl** subsessile; **Sep** 6.5 × 1.3–1.5 mm, narrowly oblong, thin, with broad hyaline margins and apex, 3- to 5-veined with weakly developed vein branches, unequally connate for 1 or 5 mm, adaxial ones connate for ¾ or more, ecarinate but

sometimes with pronounced midvein, green but often purple-speckled above the middle, obtuse or rounded; **Pet** tongue-shaped or linear or spatulate, 9–11.5 × 1 (–2) mm, white or yellow or brown, rounded or obtuse; **St** 3–4.5 mm, deeply included, exceeding the style; **Fil** thread-like, straight; **Anth** basifixed, 1–1.5 mm, linear, apex obtuse, green or cream-coloured; **Ov** 2 × 1.5 mm, subglobose; **Sty** stout, 1 mm; **Sti** disc-shaped, gemmate.

Difficult to distinguish from *T. capillaris*, which is also highly variable in habit and succulence. The main difference are the highly connate adaxial sepals (vs. < ½ connate in *T. capillaris*), but intermediate specimens are occasionally found.

**T. weberi** L. Hromadnik & P. Schneider (J. Bromeliad Soc. 37: 105, ills., 1987). **Type:** Mexico, Jalisco (*Hromadnik & Schneider* 12117 [JE, HAL, WU]). — **Distr:** S Mexico (Jalisco); epiphyte, ±800 m. — Fig. 31.

[5] Plant stemless, flowering to 30 cm, solitary or in small clusters; **L** few, to 10 cm, succulent, stiff, velvety white-lepidote with distinct fine longitudinal veining; **L** sheaths forming a pseudo-bulb almost closed at the top, conspicuous, 3 × 2.7 cm, ovate, inflated, abaxially densely cinereous-lepidote like the lamina except the lowest 3 mm of the base which are glabrous, inside brownish and with a ± distinct violet band about 2 mm wide, merging into the lamina; **L** lamina narrowly triangular, to 8 × 1.8–2 cm wide at the base, cinereous-lepidote, usually secund or erect, finely veined, the margins involute forming a seemingly subulate tip, apex stiffly pungent; **Inf** simple or rarely with 2 spikes; peduncle completely covered by its bracts, curved to ascending, to 15 cm, stout, glabrous, bright salmon-red; lowest peduncular **Bra** somewhat leaf-like, ±2.7 × 1 cm, enveloping the peduncle, membranous, veined, densely lepidote, green but the upper ones dark pink, acuminate and carinate at the tip; spikes to 14 × 0.6–0.8 cm, linear-lanceolate, complanate, (4- to) 10- (to 15-) flowered, rachis straight, completely covered by the bracts, internodes 9 mm; floral **Bra** exceeding the sepals, 25–30 × 9 mm, narrowly ovate, coriaceous, margins membranous and somewhat wavy and smooth,

**Fig. 31** *Tillandsia weberi*. (Copyright: E. J. Gouda)



veined, ecarinate, abaxially lepidote or becoming subglabrous, pink, acute; **Fl** sessile, to 50 mm; **Sep**  $20 \times 5$  mm, lanceolate, membranous, faintly veined, adaxial ones connate for 3–4 mm, thickened at the base, adaxial ones carinate, whitish-green with reddish tips, glabrous, acute; **Pet** forming an erect narrow tube clasping the filaments at the apex,  $40 \times 7$  mm (3 mm at the base), upper  $\frac{1}{2}$  blue-violet, white below, blade tip margins recurving, apiculate; **St** exerted; **Fil** to 45 mm, slender and flattened at the base and dilated becoming terete at the distal end, spirally twisted around the pistil in the lower  $\frac{1}{2}$ , thin, upper part blue-violet, otherwise white; **Anth**  $3 \times 1.5$  mm; **Ov**  $6 \times 2$  mm; **Sty** slender, 42 mm, exceeding the stamens; **Sti** shortly conduplicate-spiralized, spreading, dilated, white.

**T. xiphioides** Ker Gawler (Bot. Reg. 2: t. 105 + text, 1816). **Type**: [icono]: l.c. t. 105. — **Lit**: Gouda (2015). **Distr**: S Brazil (Rio Grande do Sul), S Uruguay, S Paraguay, Bolivia (Chuquisaca, La Paz, Potosí, Santa Cruz), Argentina (Jujuy, Salta, La Rioja, Córdoba, San Juan, Santiago del Estero, Mendoza); epiphytic and saxicolous in dry habitats, 1000–2700 m. **I**: Till & Barfuss (2014: 101, as var. *minor*). – Fig. 32.

≡ *Anoplophytum xiphioides* (Ker Gawler) Beer (1856) ≡ *Phytarrhiza xiphioides* (Ker Gawler

E. Morren (1879); **incl.** *Tillandsia suaveolens* Lemaire (1843); **incl.** *Tillandsia macrocnemis* Grisebach (1879); **incl.** *Tillandsia sericea* Hort. Ruch ex E. Morren (1879) (*nom. inval.*, Art. 32.1c); **incl.** *Tillandsia unca* Hicken (1912) (*nom. illeg.*, ICN Art. 53.1); **incl.** *Tillandsia xiphioides* var. *minor* L. Hromadnik (1989).

[2] Plant flowering 15–30 cm tall or taller, not or few-branched, stem shorter than the leaves; **L** laxly polystichous or sometimes almost distichous, few to many, erect to spreading or  $\pm$  curved, densely cinereous- or ferruginous-lepidote, scales mostly with broad lobes; **L** sheaths large, densely imbricate making the stem appear 1–2 cm thick, passing almost imperceptibly into the lamina; **L** lamina narrowly triangular, to  $25 \times 2$  cm but often much shorter, flat at the base but mostly with involute margins upwards, apex attenuate-subulate; **Inf** always simple; peduncle hidden by the inner leaves and bracts, erect, almost none to 12 cm; peduncular **Bra** densely imbricate and hiding the peduncle, elliptic-oblong, thin, lepidote or quite glabrous or sparsely pale-lepidote, caudate (lower ones) to apiculate (upper ones); spike with several sterile bracts at the base, to 12 cm (excl. petals), lanceolate or oblong, 2- to 10-flowered, acute, rachis narrowly alate, flexuous, to 3 mm  $\varnothing$ ; floral **Bra** densely imbricate, much exceeding the sepals,  $40\text{--}56$  ( $-70$ )  $\times$   $11\text{--}13$  mm,

**Fig. 32** *Tillandsia xiphioides*. (Copyright: E. J. Gouda)



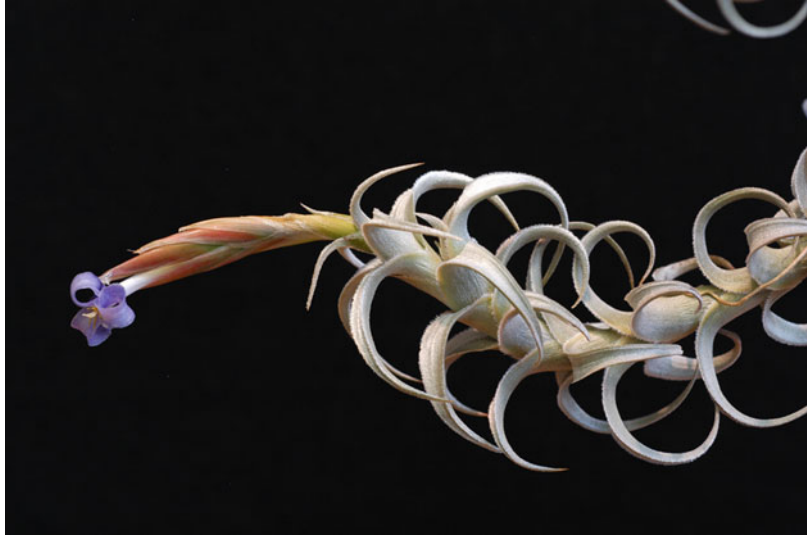
lanceolate-oblong, somewhat incurved at the apex, submembranous, margins broadly hyaline, veinless but finely to strongly veined when dry, ecarinate, usually many times longer than the internodes, glabrous or sometimes the lower ones sparsely lepidote, mostly greenish or stramineous or suffused with red or violet, attenuate or acutish; **Fl** sessile or subsessile, distichous, to 100 mm, fragrant; **Sep** (25–) 35 (–42) × (6–) 7–9 mm, linear-lanceolate, submembranous, prominently veined, free or subfree, adaxial ones finely carinate from base to apex, pale green, glabrous, acuminate or acutish; **Pet** forming a narrow tube exceeding the floral bracts, then spreading, claw narrow with suborbicular blade, 70–85 × 10–15 (–20) mm, margins conspicuously crenate-serrate, white, blade subrhombic or obovate, recurved to weakly helicoid, obtuse; **St** 43–53 mm, included or visible in the throat; **Fil** flaccid, becoming filiform upwards, straight; **Anth** basifixed, 8 mm, linear; **Ov** slenderly prismatic-ovoid, 6–10 mm, tapering into the style; **Sty** slender, including stigma 55–68 mm, exerted from the corolla throat at late anthesis; **Sti** recurved, linear.

A very variable species as to size, succulence and indumentum, with many microspecies. The leaves vary from long and leathery to short and fleshy.

**T. yuncharaensis** W. Till (J. Bromeliad Soc. 40: 214, ill., 1990). **Type**: Bolivia, Tarija (*Haugg & al.* WT55 [WU]). — **Distr**: S Bolivia (Tarija); saxicolous, ±3000 m. — Fig. 33.

[2] Plant long-caulescent, stem to 30 cm; **L** laxly polystichous; **L** sheaths 0.7 × 1.8 cm, broadly triangular, amplexicaul, glabrous in most parts, brownish, merging into the lamina; **L** lamina with subciliate scales at the margins, to 5 × 1 cm, spreading to recurved, not secund, canaliculate, veined when dry, ± appressed-lepidote, apex attenuate and acute; **Inf** simple; peduncle completely covered by its bracts, only 2–3 cm, 2 mm Ø, angled when dry, glabrous; peduncular **Bra** few (3–4), the lowest somewhat leaf-like, the upper ones like the floral bracts, much exceeding the internodes, veined, lepidote at least towards the apex, reddish, acuminate or broadly acute; spike 5.5–6.5 × 0.8–1.2 cm, linear-lanceolate, slightly to strongly complanate, (1- to) 2- to 4- (to 6–) flowered, acute, rachis glabrous; floral **Bra** exceeding the sepals, 35–42 × 11–13 mm, margins hyaline, even, ecarinate, concealing the rachis, glabrous in part with very few scale-hairs near the apex, carmine-red with greenish margins, acute; **Fl** distichous, 37–40 mm, strongly fragrant; **Sep** 23–25 × 6–7 mm, ovate-lanceolate, smooth, evenly short-connate for 1 mm, adaxial ones very

**Fig. 33** *Tillandsia yuncharaensis*.  
(Copyright: E. J. Gouda)



**Fig. 34** *Tillandsia zecheri*. (Copyright: E. J. Gouda)



bluntly carinate, subulate only at the apex, green tinged with purple, glabrous, subobtusely; **Pet** forming a narrow tube exceeding the floral bracts, then spreading,  $45\text{--}47 \times 7$  mm, margins slightly undulate, violet or white (sometimes with blue margins), claw  $30 \times 3\text{--}3.5$  mm, blade 17 mm, subrhombic, curved-spreading; **St** in 2 whorls of unequal length, 24–30 mm, visible in the throat; **Fil**  $28\text{--}29 \times 1$  mm, ribbon-like or filamentous upwards, not plicate, white; **Anth** subbasifixed,  $2.5$  (5 when fresh)  $\times 0.5$  mm, linear; **Ov**  $5 \times 2\text{--}2.5$  mm, conical-cylindrical or ovoid, contracted

into the style; **Sty** slender, 33 mm (incl. stigma), slightly exceeding the petal tube and the stamens; **Sti** dilated-conduplicate, spreading.

**T. zecheri** W. Till (Bromeliæ 1983(1–2): 6–7, ill., 1983). **Type:** Argentina, Salta (*Hromadnik & Hromadnik* 7162 [WU]). — **Distr:** NE Argentina (Salta); saxicolous on river banks, 1900–2500 m. — Fig. 34.

[1] Plant short-stemmed, branched or solitary; **L** suberect, densely cinereous or densely tomentose-lepidote in some forms; **L** sheaths veined,

lepidote, indistinctly merging into the lamina; **L** lamina narrowly triangular, 13–17 cm, rigid or succulent in some forms, slightly secund to curved, densely cinereous-lepidote, often veined with the trichomes in longitudinal lines, trichomes with elongated wings esp. at the leaf base, lamina with involute margins forming a channel, apex obtuse or pungent; **Inf** simple; peduncle completely covered by its bracts, slightly curved, short and concealed by to equalling the leaves, 2–7 cm, straight; lowest peduncular **Bra** with short leaf-like lamina, erect, imbricate, 3–4 cm, the upper ones lanceolate, enveloping the peduncle, greyish, acute; spike with a sterile bract at the base, recurved, 14 × to 3 cm, lanceolate, complanate, densely (3- to) 4- to 6- (to 8-) flowered, acute, rachis laterally compressed, slightly flexuous, glabrous, normally hardly visible at anthesis, green; floral **Bra** ± densely imbricate but partially exposing the rachis after anthesis, exceeding the sepals, (18–) 27–35 (–48) × 9–11 mm, often greenish, margins finely veined or even and sometimes waxy, ecarinate, glabrous, reddish, obtuse; **Fl** sessile, not fragrant; **Sep** (18–) 20–26 × 4.5–5 mm, oblong-lanceolate, equally free or evenly short-connate for 1–2 mm, adaxial ones carinate, green, (obscurely) acuminate; **Pet** tongue-shaped, 37–40 × ±5 mm, dark purple-violet or bluish, blade spreading to recurved, obtuse; **St** unequal in length, ± equaling the petal claw at anthesis; **Fil** slightly (if at all) plicate in the middle; **Anth** dorsifixed near the base, linear, apex apiculate; **Ov** ovoid, 5 mm; **Sty** exceeding the stamens and exerted from the throat; **Sti** weakly conduplicate, erect or slightly divergent.

## References

- Barfuss, M. H. J. [et al. 2016], Till, W., Leme, E. M. C., Pinzón, J. P., Manzanares, J. M., Halbritter, H., Samuel, R. & Brown, G. K. (2016) Taxonomic revision of *Bromeliaceae* subfam. *Tillandsioideae* based on a multi-locus DNA sequence phylogeny and morphology. *Phytotaxa* 279(1): 1–97, ills., key. <https://doi.org/10.11646/phytotaxa.279.1.1>.
- Brown, G. K. & Terry, R. G. (1992) Petal appendages in *Bromeliaceae*. *Amer. J. Bot.* 79(9): 1051–1071. <https://doi.org/10.2307/2444915>.
- Castello, L. V. & Galetto, L. (2013) How many taxa can be recognized within the complex *Tillandsia capillaris* (*Bromeliaceae*, *Tillandsioideae*)? Analysis of the available classifications using a multivariate approach. *PhytoKeys* 23: 25–39, ills., key. <https://doi.org/10.3897/phytokeys.23.4507>.
- Donadio, S. [et al. 2015], Pozner, R. & Giussani, L. M. (2015) Phylogenetic relationships within *Tillandsia* subgenus *Diaphoranthema* (*Bromeliaceae*, *Tillandsioideae*) based on a comprehensive morphological dataset. *Pl. Syst. Evol.* 301: 387–410. <https://doi.org/10.1007/s00606-014-1081-1>.
- Gouda, E. J. (1987) 189. *Bromeliaceae*, subfamily *Tillandsioideae*. In: Görts-van Rijn, A. R. A. (ed.): *Flora of the Guianas*. Series A: Phanerogams, fascicle 3. Koenigstein (DE): Koeltz Scientific Books.
- Gouda, E. J. (1995) *Bromeliaceae* — anpassingen aan epifytische en epilithische leefwijze. Utrecht (NL): University Botanic Gardens.
- Gouda, E. J. (2015) Notes on the polymorphic *Tillandsia xiphioides* Ker Gawler. *J. Bromeliad Soc.* 65(2): 111–121, ills.
- Gouda, E. J. [et al. 2012+], Butcher, D. & Gouda, C. S. (2012+) *Encyclopaedia of Bromeliads*, Version 3.1 (2012). Utrecht (NL): University Botanic Gardens, Utrecht. <http://bromeliad.nl/encyclopedia/>
- Granados Mendoza, C. [et al. 2017], Granados-Aguilar, X., Donadio, S., Salazar, G. A., Flores-Cruz, M., Hagsater, E., Starr, J. R., Ibarra-Manríquez, G., Fragosó-Martínez, I. & Magallón, S. (2017) Geographic structure in two highly diverse lineages of *Tillandsia* (*Bromeliaceae*). *Botany* 95(7): 641–651. <https://doi.org/10.1139/cjb-2016-0250>.
- Grant, J. R. (1993) True tillandsias misplaced in *Vriesea* (*Bromeliaceae*: *Tillandsioideae*). *Phytologia* 75: 170–175.
- Hromadnik, L. (2005) Der Verwandtschaftskreis um *Tillandsia tectorum* — The *Tillandsia tectorum* complex. *Bromelie Sonderheft* 5: 120 pp., key, map.
- Isley, P. T. III. (1987) *Tillandsia*. The world's most unusual air plants. Gardena (US): Botanical Press.
- Isley, P. T. III. (2009) *Tillandsia*. The world's most unusual air plants. 2. Edition. Redondo Beach (US): Botanical Press.
- Magalhães, R. I. & Mariath, J. E. A. (2012) Seed morphoanatomy and its systematic relevance to *Tillandsioideae* (*Bromeliaceae*). *Pl. Syst. Evol.* 298(10): 1881–1895, ills. <https://doi.org/10.1007/s00606-012-0688-3>.
- Maruska, J. (2012) Die Variabilität von *Tillandsia virescens*. The variability of *Tillandsia virescens*. *Bromelie* 2012(2): 66–72, ills.
- Mez, C. (1896) *Bromeliaceae*. In: Candolle, C. De (ed.): *Monographiae phanerogamarum*. Vol. 9. Paris (FR): Masson & Cie. <https://doi.org/10.5962/bhl.title.45961>.
- Morra, L. [et al. 2002], Dottori, N. & Cosa, M. T. (2002) Ontogenia y anatomía de semilla y fruto en *Tillandsia tricholepis* (*Bromeliaceae*). *Bol. Soc. Argent. Bot.* 37 (3–4): 193–201.



- Rauh, W. (1970) Bromelien für Zimmer und Gewächshaus. Band 1: Die Tillandsioideen. Stuttgart (DE): Verlag Eugen Ulmer.
- Rauh, W. (1979) Bromelienstudien (Mitteilung 9). I. Neue und wenig bekannte Arten aus Peru und anderen Ländern. Trop. subtrop. Pfl.-welt 31: 5–29, ills.
- Rauh, W. (1990) Bromelien. Ed. 3. Stuttgart (DE): Verlag Eugen Ulmer.
- Rauh, W. & Bismarck, K. von (1996) Über präkolumbianische Darstellungen von Bromelien in Peru. Trop. subtrop. Pfl.-welt 94: 46 pp., ills., map.
- Roguenant, A. (2001) Les *Tillandsia* et les *Racinaea*. Paris (FR): Editions Belin.
- Schulte, K. & Zizka, G. (2008) Multi locus plastid phylogeny of *Bromelioideae* (*Bromeliaceae*) and the taxonomic utility of petal appendages and pollen characters. *Candollea* 63(2): 209–225. [http://www.ville-ge.ch/cjb/publications\\_candollea\\_632.php](http://www.ville-ge.ch/cjb/publications_candollea_632.php)
- Shimizu, H. (1992) *Tillandsia* handbook. Shizuoka (JP): Japan Cactus Planning Co. Press.
- Smith, L. B. & Downs, R. J. (1977) Flora Neotropica. Monograph No. 14 [*Bromeliaceae*]. Part 2: *Tillandsioideae*. New York (US): Hafner Press & New York Botanical Garden. <http://www.jstor.org/stable/i399938>
- Smith, L. B. & Spencer, M. (1993) *Racinaea*, a new genus of *Bromeliaceae* (*Tillandsioideae*). *Phytologia* 74(2): 151–160.
- Till, W. (1986) Was ist *Tillandsia ehrenbergii*? *Bromelie* 1986(3): 39–41.
- Till, W. (1989) Die Untergattung *Diaphoranthema* (Beer) C. Koch von *Tillandsia* Linnaeus. *Bromelie* 1989(2): 31–34, (3): 55–59, ills.
- Till, W. (1991) Die Untergattung *Diaphoranthema* (Beer) C. Koch von *Tillandsia* Linnaeus. 3. Teil: Das *Tillandsia rectangula* Aggregat. *Bromelie* 1991(1): 15–19, ills.
- Till, W. & Barfuss, M. H. J. (2014) A new epilithic *Tillandsia* from Central Bolivia: *Tillandsia lechneri*. *J. Bromeliad Soc.* 64(2): 96–101, ills.

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**Part VIII**

**The Family Commelinaceae**





## Commelinaceae

D. R. Hunt

**Including** *Cartonemataceae* Pichon.

**Including** *Ephemeraceae* Batsch.

**Including** *Tradescantiaceae* Salisbury.

Herbs, mostly perennial, often with a rhizomatous base or root tubers, more rarely annual, often grass-like when not in flower; stems usually succulent or subsucculent, often swollen at the nodes; **Int** usually marked with a line of hairs; **L** simple, entire, often longitudinally striped with whitish, silvery or purplish bands, arranged spirally or distichous, or sometimes in mainly terminal or basal **Ros**; leaf base forming a closed (i.e. tubular) sheath around the stem (as in many grasses, but without a projecting ligule), margins of young leaves involute or convolute, venation clear or obscure; **Fl** actinomorphic or zygomorphic, bisexual or rarely unisexual and plants polygamous, in terminal or axillary 1- to many-flowered cincinni (helicoid cymes) often aggregated in thyrses or fused in pairs, cincinni usually bracteate and bracteolate; **Bra** often spathaceous or beak-like; **Sep** usually 3, free (rarely connate, very rarely 2); **Pet** 3 (very rarely 2), free, sometimes clawed and/or connate at the base, equal or unequal; **St** typically 6 in 2 whorls of 3, but all or some of one or other whorl sometimes missing, variously differentiated or staminodal; **Ov** superior, 3- or

rarely 2-locular with several to 2, or rarely 1, biseriate or uniseriate, ovules per locule; **Fr** capsules, splitting loculicidally, or rarely berry-like and indehiscent; **Se** with mealy endosperm, position of micropyle and embryo marked by a callosity (operculum or embryotega) on the testa.

**Order:** Commelinales

**Important Literature:** Clarke (1881: monograph); Rohweder (1956: systematics); Faden (1985: synopsis); Obermeyer & Faden (1985: Flora S Africa); Tucker (1989: synopsis SE USA); Faden & Hunt (1991: classification); Hunt (1993a: Flora Novo-Galiciana); Hunt (1993b: diversity Mexico); Hunt (1994: Flora Mesoamericana); Faden (1998: synopsis); Evans & al. (2001: morphological phylogeny); Evans & al. (2003: phylogeny); Wade & al. (2006: tribe *Tradescantieae*); Burns & al. (2011: molecular phylogeny); Faden (2012: Flora Tropical E Africa); Hertweck & Pires (2014: systematics, inflorescence structure); Hunt (2015: systematics).

**Distribution:** Mostly tropics and subtropics worldwide.

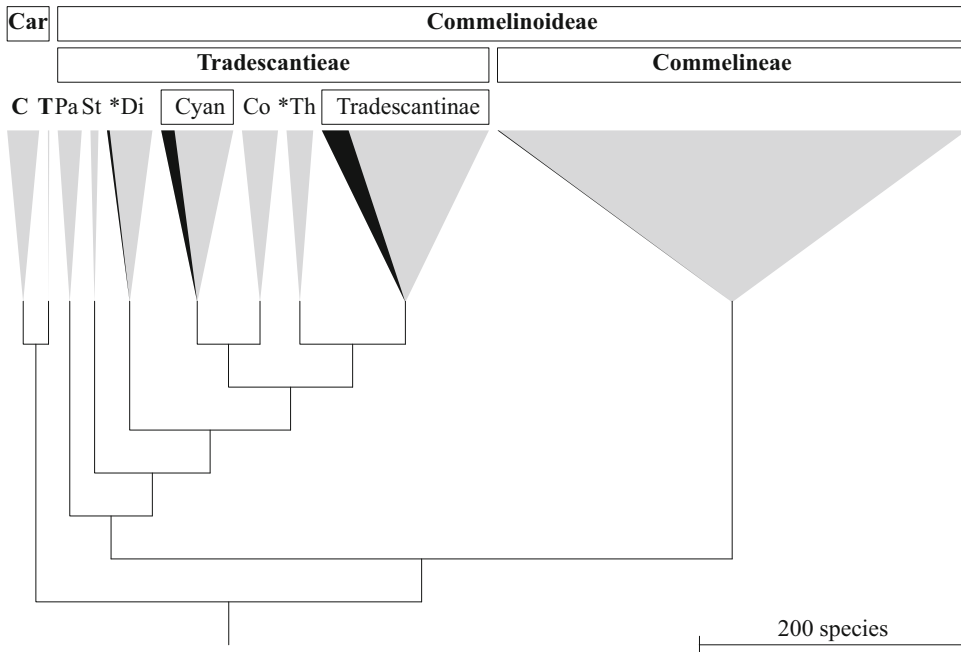
A family with about 40 genera and 650 species in 2 very unequal subfamilies: *Cartonematoideae* (only *Cartonema* and *Triceratella* from Australia and Africa; no succulents), and *Commelinoideae* (all other genera, widely distributed). *Commelinaceae* are unambiguously monophyletic, and diagnostically circumscribed on the base of their

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D. R. Hunt: deceased.

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**Fig. 1** Summary phylogeny of *Commelinoideae* based on Wade & al. 2006 (660 species total, data from Faden 1998). C = Cartonemateae, Car = Cartonematoideae, Co = Coleotrypinae, Cyan = Cyanotidinae, \*Di =

\*Dichorisandrinae, Pa = Palisotinae, St = Streptoliriinae, T = Triceratelleae, \*Th = \*Thyrsantheminae. (Copyright: U. Eggli)

morphology (closed leaf sheath, deliquescent flowers, and absence of nectaries) (Burns & al. 2011). Wade & al. (2006) provide a complete subtribal classification of *Tradescantieae*, but not all these taxa are monophyletic in the molecular studies of Burns & al. (2011) and Hertweck & Pires (2014) – Fig. 1.

Molecular data places the *Commelinoideae* as sister to the *Hanguanaceae* (only genus *Hanguana*, no succulents), and the combined clade is sister to a clade formed by the remaining families (*Haemodoraceae*, *Philydraceae*, *Pontederiaceae*) of the order (Chase & al. 2006, Saarela & al. 2008).

**Succulence:** Many members of the family exhibit a tendency to succulence in the stems and/or leaves, but even in the very few species occasionally seen in collections of succulent plants, such as *Callisia navicularis* and *Tradescantia sillamontana*, stems and leaves die down at the commencement of the winter dry season, i.e. the plants are hemicryptophytes. Many other members of the family in seasonally dry and/or

cold habitats are hemicryptophytes or geophytes with tubers or thickened roots. The succulent tissue in the leaves is reported to be derived from parenchyma (Metzler 1924), and it is often hardly differentiated from the epidermis.

The following account is confined to the most xerophytic species with succulent or subsucculent leaves in the genera *Aneilema*, *Callisia*, *Cyanotis*, *Tradescantia* and *Tripogandra* and concentrates on those of potential interest to collectors of succulents. Most of the species are easily cultivated and readily propagated by cuttings.

Species of *Dichorisandra* are sometimes mentioned as succulents because of the tuberous roots. Tuberous roots are widespread in the family, however, and are not considered to be primarily water-storage organs.

Identification of individual genera is usually not possible by vegetative features alone and depends in the first instance on features of the inflorescence, which is composed of one to many helicoid cymes or cincinni. The cincinnus may be relatively lax, with visible internodes



**Key to genera with succulents:**

<b>1a</b>	Cincinni single, not fused in pairs	2
<b>1b</b>	Cincinni fused in bifacial pairs	3
<b>2a</b>	<b>St</b> dimorphic	<i>Aneilema</i>
<b>2b</b>	<b>St</b> all similar	<i>Cyanotis</i>
<b>3a</b>	<b>St</b> dimorphic	<i>Tripogandra</i>
<b>3b</b>	<b>St</b> all similar	4
<b>4a</b>	<b>Bra</b> paired or very rarely 3 or more	<i>Tradescantia</i>
<b>4b</b>	<b>Bra</b> solitary or absent	5
<b>5a</b>	Paired cincinni stipitate, or if sessile then <b>Fl</b> also sessile	<i>Callisia</i>
<b>5b</b>	Paired cincinni sessile, <b>Fl</b> pedicellate	<i>Tradescantia</i>

between the flowers, as usually in species of *Aneilema*, or very condensed, so that the flowers appear crowded, as in a small umbel. The diagnostic feature of the large American genus *Tradescantia* and its immediate allies, *Callisia* and *Tripogandra*, is that the cincinni are fused in pairs, back to back. This may not be immediately apparent, because of the crowding of the flowers, but is often indicated by the presence of paired bracts beneath the flower-heads, or else by an open flower on each side (normally each cincinnus opens one flower at a time). *Callisia* includes several of the most succulent species in the family, but its characters are more obscure (seeds, chromosomes), with affinities to both *Tradescantia* and *Tripogandra*. *Cyanotis* is the Old World equivalent of *Tradescantia*, but the cincinni are single, not fused in pairs.

**Horticultural Importance:** Many species are cultivated, primarily for their ornamental foliage. Apart from this the family is of little economic value.

**References**

- Burns, J. H. [& al. 2011], Faden, R. B. & Steppan, S. J. (2011) Phylogenetic studies in the *Commelinaceae* subfamily *Commelinoideae* inferred from nuclear ribosomal and chloroplast DNA sequences. *Syst. Bot.* 36(2): 268–276. <https://doi.org/10.1600/036364411X569471>.
- Chase, M. W. [& al. 2006], Fay, M. F., Devey, D. S., Maurin, O., Rønsted, N., Davies, T. J., Pillon, Y., Peterson, G., Seberg, O., Tamura, M. N., Asmussen, C. B., Hilu, K., Borsch, T., Davis, J. I., Stevenson, D. W., Pires, J. C., Givnish, T. J., Sytsma, K. H., McPherson, M. A. & Graham, S. W. (2006) Multigene analyses of monocot relationships: A summary. In: Columbus, J. T. & al. (eds.): *Comparative biology and evolution (excluding Poales)*. *Aliso* 22: 63–75.
- Clarke, C. B. (1881) *Commelinaceae*. In: Candolle, A. & C. (eds.): *Monographiae Phanerogamarum Prodromi*, Vol. 3; pp. 113–324. Paris (FR): G. Masson. <http://biodiversitylibrary.org/page/32081052>
- Evans, T. M. [& al. 2001], Faden, R. B., Simpson, M. G. & Sytsma, K. J. (2001) Phylogenetic relationships in the *Commelinaceae*: I. A cladistic analysis of morphological data. *Syst. Bot.* 25(4): 668–691, diags. <https://doi.org/10.2307/2666727>.
- Evans, T. M. [& al. 2003], Sytsma, K. J., Faden, R. B. & Givnish, T. J. (2003) Phylogenetic relationships in the *Commelinaceae*: II. A cladistic analysis of rbcL sequences and morphology. *Syst. Bot.* 28(2): 270–292. <https://doi.org/10.1043/0363-6445-28.2.270>.
- Faden, R. B. (1985) *Commelinaceae*. In: Dahlgren, R. M. T. & al. (eds.): *The families of Monocotyledons*; pp. 381–387. Berlin/Heidelberg (DE) etc.: Springer-Verlag.
- Faden, R. B. (1998) *Commelinaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 4: 109–128, ills., key. Berlin (DE) etc.: Springer-Verlag.
- Faden, R. B. (2012) *Commelinaceae*. In: Beentje, H. J. (ed.): *Flora of Tropical East Africa*. Richmond (GB): Royal Botanic Gardens, Kew, on behalf of the East African Governments.
- Faden, R. B. & Hunt, D. R. (1991) The classification of the *Commelinaceae*. *Taxon* 40(1): 19–32. <http://www.jstor.org/stable/1222918>
- Hertweck, K. L. & Pires, J. C. (2014) Systematics and evolution of inflorescence structure in the *Tradescantia* alliance (*Commelinaceae*). *Syst. Bot.* 39(1): 105–116. <https://doi.org/10.1600/036364414X677991>.
- Hunt, D. R. (1993a) *Commelinaceae*. In: McVaugh, R. (ed.): *Flora Novo-Galiciana*; 13: 130–201, ills. Ann Arbor (US): University of Michigan Herbarium.
- Hunt, D. R. (1993b) The *Commelinaceae* of Mexico. In: Ramamoorthy, T. P. & al. (eds.): *Biological diversity of Mexico: Origins and distribution*; pp. 421–446. Oxford (GB)/New York (US): Oxford University Press.
- Hunt, D. R. (1994) *Commelinaceae*. In: Davidse, G. & al. (eds.): *Flora Mesoamericana*. Volumen 6: *Alismataceae a Cyperaceae*; pp. 157–173. México, D.F. (MX): Universidad Nacional Autónoma de México. <http://www.tropicos.org/Project/FM>
- Hunt, D. R. (2015) Further notes on American *Commelinaceae*. *Opusc. Neotrop.* 1: 1–5.
- Metzler, W. (1924) Beiträge zur vergleichenden Anatomie blattsukkulenter Pflanzen. *Bot. Arch.* 6(1–3): 50–83, ills.
- Obermeyer, A. A. & Faden, R. B. (1985) *Commelinaceae*. In: Leistner, O. A. (ed.): *Flora of southern Africa*, Volume 4, Part 2; pp. 23–60, ills., keys. Pretoria (ZA): Botanical Research Institute.

- Rohweder, O. (1956) Die *Farinosae* in der Vegetation von El Salvador. *Commelinaceae*. Abh. Auslandsk., Reihe C, Naturwiss. 61(C18): 98–178.
- Saarela, J. M. [& al. 2008], Prentis, P. J., Rai, H. S. & Graham, S. W. (2008) Phylogenetic relationships in the Monocot order *Commelinales*, with a focus on *Philydraceae*. *Botany* 86: 71–9731. <https://doi.org/10.1139/B08-063>.
- Tucker, G. C. (1989) The genera of *Commelinaceae* in the southeastern United States. *J. Arnold Arbor.* 70: 97–130.
- <http://www.biodiversitylibrary.org/page/9251162#page/99/>
- Wade, D. J. [& al. 2006], Evans, T. M. & Faden, R. B. (2006) Subtribal relationship in tribe *Tradescantieae* (*Commelinaceae*) based on molecular and morphological data. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 520–526. <https://doi.org/10.5642/aliso.20062201.40>

## Aneilema COMMELINACEAE

D. R. Hunt

**Aneilema** R. Brown (Prodr., 270, 1810). **Type:** *Aneilema biflorum* R. Brown. — **Commelinoideae** — **Commelineae** — **Lit:** Faden (1991: morphology, taxonomy); Davis & Evans (2009: preliminary molecular phylogeny); Faden (2012: 66–127, Flora Tropical E Africa); Lebrun & Stork (2012: 54–66, synopsis tropical Africa). **Distr:** Africa (55 species + 1 extending to the Arabian Peninsula and 1 to tropical America), Yemen (1 species), Madagascar (1 species), Australia (5 species). **Etym:** Gr. ‘a-, an-’, without; and Gr. ‘eilema’, involucre; because the inflorescences are without conspicuous subtending bracts.

**Incl.** *Lamprodirhizos* Hasskarl (1864). **Type:** not designated.

**Incl.** *Bauschia* Seubert ex Warming (1872). **Type:** *Aneilema bracteolata* Martius.

**Incl.** *Amelina* C. B. Clarke (1874). **Type:** *Amelina wallichii* C. B. Clarke.

**Incl.** *Ballya* Brenan (1964). **Type:** *Aneilema zebrinum* Chiovenda.

**Incl.** *Perosanthera* Fenzl ex Lebrun & Stork (2012) (*nom. inval.*, ICN Art. 36.1b,c). **Type:** not typified.

Annual or perennial herbs; **R** sometimes tuberous; **L** various; **Inf** single cincinni or thyrses of

cincinni, without conspicuous **Bra**; **Fl** bisexual, zygomorphic; **Sep** 3, free, equal; **Pet** 3, free, often unequal and differing in colour, upper pair clawed, white to lilac or lavender, or yellow to orange, lower much reduced (rarely enlarged), often inconspicuous; **St** (5-) 6, the 3 anterior fertile (sometimes the median sterile), the (2-) 3 posterior staminodal; **Fil** equal, or more commonly the median shorter, all glabrous or the lateral bearded; **Anth** of median stamen usually different from those of the lateral, antherodes usually bilobed; **Ov** 3- or 2-locular, ventral locules with 1–6 uniseriate ovules, dorsal not developed or with usually 1 ovule only; **Fr** capsules, usually 2-valved; **Se** with linear hilum and dorsal embryotega.

The genus embraces 64 species and has been found to be monophyletic in a preliminary molecular analysis, with *Rhopalephora* imbedded (Evans & al. 2003, Davis & Evans 2009). 7 sections are recognized based on morphological characters (Faden 1991), but only sections *Aneilema*, *Brevibarbata* and *Lamprodirhizos* were recovered in the molecular analysis of Davis & Evans (2009). The species treated here belong to sect. *Lamprodirhizos* (Hasskarl) C. B. Clarke 1881.

*Ballya* was separated on the grounds of 3 characters, but 2 have been shown by Faden (1991) to be found in other species of *Aneilema* sect. *Lamprodirhizos*, whilst the third was atypical of *A. zebrinum* itself.

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**Fig. 1** *Aneilema zebrinum*. (Copyright: U. Eggli)

**A. succulentum** Faden (Smithsonian Contr. Bot. 76: 136, fig. 55, t. 4e, f, t. 6j, 1991). **Type:** Kenya, Tana River Distr. (Faden & Faden 74/1152 [US, BR, EA, FT, K, MO, PRE]). — **Distr:** E Kenya; dry deciduous bushland and thickets on sandy to clayey soils, 10–600 m.

Creeping perennials with very succulent long **Int** forming mats; **R** fibrous; **L** distichous, succulent, often  $\pm$  falcate and/or conduplicate, narrowly lanceolate-elliptic to elliptic, (1.3–) 1.5–4 (–6)  $\times$  (0.4–) 0.7–1.3 (–1.9) cm, slightly lustrous, puberulous or pilose-puberulous, margin flat or undulate, scabrid, sparsely ciliate towards the slightly asymmetrical base; **Inf** terminal on the ascending flowering shoots, usually a single cincinnus enclosed in a subopposite pair of bracts; **Fl** up to 10, 9–14 (–17) mm  $\varnothing$ ; **Pet** white to pale lilac, lower petal boat- or cup-shaped; **Ov** 3-locular; **Fr** 2.8–4.3  $\times$  1.5–2.5 mm, puberulous.

One of the most succulent species of the genus, and when sterile confusable with *A. zebrinum* according to the protologue. — [U. Eggli]

**A. zebrinum** Chiovenda (Webbia 8: 38, t. 12, 1951). **Type** [lecto]: Ethiopia, Gemu-Gofa Prov. (Corradi 2155 [FT, K [photo]]). — **Distr:** SW Ethiopia, Kenya, Tanzania, RSA (NE KwaZulu-Natal); deciduous or semi-evergreen bushland to light forest in partial to dense shade, 10–1150 m. **I:** Obermeyer & Faden (1985: 41, fig. 8); Faden (1991: 140–143). – Fig. 1.

$\equiv$  *Ballya zebrina* (Chiovenda) Brenan (1964).

Creeping perennials; **R** fibrous; **L** distichous, lamina to 4  $\times$  2 cm, shiny, greyish-green, striped paler and sometimes with maroon lines, moderately succulent, base symmetrical; **Inf** lateral, piercing the leaf sheath, usually a single cincinnus; **Fl** 4 (–6), to 10 mm  $\varnothing$ ; **Pet** pale lilac, lower **Pet** cup-like; **Ov** 3-locular; **Fr** 3–4  $\times$  2–3 mm, puberulous.

## References

- Davis, C. & Evans, T. M. (2009) An examination of speciation, extinction, and evolutionary relationships in plants from two continents. Allendale (US): Grand Valley State University, Student Summer Scholars, Paper 34. <http://scholarworks.gvsu.edu/sss/34>
- Evans, T. M. [ & al. 2003], Sytsma, K. J., Faden, R. B. & Givnish, T. J. (2003) Phylogenetic relationships in the *Commelinaceae*: II. A cladistic analysis of rbcL sequences and morphology. Syst. Bot. 28(2): 270–292. <https://doi.org/10.1043/0363-6445-28.2.270>.
- Faden, R. B. (1991) The morphology and taxonomy of *Aneilema* R. Brown (*Commelinaceae*). Smithsonian Contr. Bot. 76: 166 pp., ills., keys, maps. <https://doi.org/10.5479/si.0081024X.76>.
- Faden, R. B. (2012) *Commelinaceae*. In: Beentje, H. J. (ed.): Flora of Tropical East Africa. Richmond (GB): Royal Botanic Gardens, Kew, on behalf of the East African Governments.
- Lebrun, J.-P. & Stork, A. L. (2012) Tropical African flowering plants. Ecology and distribution. Volume 7: Monocotyledons 1 (*Limnocharitaceae* - *Agavaceae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Obermeyer, A. A. & Faden, R. B. (1985) *Commelinaceae*. In: Leistner, O. A. (ed.): Flora of southern Africa, Volume 4, Part 2; pp. 23–60, ills., keys. Pretoria (ZA): Botanical Research Institute.

## Callisia COMMELINACEAE

D. R. Hunt

**Callisia** Loefling (Iter Hispan., 305, 1758). **Type:** *Callisia repens* Linné. — **Commelinoideae** — **Tradescantieae** — **Tradescantiinae** — **Lit:** Moore (1958: classification); Hunt (1986: classification); Hunt (1994: 165–168, Flora Mesoamerica). **Distr:** Tropical America from SE USA to Argentina. **Etym:** Gr. ‘kallos’, beauty.

**Incl.** *Aploleia* Rafinesque (1837). **Type:** *Aploleia diffusa* Rafinesque [*nom. illeg.*, = *Callisia monandra* (Swartz) Schultes *fil.*].

**Incl.** *Phyodina* Rafinesque (1837). **Type:** *Tradescantia gracilis* Kunth.

**Incl.** *Spironema* Lindley (1840) (*nom. illeg.*, Art. 53.1). **Type:** *Spironema fragrans* Lindley.

**Incl.** *Cuthbertia* Small (1903). **Type:** *Tradescantia rosea* Ventenat.

**Incl.** *Rectanthera* O. Degener (1932). **Type:** *Spironema fragrans* Lindley.

**Incl.** *Leptocallisia* (Bentham & Hooker *fil.*) Pichon (1946). **Type:** *Callisia umbellulata* Lamarck.

**Incl.** *Hadrodemas* H. E. Moore (1963). **Type:** *Tradescantia warszewicziana* Kunth & Bouché.

Perennial or rarely annual or short-lived herbs; **L** succulent; **Inf** various, cincinni typically fused

in pairs, without conspicuous **Bra**; **Fl** usually actinomorphic and bisexual, sessile or pedicellate; **Sep** 3 or very rarely 2, sometimes hyaline; **Pet** 3 or very rarely 2, free, usually white or pink; **St** 6, all similar or subsimilar, or reduced to 3 or 1; **Fil** typically hairless, sometimes bearded; **Anth** versatile, connectives usually broad; **Ov** (2- to 3-locular; ovules 2 or very rarely 1 per locule; **Sti** usually penicillate or minutely capitate; **Fr** small capsules; **Se** with punctiform (dot-like) hilum.

A genus of  $\pm 20$  species. *Callisia* has always been difficult to classify, whether by morphological characters (Hunt 1986) or by molecular approaches (Bergamo 2003). *Callisia* appears to be polyphyletic in recent molecular studies, and not all sections were recovered as monophyletic (Burns & al. 2011, Hertweck & Pires 2014). Recircumscription of the genus, either to include *Tripogandra* or else to admit several small or monotypic genera, would not be appropriate, however, as molecular data are not yet available for various relevant taxa of ‘particular systematic interest’ (Hertweck & Pires 2014) included in this and allied genera, potentially impacting on the circumscription of *Tradescantia* and the classification of tribe *Tradescantieae* as a whole (Hunt 2015).

*Callisia* is closely related to *Tradescantia*, but mostly lacking paired bracts below the inflorescence, and having different seeds and chromosomes. The smaller-growing species die back to dwarf shoots or to tubers during the resting-

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period. As in *Tradescantia*, the cincinni are fused in pairs (in 1 species associated in pairs or threes), and the flowers are regular with the stamens all similar (though sometimes reduced in number). Various species have been placed in separate genera, treated by Hunt (1986) as six sections. Those including succulent species treated here are as follows:

- [1] Sect. *Hadrodemas* (H. E. Moore) D. R. Hunt 1986: Cincinni incompletely fused in pairs or threes; **Fl** pedicellate; **Sep** fleshy; **Pet** pink; **St** 6; robust *Aloe*-like plant.
- [2] Sect. *Brachyphylla* D. R. Hunt 1986: Cincinni strictly fused in pairs; **Fl** pedicellate; **Sep** boat-shaped; **Pet** pink; **St** 6, bearded; **Sti** capitate or dot-like.
- [3] Sect. *Leptocallisia* Benth. & Hooker *fil.* 1883: Cincinni strictly fused in pairs; **Fl** pedicellate; **Sep** boat-shaped; **Pet** white; **St** (1-) 3, glabrous (in treated taxa); **Sti** capitate or dot-like.
- [4] Sect. *Callisia*: Cincinni strictly fused in pairs; **Fl** sessile or nearly so; **Sep** narrowly acute; **Sti** penicillate.

**C. elegans** Alexander *ex* H. E. Moore (Baileya 6: 140, Fig. 28, 1958). **Type**: Cult. USA (*Alexander* s.n. [NY]). — **Distr**: Guatemala, Honduras; dry to moist river or creek banks, 600–1100 m.

≡ *Callisia gentlei* var. *elegans* (Alexander *ex* H. E. Moore) D. R. Hunt (1986).

[4] Decumbent perennials; **L** 3.5 – 10 × 1.5 – 3 cm, distichous, dark green above with paler longitudinal stripes, commonly purplish beneath, velutinous; **Inf** 6–15 cm or more, paired cincinni mostly sessile, some pedunculate; **Fl** sessile; **Pet** white, to 9.5 × 6.5 mm.

Allegedly found in Mexico but not known there in the wild. Treated by Hunt (1986: 411) as a variety of *C. gentlei* Matuda from Belize, which has pink flowers and unstriped, scarcely succulent leaves.

**C. fragrans** (Lindley) Woodson (Ann. Missouri Bot. Gard. 29: 154, 1942). **Type**: [lecto — icono]: Edward's Bot. Reg., 26: t. 47, 1840. — **Distr**: Mexico (Tamaulipas to Yucatán).

≡ *Spironema fragrans* Lindley (1840) ≡ *Rectanthera fragrans* (Lindley) O. Degener (1932).

[4] Robust perennials to 1.5 m, flowering plants bromeliad-like and stout, with subrosulate leaves, sparsely branched but producing long, relatively slender stolons with distichous leaves from the lower nodes; **L** of flowering stems to 30 × 7 cm, narrowly elliptic-lanceolate, acute, subamplexicaul, usually glabrous, bright light green; **Inf** ample terminal panicles, **Br** crowded with sessile paired cincinni subtended by papery **Bra** to 2 cm; **Fl** almost sessile, small, fragrant; **Sep** 3.5 – 5 × 1.5 – 2 mm, bristly; **Pet** 5 – 6 × 2.5 – 3.5 mm, spreading, lacking an expanded blade, lanceolate to ovate, white; **St** 6, long-exserted, **Anth** connectives membranous, white, more conspicuous than the petals; **Sti** penicillate.

A cultivar with pale-striped leaves has been named 'Melnickoff'.

**C. micrantha** (Torrey) D. R. Hunt (Kew Bull. 38: 131, 1983). **Type**: USA, Texas (*Schott* s.n. [US]). — **Distr**: USA (SE Texas), Mexico (NE Tamaulipas); open oak or mesquite woods and prairies, sandy or clayey soils. **I**: Vich (2014: 118–119).

≡ *Tradescantia micrantha* Torrey (1859) ≡ *Phyodina micrantha* (Torrey) D. R. Hunt (1979).

[2] Tufted or creeping, sometimes trailing to 1 m or more, succulent; **L** narrowly lanceolate to oblong-lanceolate, ± falcate and canaliculate, acute, mostly 1.5 – 2.5 × 0.5 – 0.6 cm, succulent, green with purplish striation below, virtually glabrous; **Inf** of paired cincinni mostly terminal and sessile, closely subtended by the uppermost 1–2 leaves; **Ped** 8–12 mm; **Fl** 10–15 mm Ø, bright purplish-pink; **St** bearded, connective yellow; **Sti** capitate.

Resembling *C. navicularis*, but smaller in all parts and lacking overwintering dwarf shoots. The karyotype is also different.

**C. multiflora** (M. Martens & Galeotti) Standley (J. Washington Acad. Sci. 15: 457, 1925). **Type**: Mexico, Veracruz (*Galeotti* 4964 [BR, K, W]). — **Distr**: Mexico (from Jalisco

S-wards), Belize, Guatemala, Honduras, Nicaragua; deciduous forests, rocky places and cultivated fields. **I:** Curtis's Bot. Mag. 81: t. 4849, 1855.

≡ *Commelina multiflora* M. Martens & Galeotti (1842) ≡ *Leptocallisia multiflora* (M. Martens & Galeotti) Pichon (1946) ≡ *Aploleia multiflora* (M. Martens & Galeotti) H. E. Moore (1961); **incl.** *Tradescantia martensiana* Kunth (1843) ≡ *Callisia martensiana* (Kunth) C. B. Clarke (1881).

[3] Perennials with ascending or procumbent stems to 80 cm, rooting and branching at the lower nodes; **L** 3–9 × 1–2.5 cm, ovate or oblong to elliptic-lanceolate, acute or acuminate, base rounded to subcordate, pale green, succulent, densely and minutely hairy; **Inf** slender terminal panicles to 30 cm with numerous paired cincinni; **Ped** 6–7 mm, usually minutely glandular-pubescent; **Fl** 6–8 mm Ø, white, fragrant; **St** 3, opposite to the sepals; **Fil** ± 1.5 mm, glabrous or bearded; **Anth** linear, yellow; **Ov** 3-locular; **Sty** very short; **Sti** shallowly 3-lobed.

**C. navicularis** (Ortgies) D. R. Hunt (Kew Bull. 38(1): 132, 1983). **Type:** [lecto — icono]: Gartenflora, 26: t. 901, 1877. — **Distr:** E Mexico (Sierra Madre Oriental: Coahuila, Nuevo León, S to Puebla); spiny matorral on limestone and gypsum, 1500–2400 m. — Fig. 1.

≡ *Tradescantia navicularis* Ortgies (1877) ≡ *Phyodina navicularis* (Ortgies) Rohweder (1956); **incl.** *Tradescantia brachyphylla* Greenman (1898).

[2] Stems tufted or trailing, succulent, of 2 intergrading types, bulbil-like short shoots with ± tightly imbricate leaves, and stolons with long internodes rooting and producing short shoots or inflorescences; **L** lanceolate to broadly ovate, canaliculate and somewhat falcate, tip acute, mostly 2–3 × 1–2 cm, very succulent, green above, purple striate beneath, virtually glabrous; **Inf** terminal, closely subtended by the uppermost leaf or more rarely by 2 leaves; **Ped** 10–20 mm; **Sep** lanceolate, canaliculate and strongly keeled, ± 7 × 3–4 mm, keel ciliate, margins hyaline; **Pet** very broadly ovate, ± 10 × ± 9 mm, bright purplish-pink; **St** equal, 5–6 mm; **Fil** bearded; connectives yellow; **Sti** capitate.

The original material was allegedly collected in Peru and was cultivated in the Zürich Botanical Garden. The taxon is not known outside Mexico, however.

**C. repens** (Jacquin) Linné (Spec. Pl., ed. 2, 1: 62, 1762). **Type:** Martinique (*Jacquin* s.n. [[lecto — icono]: *Jacquin*, Select. Stirp. Amer. Hist., 11, t. 11, 1763]). — **Distr:** USA (Texas) to Argentina, West Indies; forest margins to stream banks. — Fig. 2.

**Fig. 1** *Callisia navicularis*. (Copyright: U. Egli)



**Fig. 2** *Callisia repens*.  
(Copyright: U. Eggli)



≡ *Hapalanthus repens* Jacquin (1760); **incl.** *Tradescantia callisia* Swartz (1797); **incl.** *Callisia repens* var. *ciliata* Roemer & Schultes (1817); **incl.** *Spironema robbinsii* C. Wright (1871); **incl.** *Callisia repens* var. *mandonii* C. B. Clarke (1881).

[4] Variable perennials with slender creeping stems, rooting at the nodes and forming mats; **L** 1–4 × 1–2 cm, variable, narrowly to broadly ovate, acute, rounded to subcordate at the base, virtually glabrous; **Inf** typically spiciform, ascending, paired cincinni sessile, typically subtended by leaves reduced to a mucro on the membranous sheath; **Ped** 0.5–1.5 mm; **Sep** 2–3.5 mm, becoming scarious; **Pet** 3–5 × 1–1.5 mm, narrowly oblong acute, translucent white; **St** 3 or 6 (1 or more often staminodal), long-exserted; **Fil** 6–10 mm; **Anth** connective ± 1 × 1.5 mm, broadly reniform, thin; **Ov** 2-locular; **Sti** penicillate.

The form of *C. repens* in commercial cultivation is distinctive. It has small rounded leaves and inconspicuous inflorescences in the axils of normal leaves. Its wild origin is uncertain. It has been confused with *C. cordifolia* (sect. *Leptocallisia*) which has a different inflorescence and thin leaves.

**C. tehuantepecana** Matuda (Anales Inst. Biol. UNAM 27: 356, 1957). **Type:** Mexico, Oaxaca (*MacDougall* s.n. [MEXU]). — **Distr:** S Mexico (Oaxaca); ecology not recorded.

[4] Stems decumbent or erect to 60–80 cm; **L** lanceolate, acuminate, 7–9 × 1.5–2 cm, glabrous, not striate, margins white-ciliate, sheaths papery; **Inf** spiciform, paired cincinnati terminal and lateral, sessile or shortly pedunculate, 6- to 8-flowered; **Ped** short; **Fil** 10–15 mm Ø, pink; **St** glabrous, connective broadly quadrate; **Sti** capitate.

Closely related to *C. gentlei* and *C. elegans*, but differing in the longer and narrower leaves, somewhat laxer habit, etc. *C. gentlei*, though it has subsucculent leaves, is of less interest than the closely related *C. elegans* and *C. tehuantepecana*, and is not treated here.

**C. warszewicziana** (Kunth & C. D. Bouché) D. R. Hunt (Kew Bull. 38: 132, 1983). **Type:** Guatemala (*Warszewicz* s.n. [B]). — **Distr:** S Mexico (Chiapas), Guatemala; rocks in pine-oak forsts, 1200–1500 m. **I:** Moore (1963: 134).

≡ *Tradescantia warszewicziana* Kunth & C. D. Bouché (1847) ≡ *Dichorisandra warszewicziana* (Kunth & C. D. Bouché) Pichon (1854) ≡ *Spironema warszewicziana* (Kunth & C. D. Bouché) G. Brückner (1927) ≡ *Tripogandra warszewicziana* (Kunth & C. D. Bouché) Woodson (1942) ≡ *Phyodina warszewicziana* (Kunth & C. D. Bouché) Rohweder (1956) ≡ *Hadrodemas warszewiczianum* (Kunth & C. D. Bouché) H. E. Moore (1963); **incl.** *Tradescantia subscaposa* C. B. Clarke (1890).

[1] Robust bromeliad-like herbs; stems eventually 1 m or more, stout; **L** to 30 × 6.5 cm, spirally arranged and densely imbricate towards the apical **Ros**, narrowly oblong, acuminate, sessile, succulent, glabrous except for the sometimes ciliate, often purple margin; **Inf** to 35 cm overall, appearing axillary, branched below and sometimes viviparous, cincinni fused at the base in pairs or threes, sessile or subsessile, many-flowered; **Ped** 10–13 mm; **Sep** 4–5 mm, succulent, persistent, glabrous; **Pet** 6 × 6 mm, purplish-pink; **St** 6, ± 5 mm; **Fil** usually glabrous; **Anth** connectives broad, yellow; **Ov** 3-locular, ovules 2 per locule.

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## References

- Bergamo, S. (2003) A phylogenetic evaluation of *Callisia* Loeffl. (*Commelinaceae*) based on molecular data. Athens (US): University of Georgia, unpublished Ph.D. thesis.
- Burns, J. H. [et al. 2011], Faden, R. B. & Steppan, S. J. (2011) Phylogenetic studies in the *Commelinaceae* subfamily *Commelinoideae* inferred from nuclear ribosomal and chloroplast DNA sequences. *Syst. Bot.* 36(2): 268–276. <https://doi.org/10.1600/036364411X569471>.
- Hertweck, K. L. & Pires, J. C. (2014) Systematics and evolution of inflorescence structure in the *Tradescantia* alliance (*Commelinaceae*). *Syst. Bot.* 39(1): 105–116. <https://doi.org/10.1600/036364414X677991>.
- Hunt, D. R. (1986) Amplification of *Callisia* Loeffl. American *Commelinaceae* XV. *Kew Bull.* 41(2): 407–412. <https://doi.org/10.2307/4102950>.
- Hunt, D. R. (1994) *Commelinaceae*. In: Davidse, G. & al. (eds.): *Flora Mesoamericana*. Volumen 6: *Alismataceae* a *Cyperaceae*; pp. 157–173. México, D.F. (MX): Universidad Nacional Autónoma de México. <http://www.tropicos.org/Project/FM>
- Hunt, D. R. (2015) Further notes on American *Commelinaceae*. *Opusc. Neotrop.* 1: 1–5.
- Moore, H. E. (1958) *Callisia elegans*, a new species, with notes on the genus. *Baileya* 6: 135–147.
- Moore, H. E. (1963) *Hadrodemas*, a new genus of *Commelinaceae*. *Baileya* 10: 131–136.
- Vích, J. (2014) [Czech:] *Callisia* — extremely resistant succulents from Mexico. *Kaktusy* 50(4): 118–120, ill.







## Cyanotis COMMELINACEAE

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**Cyanotis** D. Don (Prodr. Fl. Nepal., 45, 1825). **Type:** *Cyanotis barbata* D. Don. — **Commelinoideae** — **Tradescantieae** — **Cyanotinae** — **Lit:** Faden & Cameron (2005: cytology); Faden (2012: 12–31, Flora Tropical E Africa); Lebrun & Stork (2012: 95–100, synopsis tropical Africa). **Distr:** Old World tropics. **Etym:** Gr. ‘kyanos’, dark blue; and Gr. ‘ous, otos’, ear; for the colour of the flower of many species.

**Incl.** *Tonningia* Necker ex Jussieu (1829) (*nom. illeg.*, Art. 53.1). **Type:** *Commelina axillaris* Linné.

**Incl.** *Belosynapsis* Hasskarl (1871). **Type:** *Belosynapsis kewensis* Hasskarl.

**Incl.** *Amischophacelus* R. S. Rao & Kammathy (1966). **Type:** *Commelina axillaris* Linné.

Usually perennial, often tuberous-rooted herbs, or with underground corms, rhizomes or bulbs; **L** narrow, often distichous,  $\pm$  succulent and sometimes ciliate; **Fl** violet-blue or purplish-pink, bisexual, actinomorphic or nearly so, generally almost stalkless in dense single axillary cincinni subtended by a leaf-like or reduced **Bra** and with conspicuous sickle-shaped bracteoles; **Sep** 3, free or joined below; **Pet** 3, free or joined with the filament bases to form a short tube; **St** 6, equal,

fertile; **Fil** nearly always bearded, often swollen subterminally, connectives narrow; **Ov** 3-locular with 2 ovules per locule; **Fr** dry dehiscent capsules; **Se** with punctiform (dot-like) hilum, embryotega terminal.

The genus embraces  $\pm$  50 species, of which the majority is subsucculent to succulent. *Cyanotis* has been found to be monophyletic in the molecular study of Burns & al. (2011), and it is placed near the base of tribe *Tradescantieae*. Most species of the genus are pronouncedly variable and therefore difficult to separate in keys (Faden 2012). The underground parts can be quite diagnostic but present some variability, with both rhizomatous and bulb-forming individuals known for some species (Faden 2012: 13). Most species of *Cyanotis* are of little horticultural interest, but the following are valued for their attractive succulent foliage.

**C. kewensis** (Hasskarl) C. B. Clarke (in A. & C. de Candolle, Monogr. Phan. 3: 243, 1881). **Type:** Cult. RBG Kew (*Anonymous* s.n. [not located]). — **Distr:** India (Madras).

$\equiv$  *Belosynapsis kewensis* Hasskarl (1871); **incl.** *Erythrotis beddomei* Hooker *fil.* (1875); **incl.** *Cyanotis kewoides* Christenhusz & Byng (2018) (*nom. illeg.*, ICN Art. 52.1).

Prostrate perennials creeping from its initial **Ros**, internodes and leaf sheaths densely brown-hairy; **L** of the rosettes lanceolate, acute, rounded at the base, to 5  $\times$  2 cm, **L** of the side-shoots overlapping in 2 ranks, often smaller, succulent,

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dark green above, deep purple beneath, densely velvety; **Inf** lax, to 3 cm, with up to 8 **Fl**  $\pm$  8 mm  $\emptyset$ ; **Ped** 3–4 mm; **Pet** free, purplish-pink; **St**  $\pm$  6 mm, **Fil** bearded with violet hairs; **Anth** yellow with orange pollen.

**C. somaliensis** C. B. Clarke (Bull. Misc. Inform. Kew 1895: 229, 1895). **Type** [syn]: Somalia (*Cole* s.n. [K]). — **Distr**: Somalia; open woodland on gneiss slopes, under shrubs on rocks, 915–1770 m. **I**: Brewerton (1977); Thulin (1995: 80 (but not p. 81)); Thulin (2006: 585). — Fig. 1.

Succulent perennials with non-flowering basal **Ros** (usually lacking in cultivated specimens) and stolon-like creeping shoots to  $\pm$ 25 cm which can produce inflorescences or roots and form new rosettes; **L** oblong-linear, acute and with a small point, sessile, **L** of the rosettes to  $12 \times 1.5$  cm, **L** of the lateral shoots  $1.5 - 4 \times 0.5 - 1$  cm, short leaves U-shaped in section, and often recurved, succulent, densely hairy below, margins long-ciliate, sheaths inflated, persistent, becoming papery; **Inf** short, scarcely exceeding the bracts, with several flowers; **Fl**  $\pm$  5 mm  $\emptyset$ , purplish-blue.



**Fig. 1** *Cyanotis somaliensis*. (Copyright: U. Eggli)

The origin and status of the widespread cultivated form of *C. somaliensis* (see e.g. the illustration cited above), which generally lacks basal rosettes, is uncertain. According to Lebrun & Stork (2012: 99), it can be confused with the hardly succulent *C. repens* and *C. foecunda*.

**C. speciosa** (Linné *fil.*) Hasskarl (Commelin. Ind., 108, 1870). **Type**: RSA, Western Cape (*Thunberg* s.n. [LINN 406.8, UPS?]). — **Distr**: S and E Africa. **I**: Obermeyer & Faden (1985: 54, Fig. 14).

$\equiv$  *Tradescantia speciosa* Linné *fil.* (1782)  $\equiv$  *Commelina speciosa* (Linné *fil.*) Thunberg (1794)  $\equiv$  *Tonningia speciosa* (Linné *fil.*) Rafinesque (1837) (*incorrect name*, Art. 11.4).

Variable perennial succulent herbs with basal **Ros** and stolons to 50 cm, often forming loose mats; **L** narrowly oblong, acute, channelled, to  $\pm 10 \times 2$  cm in the best forms,  $\pm$  densely clothed with white silky hairs, or nearly glabrous; **Inf** spiciform, arching to 30 cm with sessile cincinni subtended by reduced leaves; **Fl** numerous, bracteoles  $\pm$  8 mm, falcate; **Pet** blue to mauve or pink.

Faden (2012) and Lebrun & Stork (2012) distinguish 3 subspecies:

**C. speciosa** ssp. **bulbosa** Faden (Fl. Trop. East Afr., Commelinaceae, 31, 2012). **Type**: Zambia, Mpika Distr. (*Faden & Faden* 74/120 [US, K, MO]). — **Distr**: Tanzania, Democratic Republic of the Congo, Angola?, Burundi?, Zambia, Malawi, N Moçambique.

Basal bulb surrounded by papery and long-hairy leaf bases; **R** clustered,  $\pm$  tuberous.

**C. speciosa** ssp. **madagascarica** (C. B. Clarke) Faden (Kew Bull. 62(1): 140, 2007). **Type** [lecto]: Madagascar, Antananarivo (*Bojer* s.n. [K, P]). — **Distr**: C Madagascar (Antananarivo).

$\equiv$  *Cyanotis nodiflora* var. *madagascarica* C. B. Clarke (1881).

Flowering shoots prostrate, often branched and rooting at the nodes.

**C. speciosa** ssp. **speciosa** — **Distr**: S Moçambique, Zimbabwe, Botswana, Swaziland, RSA (widespread), Namibia?; 1200–2100 m.

**Incl.** *Tradescantia nodiflora* Lamarck (1786)  
 ≡ *Cyanotis nodiflora* (Lamarck) Kunth (1843)  
 ≡ *Tonningia nodiflora* (Lamarck) Kuntze (1891)  
 (*incorrect name*, Art. 11.4); **incl.** *Tradescantia for-  
 mosa* Willdenow (1799); **incl.** *Cyanotis gryphaea*  
 Dinter (1920).

Rhizome vertical to sigmoid, with fibrous roots.

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## References

- Brewerton, D. V. (1977) *Cyanotis somaliensis* Clarke. *Kakt. and. Sukk.* 28(4): 98, ill.
- Burns, J. H. [ & al. 2011], Faden, R. B. & Steppan, S. J. (2011) Phylogenetic studies in the *Commelinaceae* sub-family *Commelinoideae* inferred from nuclear ribosomal and chloroplast DNA sequences. *Syst. Bot.* 36(2): 268–276. <https://doi.org/10.1600/036364411X569471>.
- Faden, R. B. (2012) *Commelinaceae*. In: Beentje, H. J. (ed.): *Flora of Tropical East Africa*. Richmond (GB): Royal Botanic Gardens, Kew, on behalf of the East African Governments.
- Faden, R. B. & Cameron, D. M. (2005) *Cyanotis repens* (*Commelinaceae*): A new species from Tropical Africa. *Novon* 15: 110–116, ills., map.
- Lebrun, J.-P. & Stork, A. L. (2012) *Tropical African flowering plants. Ecology and distribution. Volume 7: Monocotyledons 1 (Limnocharitaceae- Agavaceae)*. Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Obermeyer, A. A. & Faden, R. B. (1985) *Commelinaceae*. In: Leistner, O. A. (ed.): *Flora of southern Africa*, Volume 4, Part 2; pp. 23–60, ills., keys. Pretoria (ZA): Botanical Research Institute.
- Thulin, M. (ed.) (1995) *Flora of Somalia. Volume 4. Angiospermae (Hydrocharitaceae - Pandanaceae)*. Richmond (GB): Royal Botanic Gardens Kew.
- Thulin, M. (ed.) (2006) *Flora of Somalia. Volume 3. [Angiospermae (Ericaceae - Asteraceae)]*. With cumulative index to volumes 1–4. Richmond (GB): Royal Botanic Gardens Kew.





## Tradescantia COMMELINACEAE

D. R. Hunt

**Tradescantia** Linné (Spec. Pl. [ed. 1], 288, 1753). **Type:** *Tradescantia virginiana* Linné. — **Commelinoideae** — **Tradescantieae** — **Tradescantiinae** — **Lit:** Anderson & Woodson (1935: synopsis USA); Hunt (1980: classification); Hunt (1986: classification); Hunt (1994: 161–165, Flora Mesoamerica); Pellegrini & al. (2017: morphology S America). **Distr:** America (USA to N Argentina). **Etym:** For John Tradescant ( $\pm$ 1570–1638), gardener to Charles I of England.

**Incl.** *Campelia* L. Richard (1808). **Type:** *Commelina zanoniana* Linné.

**Incl.** *Tropitria* Rafinesque (1837). **Type:** *Tradescantia crassula* Link & Otto [typification by inference, only element included].

**Incl.** *Zebrina* Schnizlein (1849). **Type:** *Zebrina pendula* Schnizlein.

**Incl.** *Rhoeo* Hance (1853). **Type:** *Tradescantia discolor* L'Héritier [= *T. spathacea* Swartz].

**Incl.** *Treleasea* Rose (1899) (*nom. illeg.*, Art. 53.1). **Type:** *Tradescantia brevifolia* (Torrey) Rose.

**Incl.** *Setcreasea* K. Schumann & Sydow (1901). **Type:** *Tradescantia brevifolia* (Torrey) Rose.

**Incl.** *Cymbispatha* Pichon (1946). **Type:** *Tradescantia commelinoides* Schultes *fil.*

**Incl.** *Separothea* Waterfall (1959). **Type:** *Zebrina pumila* E. L. Greene.

Perennial or very rarely annual or short-lived herbs of diverse habit; **R** fibrous or tuberous; **L** various, rarely somewhat succulent; **Inf** of bifacially fused and paired sessile cincinni subtended and  $\pm$  enclosed by paired boat-shaped **Bra** similar to or  $\pm$  differentiated from the leaves; **Fl** actinomorphic or almost so, bisexual; **Ped** often recurved after anthesis; **Sep** 3, usually equal, free, rarely somewhat unequal or fused or in 1 species accrescent (*T. andrieuxii*) and fleshy in fruit; **Pet** 3, equal, usually free, sometimes clawed at the base, rarely united into a slender tube, blue-violet, purple, pink or white; **St** 6, all fertile, all similar and equal or subequal; **Fil** free or the antipetalous rarely connate with the petal bases; **Anth** versatile, connectives broad; **Ov** 3-locular; ovules 2 or very rarely 1 per locule; **Sti** minutely capitate; **Fr** capsules; **Se** with linear or very rarely punctiform (dot-like) hilum and dorsal or lateral embryotega.

The genus, which numbers 70 species, has been found to be monophyletic in the molecular phylogenetic study of Burns & al. (2011), but includes a single species of *Gibasis* (which must have been misidentified). The species of sect. *Austrotradescantia* are placed as basal sister to the remaining clades of the genus.

*Tradescantia* was divided into 12 sections by Hunt (1980) and Hunt (1986), some of which (see synonymy) have previously been treated as independent genera.

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The sections relevant to this account can be recognized as follows:

- [1] Sect. *Zebrina* (Schnizlein) D. R. Hunt 1986: **Pet** united below into a slender tube; **L** striped silvery (*T. zebrina* only).
- [2] Sect. *Rhoeo* (Hance) D. R. Hunt 1986: Plants evergreen, bromeliad-like with **Ros** of fleshy linear-ensiform leaves; **Bra** of the inflorescence well-differentiated from the foliage leaves; **Fl** mostly white; **Pet** free (*T. spathacea* only).
- [3] Sect. *Austrotradescantia* D. R. Hunt 1980: Plants evergreen, creeping or decumbent herbs with relatively small, thin or fleshy leaves; **Fl** mostly white; **Pet** free; **Cal** not fleshy or accrescent.
- [4] Sect. *Tradescantia*: Plants dying back annually to the shortly rhizomatous **Rstock**; **Inf** appearing mainly terminal; **Bra** of the inflorescence similar to the foliage leaves; **Fl** usually blue, violet or purple; **Pet** free.
- [5] Sect. *Setcreasea* (K. Schumann & Sydow) D. R. Hunt 1975: **Pet** united, but at the base only; **L** not striped.
- [6] Sect. *Mandonia* D. R. Hunt 1980: Plants dying back annually to the tuberous **Rstock**; **Inf** terminal or lateral, forming a compound spike; **Bra** of the inflorescence similar to the foliage leaves; **Fl** usually blue, violet or purple; **Pet** free.

The type species, *T. virginiana*, and its allies, native to the USA, are reliably hardy in temperate gardens, perennating as hemicytrophites. A few other species will survive mild winters out-of-doors in the cool-temperate N hemisphere, but the deciduous species require protection from damp conditions, while the evergreen taxa need cool or (in a few cases) warm greenhouse treatment.

*T. spathacea* and *T. zebrina* are popular indoor plants grown for their patterned foliage. Several species have become established as neophytes throughout the world in appropriate climates.

**T. cerinthoides** Kunth (Enum. Pl. 4: 83, 1843). **Type** [lecto]: Brazil, Rio Grande do Sul (*Sellow* 2963 [B]). — **Distr**: SE Brazil (Paraná, Rio

Grande do Sul, Santa Catarina); neophyte in New Zealand and elsewhere. **I**: Curtis's Bot. Mag. 170: t. 247, 1955, as *T. blossfeldiana*.

**Incl.** *Tradescantia koernickeana* Seubert (1855); **incl.** *Tradescantia cymbispatha* var. *villosissima* C. B. Clarke (1881); **incl.** *Tradescantia blossfeldiana* Mildbraed (1940).

[3] Stems decumbent, rooting at the nodes and becoming shortly rhizomatous; **L** elliptic-oblong to ovate, to 15 × 3.5 cm, sessile, somewhat fleshy, glossy dark green and hairy to glabrous above, green or often purple and densely hairy beneath; **Inf** terminal and lateral; peduncles to 5 cm; **Bra** 2 – 2.5 × 1 – 1.5 cm; **Ped** to 25 mm, hairy; **Fl** 15–20 mm Ø, purplish-pink in the upper ½, white below, or all white.

Similar to *T. crassula*, but more hairy, with broader leaves, and leaves and flowers usually suffused with purple. *T. cerinthoides* is better known as *T. blossfeldiana*, which was introduced via Argentina by Blossfeld, who offered it in his 1939 catalogue, but all wild plants seen by the present writer were collected in SE Brazil.

**T. crassula** Link & Otto (Icon. Pl. Rar. Hort. Reg. Bot. Berol. 13, t. 7, 1828). **Type** [lecto]: Brazil, Rio Grande do Sul (*Sellow* 3033 [B]). — **Lit**: Pellegrini & al. (2017: with ills.). **Distr**: S Brazil (Paraná, Rio Grande do Sul, Santa Catarina, São Paulo, Minas Gerais), Paraguay (Paraguari), NE Argentina (Misiones); rocky outcrops, grasslands and open areas, usually in full sun.

≡ *Tropitria crassula* (Link & Otto) Rafinesque (1837); **incl.** *Tradescantia crassipes* Graham (1829); **incl.** *Tradescantia crassula* var. *gaudichaudii* C. B. Clarke (1881); **incl.** *Tradescantia schwirkowskiana* Funez & al. (2016).

[3] Stem decumbent, rooting at the nodes and becoming rhizomatous at the base; **L** oblong-elliptic, obtuse, channelled, to 15 × 3 cm, somewhat fleshy, shiny green, glabrous except the minutely ciliate margins and sometimes minutely pubescent beneath; **Inf** terminal and lateral; peduncle to 6 cm; **Bra** unequal, the longer to ±4 × 1.5 cm (unfolded); **Ped** to 20 mm; **Fl** 10–20 mm Ø, white.



**Fig. 1** *Tradescantia fluminensis*. (Copyright: U. Eggli)

**T. fluminensis** Vellozo (Fl. Flumin., 140, 1829). **Type:** [lecto — icono]: Original parchment plate of Vellozo, Icones 3: t. 153, 1831. — **Distr:** SE Brazil (Minas Gerais to Rio Grande do Sul), Paraguay, Uruguay, NE & E Argentina (Misiones, Corrientes, Buenos Aires, Salta, Jujuy, Córdoba); widely naturalized as neophyte and invasive in the S USA, Australia, New Zealand, RSA, etc. — **Fig. 1.**

**Incl.** *Tradescantia albiflora* Kunth (1843).

[3] Stems weakly ascending and decumbent or pendent, rooting at the nodes; **L** variable, broadly ovate to oblong-lanceolate, acute to acuminate,  $\pm$  unequal-sided at the base and rounded to subcordate,  $1.5\text{--}12 \times 1\text{--}3.5$  cm, subpetiolate, usually glabrous, green or purplish beneath, variegated whitish or yellowish in the more decorative forms; **Inf** terminal and lateral on peduncles  $\pm 1\text{--}5$  cm; **Bra** folded but not keeled,  $1\text{--}2 \times 0.7\text{--}1.5$  cm (unfolded); **Ped**  $\pm 10$  mm, usually glabrous; **Fl**  $12\text{--}18$  mm  $\varnothing$ , white.

The true *T. fluminensis* is a rhizomatous perennial from the region of Rio de Janeiro with subpetiolate leaves tending to the larger end of the range quoted. In different clones the leaves are all green, or variegated whitish or yellowish. The popular cultivar with sessile leaves longitudinally striped whitish, known as *T. albiflora* ‘Albovittata’, is intermediate in habit between *T. fluminensis* and *T. crassula*. The decorative, non-rhizomatous, annual or short-lived plant with small, yellow-variegated leaves and slender, often purplish, stems, known as *T. fluminensis* ‘Argenteo-variegata’, is not this species. It may be *T.*

*mundula* Kunth or *T. anagallidea* Seubert from S Brazil to N Argentina. Individual plants are self-fertile, but most of their seedlings have normal green leaves. Many named cultivars have been marketed over time.

**T. hirta** D. R. Hunt (Curtis’s Bot. Mag. 180(3): 121–123, ills., t. 686, 1975). **Type:** Cult. BG München (*Anonymus* s.n. [M]). — **Distr:** NE Mexico (Coahuila, Nuevo León, San Luis Potosí); on rocks.

$\equiv$  *Setcreasea hirsuta* Markgraf (1952).

[5] Stem-base shortly rhizomatous and branching; **L** annual, linear, thickly succulent, concave above and rounded below, long-attenuate at the tip, to  $20 \times 1$  cm, with soft tissue, glaucous green, sparingly to densely hairy with long weak hairs especially towards the sheath; **Inf** terminal, solitary, scapiform, to 20 cm or more; **Bra** foliaceous, unequal, to 1.8 cm, membranous, glabrous, greenish or hyaline, veiny; **Ped**  $\pm 3\text{--}5$  mm, glabrous or pilose at the tip; **Sep** narrowly ovate-elliptic,  $10\text{--}15 \times 3\text{--}5$  mm, membranous, whitish, glabrous; **Pet** spatulate, claw 8–9 mm, whitish, coherent with the filaments of the antisepalous stamens to form a slender tube 2–8 mm long, **Pet** blade ovate to suborbicular,  $10\text{--}15 \times 8\text{--}10$  mm, deep purplish-pink; **St** subequal, inserted on the corolla at the tube mouth; **Fil** 8–12 mm, bearded with purplish-pink hairs; connectives broadly triangular and apiculate,  $2 \times 2$  mm, yellow; **Anth** curved-oblong, 2 mm; **Ov** ellipsoid-cylindrical, 2–3 mm, glabrous; **Sty** 13–18 mm; **Sti** 3-lobed; **Fr** and **Se** not described.

**T. pallida** (Rose) D. R. Hunt (Kew Bull. 30: 452, 1975). **Type:** Mexico, Tamaulipas (*Palmer* s.n. [US]). — **Distr:** E Mexico (Tamaulipas to Yucatán); deciduous forests, rocky sites, to 600 m.

$\equiv$  *Setcreasea pallida* Rose (1911); **incl.** *Setcreasea purpurea* Boom (1955).

[5] Stems to 40 cm, ascending or decumbent; **L** oblong-elliptic to elliptic-lanceolate, usually  $7\text{--}15 \times 2\text{--}3.5$  cm, trough-shaped, acute and usually apiculate, tapering into the sheath, slightly succulent, glaucous green, edged red, or reddish to violet overall, usually glabrous, rarely pilose with long soft hairs; **Inf** mostly terminal, solitary,

on peduncles to 6–11 cm; **Bra** unequal, ovate-acuminate, folded and  $\pm$  keeled, outer to 7  $\times$  2.5 cm (unfolded), inner smaller; bracteoles thin, sheathing the buds; **Ped** short, with long soft hairs at the tip; **Fl** 20–30 mm  $\varnothing$ ; **Sep** free, hyaline; **Pet** clawed, connivent at the very base, pink or pink with white midline, rarely white; **St** slightly epipetalous, with weak hairs to 3 mm.

A purple-leaved cultivar ('Purpurea' or 'Purple Heart') is widely cultivated under glass and useful for summer bedding. Many more named cultivars have been marketed at one time or another.

**T. sillamontana** Matuda (Bol. Soc. Bot. México 18: 1, fig. 1, 1955). **Type:** Mexico, Nuevo León (*White & Chatters* 30 [MICH, GH, MEXU]). — **Lit:** Hunt (1976: with ill.). **Distr:** NE Mexico (Nuevo León); dry areas, 800–1230 (–1760) m. — Fig. 2.



**Fig. 2** *Tradescantia sillamontana*. (Copyright: U. Egli)

**Incl.** *Tradescantia pexata* H. E. Moore (1960).

[4] Stems ascending or decumbent, to 30 cm, mainly branched near the base, normally dying back in autumn to the rhizomatous base; **L** distichous, elliptic-ovate to broadly ovate-lanceolate, acute, rounded to amplexicaul at the base, mostly 3–7  $\times$  2–2.5 cm, somewhat succulent, green or becoming purplish in strong light, densely villose-lanate, esp. below with hairs to 1 cm; **Inf** terminal and usually solitary; peduncles usually <3.5 cm; **Bra** similar to the leaves but more strongly channelled or folded, somewhat unequal, 2.5–5  $\times$  2–4 cm (unfolded); **Ped** 10–15 mm; **Fl** 15–25 mm  $\varnothing$ , purplish-pink; **Sep** and **Pet** free; **St** glabrous.

**T. spathacea** Swartz (Prodr., 57, 1788). **Type:** Jamaica [cult.] (*Swartz* s.n. [S]). — **Lit:** Stearn (1957). **Distr:** S Mexico (Chiapas, Tabasco, Yucatán), Belize, Guatemala (Petén); dry limestone hills, to 500 m.

$\equiv$  *Rhoeo spathacea* (Swartz) Stearn (1957); **incl.** *Tradescantia discolor* L'Héritier (1788)  $\equiv$  *Rhoeo discolor* (L'Héritier) Hance ex Walpers (1853).

[2] Erect bromeliad-like herbs; stem usually short, rarely to 1 m; **L** 20–35  $\times$  3–5.5 cm, imbricate, subrosulate, narrowly linear-lanceolate, acuminate, scarcely narrowed above the sheath, succulent, glabrous, green on both faces or more commonly dark bluish-green above and purple beneath; **Inf** axillary; peduncle 2–4.5 cm, simple or branching; **Bra** 2–4.5  $\times$  2.5–5 cm, deeply boat-shaped, broadly ovate; **Fl** numerous, 10–15 mm  $\varnothing$ , white, scarcely exerted; **Ped**  $\pm$  15 mm, recurved in fruit; **Sep**, **Pet** and **St** free; **Se** 1 per locule.

The predominance of the form with purple pigmentation, and the common occurrence of the plant around ancient Maya sites, may be due to the use of the plant as source of a cosmetic decoction (Standley & Steyermark 1952: 23). The species is widely cultivated, world-wide, as an ornamental. 'Vittata' ('Variegata') is a cultivar with attractive leaves, cream-striped above and purple below. 'Concolor' has the leaves green throughout.

**T. zebrina** Heynhold *ex* Bosse (Vollst. Handb. Bl.-gärtn., ed. 2, 4: 655, 1849). **Type** [neo]: Mexico, Oaxaca (*Morton & Makrinius* 2712 [US]). — **Distr**: S Mexico (? , not definitely known in the wild state); moist rocks in forests, to 1500 m; neophyte in many tropical countries.

**Incl.** *Zebrina pendula* Schnizlein (1849) ≡ *Tradescantia pendula* (Schnizlein) D. R. Hunt (1981); **incl.** *Zebrina purpusii* G. Brückner (1928).

[1] Stems decumbent or creeping, rooting at the nodes; **L** 2.5 – 10 × 1.5 – 3.5 cm, ovate-oblong to broadly ovate, acute, rounded at the base, somewhat succulent, green and/or purple above, often striped with silver, usually purplish beneath; **Inf** solitary, terminal or opposite the leaves; peduncle 1.5–11 cm; **Bra** 2, unequal, the outer larger, 1.5–6 cm, the inner 0.8–3 cm, usually glabrous except for a conspicuous band of hairs on the sheath; **Ped** to 3 mm; **Sep** 5–8 mm, hyaline, connivent, or the posterior ± free; **Pet** united below into a slender tube to 10 × 1.3 mm, white, lobes free, 5 – 10 × 3 – 7 mm, ovate, purplish-pink or violet-blue; **St** epipetalous, bearded below.

This species is very commonly cultivated, and many cultivars have been formally named over the years.

## References

- Anderson, E. S. & Woodson, R. E. (1935) The species of *Tradescantia* indigenous to the United States. *Contr. Arnold Arbor.* 9: 1–132, key, ills.
- Burns, J. H. [& al. 2011], Faden, R. B. & Stepan, S. J. (2011) Phylogenetic studies in the *Commelinaceae* subfamily *Commelinoideae* inferred from nuclear ribosomal and chloroplast DNA sequences. *Syst. Bot.* 36(2): 268–276. <https://doi.org/10.1600/036364411X569471>.
- Hunt, D. R. (1976) *Tradescantia sillamontana*. *Curtis's Bot. Mag.* 181: t. 706 + text.
- Hunt, D. R. (1980) Sections and series in *Tradescantia*. *American Commelinaceae IX.* *Kew Bull.* 35(2): 437–442. <https://doi.org/10.2307/4114596>.
- Hunt, D. R. (1986) *Campelia*, *Rhoeo* and *Zebrina* united with *Tradescantia*. *American Commelinaceae XIII.* *Kew Bull.* 41(2): 401–405. <https://doi.org/10.2307/4102948>.
- Hunt, D. R. (1994) *Commelinaceae*. In: Davidse, G. & al. (eds.): *Flora Mesoamericana*. Volumen 6: *Alismataceae a Cyperaceae*; pp. 157–173. México, D.F. (MX): Universidad Nacional Autónoma de México. <http://www.tropicos.org/Name/42000348?projectid=3&langid=66>
- Pellegrini, M. O. O. [& al. 2017], Forzza, R. C. & Sakuragui, C. M. (2017) Novelty in Brazilian *Tradescantia* L. (*Commelinaceae*). *PhytoKeys* 80: 1–31, ills., key. <https://doi.org/10.3897/phytokeys.80.12232>.
- Standley, P. C. & Steyermark, J. A. (1952) *Flora of Guatemala. Commelinaceae.* *Fieldiana, Bot.* 24(3): 1–42, key, ills. <https://doi.org/10.5962/bhl.title.2255>.
- Stearn, W. T. (1957) The Boat Lily (*Rhoeo spathacea*). *Baileya* 5: 195–198.





## Tripogandra COMMELINACEAE

D. R. Hunt

**Tripogandra** Rafinesque (Fl. Tellur. 2(2): 16, 1837). **Type:** *Tradescantia multiflora* Jacquin. — **Commelinoideae** — **Tradescantieae** — **Tradescantiinae** — **Lit:** Bacigalupo (1967: synopsis Argentina); Handlos (1975: monograph); Hunt (1994: 168–170, Flora Mesoamerica). **Distr:** Tropical America from S USA to Argentina. **Etym:** Gr. ‘tri-’, three; Gr. ‘pogon’, beard; and Gr. ‘aner, andros’, man, anther; because the type species has three bearded and three glabrous stamens.

**Incl.** *Heminema* Rafinesque (1837). **Type:** *Tradescantia multiflora* Swartz.

**Incl.** *Descantaria* Schlechtendal (1853) (*nom. illeg.*, Art. 52.1). **Type:** *Tradescantia cumanensis* Kunth [*nom. illeg.*, = *Commelina floribunda* Kunth].

**Incl.** *Disgrega* Hasskarl (1866). **Type:** *Tradescantia disgrega* Kunth.

**Incl.** *Donnellia* C. B. Clarke ex Donnell Smith (1880) (*nom. illeg.*, Art. 53.1). **Type:** *Callisia grandiflora* Donnell Smith.

**Incl.** *Leptorhoeo* C. B. Clarke ex Hemsley (1880). **Type:** *Leptorhoeo filiformis* C. B. Clark ex Hemsley [*nom. illeg.*, = *Commelina floribunda* Kunth].

**Incl.** *Neodonnellia* Rose (1906). **Type:** *Callisia grandiflora* Donnell Smith.

Annual or perennial herbs, erect or trailing, rarely scandent; tubers absent; **L** ovate, narrowly ovate, oblong-lanceolate or rarely linear, sometimes somewhat succulent; **Inf** bifacially paired and fused cincinni not subtended by evident bracts but borne on a common peduncle, the paired cincinni solitary or variously clustered; **Fl** bisexual, zygomorphic; **Sep** 3, free; **Pet** 3, free, white or pink; **St** 6, dimorphic, **St** of the outer whorl usually fertile, shorter, **Fil** glabrous or bearded, **Anth**-connectives narrow, **St** of the inner whorl fertile or staminodal, longer, **Fil** curved to be erect in front of the upper petals, glabrous or variously bearded, **Anth**-connectives various; **Ov** 3-locular; ovules 2 per locule; **Sti** capitellate or capitate; **Fr** capsules; **Se** with a punctiform (dot-like) to linear hilum and dorsal embryotegea.

A genus of 22 species, of which some (e.g., *T. grandiflora*) are cultivated as ornamentals. According to molecular phylogenetic studies, the genus is monophyletic, but embedded within *Callisia* (Hertweck & Pires 2014).

**T. glandulosa** (Seubert) Rohweder (Abh. Auslandsk., Reihe C, Naturwiss. 61(C18): 156, 1956). **Type:** Brazil, Paraná (*Sello* 995 [B]). — **Distr:** Trinidad?, S Brazil (Paraná), Paraguay, Uruguay, S Bolivia, N Argentina (Formosa, Misiones, Corrientes, Santa Fé, Entre Ríos, Salta,

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Tucumán, Catamarca, Chaco); moist places along streams. **I:** Bacigalupo (1967: 404, 410).

≡ *Tradescantia glandulosa* Seubert (1855) ≡ *Descantaria glandulosa* (Seubert) G. Brückner (1927) (*incorrect name*, Art. 11.4) ≡ *Callisia glandulosa* (Seubert) Christenhusz & Byng (2018); **incl.** *Tradescantia radiata* C. B. Clarke (1903) ≡ *Descantaria radiata* (C. B. Clarke) G. Brückner (1927) (*incorrect name*, Art. 11.4) ≡ *Tripogandra radiata* (C. B. Clarke) Bacigalupo (1964); **incl.** *Descantaria pflanzii* G. Brückner (1927) (*incorrect name*, Art. 11.4) ≡ *Tripogandra pflanzii* (G. Brückner) Rohweder (1956); **incl.** *Tradescantia pflanzii* G. Brückner (1927) (*nom. inval.*, Art. 32.1d).

Perennials, decumbent and rooting at the nodes, flowering stems erect to 40 cm; **L** ovate, acute, rounded at the base, to 8 × 3 cm, weakly succulent, glabrous except towards the base of the midrib below and at the mouth of the sheath; **Inf** terminal and in the uppermost leaf axils; peduncles to 1–5 cm; cincinni with up to 5–6 flowers; **Ped** 4–5 mm, glandular-pilose; **Sep** ovate, 3–4 × 1.2–2 mm, glandular-pilose; **Pet** ovate, 3.5–5 × 2.5–3.5 mm, white or pink; outer **St** fertile, **Fil** to 1.5 mm, bearded; inner **St** fertile, **Fil** to 3.5 mm, glabrous, dilated below the tip; **Ov** globose, to 1 mm Ø; **Sty** very short; **Sti** simple or capitellate; **Fr** globose, to 2.7 × 3.1 mm; **Se** rounded-triangular, 0.8–1.4 mm, light grey to brown, ribbed, reticulate-foveate, hilum punctiform.

**T. grandiflora** (Donnell Smith) Woodson (Ann. Missouri Bot. Gard. 29: 153, 1942). **Type** [lecto]: Guatemala (*Tuerckheim* 7864 [US]). — **Distr:** S Mexico (Veracruz, Tabasco, Campeche, Yucatán, Chiapas, Quintana Róo), Belize, Guatemala; tall evergreen forest, on limestone rocks, 800–1500 m.

≡ *Callisia grandiflora* Donnell Smith (1901) ≡ *Donnellia grandiflora* (Donnell Smith) C. B. Clarke (1902) (*incorrect name*, Art. 11.4) ≡ *Neodonnellia grandiflora* (Donnell Smith) Rose (1906).

Subscandent perennials to 3 m; **L** to 15 × 4.5 cm, distichous, narrowly ovate to elliptic, somewhat succulent, acute, oblique at the base, glabrous; **Inf** paniculate; cincinni to 7-flowered;

**Ped** to 14 mm, glabrous, erect in fruit; **Fl** fragrant, to 20 mm Ø; **Sep** dull mauve; **Pet** white; outer **St** fertile, **Anth** blackish; inner **St** staminodal, S-shaped, with 2 tufts of whitish hairs in the upper ½, **Anth** orange; **Fr** ellipsoid, to 6.5 mm; **Se** 1 or 2 per locule, 3–5 mm, grey, rugose.

**T. ionantha** (Diels) J. F. Macbride (Revista Univ. (Cuzco) 33(87): 142, 1945). **Type:** Peru, Puno (*Weberbauer* 588 [B]). — **Distr:** Colombia, Peru, Bolivia; mountains.

≡ *Tradescantia ionantha* Diels (1906) ≡ *Descantaria ionantha* (Diels) G. Brückner (1930) (*incorrect name*, Art. 11.4) ≡ *Callisia ionantha* (Diels) Christenhusz & Byng (2018).

Perennials, flowering stems erect to 35 cm, often containing a purplish pigment; **L** clustered at the stem base, scattered above, 1.5–3.8 × 1–1.5 cm, rather fleshy, slightly hairy above, more so below; **Inf** ± closely subtended by 1–3 upper leaves, of which 1–2 are folded in a manner reminiscent of *Callisia navicularis*; **Fl** 5–6 mm Ø; **Sep** 2.5 × 2 mm, hairy; **Pet** 2–3 mm, lilac to deep magenta-purple; longer **St** 3 mm, bearded, shorter **St** 1.5 mm; **Fr** and **Se** not described.

Handlos (1975: 284) regarded this plant as only a mountain ecotype of *T. multiflora*, as only the flower colour, always bright purple or magenta, appeared to him to separate it from the bulk of *T. multiflora*. I have not found this difficulty myself, since the plant is also much more succulent, with shiny, often folded, leaves, giving living plants and even herbarium specimens a distinct facies. Its occurrence in Bolivia is doubtful and it is not included in the online Bolivia Checklist at [eFloras.org](http://eFloras.org).

**T. multiflora** (Swartz) Rafinesque (Fl. Tellur. 2: 16, 1837). **Type:** Jamaica (*Swartz* s.n. [B?, M]). — **Distr:** Tropical to N South America (Jamaica, Trinidad and Tobago, Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia, N Argentina); shaded or open rocky banks on slopes, to 2900 m. **I:** Bacigalupo (1967: 399).

≡ *Tradescantia multiflora* Swartz (1788) ≡ *Heminema multiflora* (Swartz) Rafinesque (1837) ≡ *Descantaria multiflora* (Swartz) G. Brückner (1927) (*incorrect name*, Art. 11.4); **incl.**

*Tradescantia parviflora* Ruiz & Pavón (1794) ≡ *Tradescantia multiflora* var. *parviflora* (Ruiz & Pavón) C. B. Clarke (1881) ≡ *Tripogandra parviflora* (Ruiz & Pavón) Steyermark (1963) ≡ *Tripogandra multiflora* fa. *parviflora* (Ruiz & Pavón) Bacigalupo (1967); **incl.** *Tradescantia procumbens* Willdenow (1799); **incl.** *Commelina floribunda* Kunth (1816) ≡ *Aneilema floribundum* (Kunth) Hooker & Arnott (1840) ≡ *Leptorhoeo floribunda* (Kunth) Baillon (1894) ≡ *Tripogandra floribunda* (Kunth) Woodson (1942); **incl.** *Tradescantia cumanensis* Kunth (1843) ≡ *Descantaria cumanensis* (Kunth) Schlechtendal ex G. Brückner (1927) (*nom. illeg.*, Art. 52.1) ≡ *Tripogandra cumanensis* (Kunth) Woodson (1942); **incl.** *Tradescantia multiflora* [?] *linnaei* C. B. Clarke (1881); **incl.** *Descantaria procumbens* Hasskarl ex C. B. Clarke (1881) (*nom. inval.*, Art. 34.1c); **incl.** *Tradescantia multiflora* var. *tobagensis* Urban (1912); **incl.** *Callisia tripogandra* Christenhusz & Byng (2018).

Perennials, trailing and rooting at the nodes; flowering stems to 80 cm, erect; **L** narrowly to broadly ovate, usually glabrous, acute, to 8 × 3 cm, oblique at the base, somewhat succulent; **Inf**

numerous, terminal and in the upper leaf axils; **Fl** 3–8 mm Ø, white or pink; **Sep** often red-spotted at the base; outer **St** very short, glabrous; inner **St** longer, S-shaped, bearded; **Ov** 3-lobed, glabrous; **Sty** short, ½ as long as the ovary; **Fr** 1.5 mm; **Se** subtetrahedral, 0.6–0.8 mm, ash-grey, reticulate-foveolate.

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## References

- Bacigalupo, N. M. (1967) Las especies de *Tripogandra* (*Commelinaceae*) en la República Argentina. *Darwiniana* 14(2–3): 396–412, key, ills.
- Handlos, W. L. (1975) The taxonomy of *Tripogandra* (*Commelinaceae*). *Rhodora* 77: 213–333, key, ills. <http://biodiversitylibrary.org/page/659862#page/219/>
- Hertweck, K. L. & Pires, J. C. (2014) Systematics and evolution of inflorescence structure in the *Tradescantia* alliance (*Commelinaceae*). *Syst. Bot.* 39(1): 105–116. <https://doi.org/10.1600/036364414X677991>.
- Hunt, D. R. (1994) *Commelinaceae*. In: Davidse, G. & al. (eds.): *Flora Mesoamericana*. Volumen 6: *Alismataceae* a *Cyperaceae*; pp. 157–173. México, D.F. (MX): Universidad Nacional Autónoma de México. <http://www.tropicos.org/Project/FM>



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**Part IX**

**The Family Cyperaceae**







# Cyperaceae

U. Eggli

**Order:** Poales

**Important Literature:** Goetghebeur (1998: synopsis).

**Distribution:** Worldwide.

A large family consisting of 98 genera and 5680 species, with a worldwide distribution, and especially frequent in water-saturated locations.

The family is not generally known to embrace succulents, although there has been a recent suggestion that *Cyperus esculentus* (“Yellow Nutsedge”) (widespread in coastal regions of the Mediterranean and the Canary Islands) qualifies as a leaf succulent. The species inhabits dry sand dunes above the high-tide mark, but can also be found further inland at least in S Spain, and these plants sometimes show leaves up to 3–4 mm thick (N. P. Taylor, personal communication 2017). It appears that succulence is, however, merely halophytic, and the plants are not genuinely succulent (T. Raus, personal communication 2017).

*Cyperus bulbosus* (in the Old World tropics to Australia) and *C. esculentus* var. *sativus*

(originally W Asia and Africa, now widespread and almost cosmopolitan) produce fleshy tubers derived from a thickened rhizome. The tubers are rich in starch, sugar and fat, and at least the tubers of *C. esculentus* var. *sativus* (widely cultivated as “Chufa” in Spain and S America) are poikilohydric rather than succulent, and thus cannot be considered as being succulent according to the definition of succulence of Eggli & Nyffeler (2009). Subterranean tubers are also found in a couple of other species, e.g., *C. rotundus* (“Purple Nutsedge”, the world’s worst weed) (Goetghebeur 1998).

## References

- Eggli, U. & Nyffeler, R. (2009) Living under temporarily arid conditions — succulence as an adaptive strategy. *Bradleya* 27: 13–36, ills. <https://doi.org/10.5167/uzh-28825>
- Goetghebeur, P. (1998) *Cyperaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants, 4: 141–190. Berlin/Heidelberg (DE): Springer Verlag. [https://doi.org/10.1007/978-3-662-03531-3\\_15](https://doi.org/10.1007/978-3-662-03531-3_15)

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**Part X**

**The Family Dioscoreaceae**







## Dioscoreaceae

U. Eggli and G. D. Rowley

**Including** *Avetraceae* Takhtajan.  
**Including** *Stenomeridaceae* J. Agardh.  
**Including** *Tamaceae* Berchtold & J. Presl.  
**Including** *Tamnaceae* J. Kichx fil.  
**Including** *Trichopodaceae* Hutchinson.

Dioecious or rarely monoecious herbaceous perennial climbers, rarely  $\pm$  woody, rarely spiny, often completely deciduous from underground or above-ground tubers (sometimes with fissured corky bark) or rhizomes; sometimes with aerial tubers from leaf axils; **L** alternate or rarely opposite, petiole mostly well-developed, lamina entire or (palmately) lobed or more often heart-shaped, with few to many curved-ascending and again converging main veins; **Inf** paniculate or spicate from leaf axils; **Fl** small and often greenish, almost always unisexual, regular;  **Tep** 6 in 2 series, basally usually united, often with nectaries;  **male Fl** with 6 **St** in 2 whorls (sometimes 1 whorl absent or as staminodes); **Anth** longitudinally dehiscent;  **female Fl** without staminodes; **Ov** inferior of 3 united **Ca** with normally 2 ovules per locule, placentation mostly axile; **Sty** 3 or 1;

**Sti** 3; **Fr** often 3-winged capsules, or fleshy berries; **Se** often winged.

**Order:** Dioscoreales

**Important Literature:** Knuth (1924: monograph); Huber (1998: synopsis); Caddick & al. (2002a: phylogeny); Caddick & al. (2002b: classification); Viruel & al. (2016: historical biogeography); Raz (2017: review fossil record).

**Distribution:** Tropics worldwide, with a few taxa (incl. *Tamus*, “Black Bryony”) extending into temperate regions.

The family has 3 genera (or 4 when *Tacca* is included, see below), but counts for species number differ between about 420 (Caddick & al. 2002b) and 870 (Stevens 2001+); 95% of them belong to *Dioscorea*. *Dioscoreaceae* is shown as sister to *Burmanniaceae* (no succulents) in recent molecular phylogenies. The traditionally separate family *Taccaceae* is sometimes included in *Dioscoreaceae* (e.g. Caddick & al. 2002a), but retained as separate by others. *Tamus* (“Black Bryony”) was traditionally considered as separate genus but should be included in *Dioscorea*, with which it shares a tuberous storage organ, and from which it differs by having juicy berry-like fruits – Fig. 1.

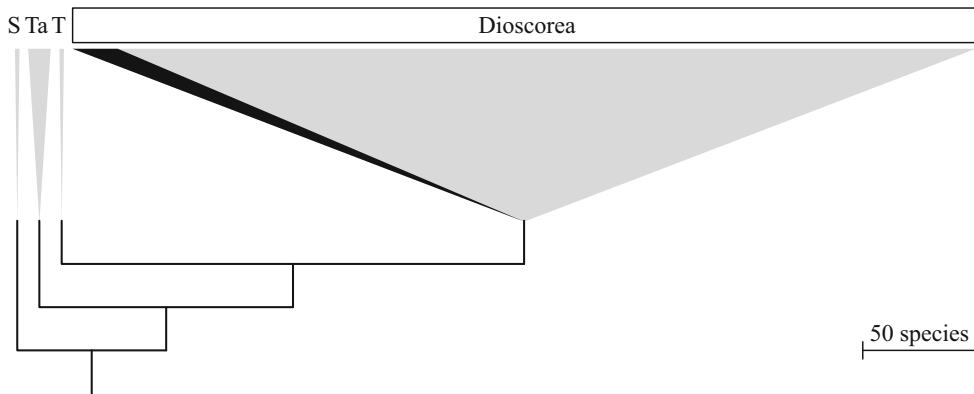
Apart from several species of *Dioscorea* which are important food plants, the family is notable for its diverse phytochemistry (primarily lactone

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**Fig. 1** Summary phylogeny of *Dioscoreaceae* based on Caddick & al. (2002a) (414 species total). S = *Stenomeris*, T = *Trichopus*, Ta = *Tacca*. (Copyright U. Eggli)

alkaloids and steroidal saponins). Succulence (as underground or rarely above-ground storage tubers, or rarely thickened stems) is restricted to *Dioscorea*, but only a few taxa can be regarded as true succulents.

## References

- Caddick, L. R. [& al. 2002a], Rudall, P. J., Wilkin, P., Hedderson, T. A. J. & Chase, M. W. (2002a) Phylogenetics of *Dioscoreales* based on combined analyses of morphological and molecular data. *Bot. J. Linn. Soc.* 138: 123–144. <https://doi.org/10.1046/j.1095-8339.2002.138002123.x>
- Caddick, L. R. [& al. 2002b], Wilkin, P. J., Rudall, P. J., Hedderson, T. A. J. & Chase, M. W. (2002b) Yams reclassified: A recircumscription of *Dioscoreaceae* and *Dioscoreales*. *Taxon* 51(1): 103–114. <http://www.jstor.org/stable/1554967>
- Huber, H. (1998) *Dioscoreaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 216–235, ill., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_28](https://doi.org/10.1007/978-3-662-03533-7_28)
- Knuth, R. (1924) *Dioscoreaceae*. In: Engler, A. (ed.): *Das Pflanzenreich*, IV. 43 (Heft 87). Leipzig (DE): W. Engelmann. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=420>
- Raz, L. (2017) A review of the fossil record for *Dioscoreaceae*. *Bot. J. Linn. Soc.* 183(4): 495–508, ill. <https://doi.org/10.1093/botlinnean/bow021>
- Stevens, P. F. (2001+) Angiosperm Phylogeny Website, Version 12, July 2012 [and more or less continuously updated since]. St. Louis (US): Missouri Botanical Garden. <http://www.mobot.org/MOBOT/research/APweb/>
- Viruel, J. [& al. 2016], Segarra-Moragues, J. G., Raz, L., Forest, F., Wilkin, P., Sanmartín, I. & Catalán, P. (2016) Late Cretaceous—Early Eocene origin of yams (*Dioscorea*, *Dioscoreaceae*) in the Laurasian Palaeartic and their subsequent Oligocene—Miocene diversification. *J. Biogeogr.* 43(4): 750–762. <https://doi.org/10.1111/jbi.12678>



## Dioscorea DIOSCOREACEAE

G. D. Rowley and U. Eggli

- Dioscorea** Linné (Spec. Pl. [ed. 1], 1032, 1753). **Type:** *Dioscorea sativa* Linné [*typ. cons.* (ICBN 2006: 263)]. — **Lit:** Burkill (1952: systematics sect. *Testudinaria*); Archibald (1967: synopsis RSA); Wilkin (2001: synopsis Fl. Zambesiaca area); Wilkin & al. (2005: molecular phylogeny); Wilkin (2009: Fl. Zambesiaca); Durst (2010: ill. synopsis); Maurin & al. (2016: evolution pachycauly); Viruel & al. (2016: historical biogeography). **Distr:** Tropics and subtropics worldwide. **Etym:** For Pedanios Dioscorides, most influential Greek physician and herbalist of the first century A.D.
- Incl.** *Rajania* Linné (1753). **Type:** *Rajania hastata* Linné.
- Incl.** *Tamus* Linné (1753). **Type:** *Tamus communis* Linné.
- Incl.** *Oncus* Loureiro (1790). **Type:** *Oncus esculentus* Loureiro.
- Incl.** *Ubium* Cothenius (1790). **Type:** *Ubium quadrifarium* J. F. Gmelin.
- Incl.** *Oncorhiza* Persoon (1805) (*nom. illeg.*, Art. 52.1). **Type:** *Oncus esculentus* Loureiro.
- Incl.** *Testudinaria* Salisbury ex Burchell (1824). **Type:** *Tamus elephantipes* L'Héritier.
- Incl.** *Rhizemys* Rafinesque (1836) (*nom. illeg.*, Art. 52.1). **Type:** *Tamus elephantipes* L'Héritier.
- Incl.** *Botryosicyos* Hochstetter (1844). **Type:** *Botryosicyos pentaphyllus* Hochstetter.
- Incl.** *Helmia* Kunth (1850). **Type:** *Helmia dregeana* Kunth [lectotype designated by Caddick & al., Taxon 51: 108, 2002].
- Incl.** *Sismondaea* Delponte (1854). **Type:** *Sismondaea dioscoreoides* Delponte.
- Incl.** *Epipetrum* Philippi (1862). **Type:** *Dioscorea humilis* Bertero ex Colla.
- Incl.** *Borderea* Miégeville (1866). **Type:** *Borderea pyrenaica* Miégeville.
- Incl.** *Elephantodon* Salisbury (1866). **Type:** *Dioscorea eburnea* Loureiro.
- Incl.** *Hamatris* Salisbury (1866). **Type:** *Dioscorea triphylla* Linné.
- Incl.** *Merione* Salisbury (1866). **Type:** *Dioscorea villosa* Linné
- Incl.** *Polynome* Salisbury (1866). **Type:** *Dioscorea alata* Linné [lectotype, designated by Caddick & al., Taxon 51: 108, 2002].
- Incl.** *Strophis* Salisbury (1866). **Type:** *Dioscorea cirrhosa* Loureiro.
- Incl.** *Higinbothamia* Uline (1899). **Type:** *Higinbothamia synandra* Uline.
- Incl.** *Peripetasma* Ridley (1920). **Type:** *Peripetasma polyanthum* Ridley.
- Incl.** *Nanarepenta* Matuda (1962). **Type:** *Nanarepenta toluicana* Matuda.

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Dioecious perennials or very rarely annuals, typically with long weak annual stems twining (mostly sinistrorsely) from underground storage organs (swollen rhizomes, potato-like tubers or caudices), rarely with above-ground caudices with strongly fissured and structured bark, or rarely with persistent woody or succulent stems; stems sometimes spiny, sometimes with aerial tubers from leaf axils; **L** alternate, usually simple and cordate with a well-developed petiole having a jointed pulvinate base; stipules absent; **Inf** panicles, racemes or spikes, axillary; **Fl** unisexual (but sometimes with staminodes or pistillodium), actinomorphic, small and greenish-yellow or greenish-whitish, or purple; **Te** 6 in 2 series, shortly united into a basal tube; **St** 6 in 2 whorls; **Ov** inferior of 3 **Ca**, each locule with 2 ovules; **Fr** 3-lobed or -winged capsules; **Se** large, flattened, with a symmetrical or 1-sided papery wing. — **Cytology**:  $n = 9, 10$ , rarely 8, or higher (Huber 1998).

The large genus with 350–400 species (Caddick & al. 2002b) (380–? 800 according to Stevens (2001+: acc. Jan. 2016)) has a predominantly tropical distribution. The tubers have a diverse morphological origin, and many species are further notable for their extrafloral nectaries (esp. found on leaves). Some 10% of its species are economically important, esp. for their starchy tubers (“Yams”, with numerous cultivars of several ploidy levels of several species cultivated throughout the tropics) or are exploited as sources of steroidal hormones used as oral contraceptives (esp. the Mexican *D. floribunda*). The succulent tissue of *D. elephantipes* and *D. sylvatica* is turnip-like and occasionally cooked and eaten in S Africa. Similar use is reported for *D. remotiflora* Kunth from Mexico, whose tuberous roots are used locally and taste like potatoes when cooked.

**Classification**: Knuth (1924) classified *Dioscorea* into 4 subgenera and 60 sections, while Huber (1998) recognized no fewer than 25 “genus-equivalent” sections and genera (incl. *Testudinaria*). He argued that a broadly circumscribed *Dioscorea* inadequately reflects the diversity of forms, and that the 24 sections in his key would merit generic status. On the other hand, Wilkin & al. (2005) found that the traditional sectional classification can be

simplified, and that only some of the traditionally recognized groups are monophyletic. Taxa with rhizomes appear to be ancestral to taxa that form tubers in this phylogeny. The caudiciform growth form of the S African “Elephant’s foot” evolved in an advanced subclade of African *Dioscoreas* since mid-miocene (Maurin & al. 2016). The parallel evolution of this growth form in the Mexican *D. remotiflora* is notable.

**Succulence**: Succulence has developed in the form of enlarged and fleshy caudices in several taxa from arid regions in Africa and Mexico (caudex normally  $\pm$  above ground) and one from arid Chile (caudex underground). A notable addition to the succulent species is *D. basi-clavicaulis* from NE Brazil with perennial thickened virgate prickly stems. Bucherer (1889) studied the anatomy of the tubers of several species and found that they are derived from the epicotyl. This contrasts with Sparshott (1935) who found that the tuber of *D. elephantipes* is derived from the hypocotyl, and with Teichman und Logischen & al. (1977) who found that the tubers of *D. cotinifolia* (not considered succulent) are also derived from the hypocotyl but represent “intermediary organs” with both shoot and root characteristics. Growth in volume is due to a monocot cambium (Huber 1998: 216) and can be asymmetrical-downwards as in the former *Tamus*, mostly lateral as in *D. sinuata*, or both lateral and vertical as in *D. elephantipes*. The interior tissue of these tubers is parenchymatic with little starch (Bucherer 1889), and tubers of *D. elephantipes* consist of up to 97% water (Marloth 1908: 318–319). Other species, e.g. *D. batatas*, have true root tubers that are annually replaced, and that form by enlargement of adventitious roots (Bucherer 1889), and store primarily starch; they are not considered as succulents. The axillary tubers (sometimes erroneously referred to as “bulbils”) of e.g. *D. batatas* are derived from axillary buds, i.e. they consist of a stem axis with contracted internodes (Huber 1998: 219).

**D. basi-clavicaulis** Rizzini & Mattos-Filho (Revista Brasil. Biol. 46(2): 317–319, ill., 1986). **Type**: Brazil, Minas Gerais (Rizzini & Mattos-

*Filho* s.n. [RB 215.073]). — **Distr:** Brazil (Minas Gerais, Bahia); in Caatinga scrub. — Fig. 1.

**R** fascicled, tuberous-elongate; stems several from a common rhizomatous rootstock, perennial, basal parts (0.5–1 m) fleshy-fibrous, narrowly fusiform, to 8 cm Ø, olive-green, terete or angled



**Fig. 1** *Dioscorea basiclavicaulis*. (Copyright: U. Eggli)

**Fig. 2** *Dioscorea elephantipes*. (Copyright: U. Eggli)



or ± longitudinally ridged, densely spiny, tip elongating whip-like, thin, to several m long, with pendent to semi-twining laxly spiny side branches; **L** narrowly triangular, to 11 × 6 cm, base auriculate, tip long-acuminate, thin-textured, grass-green, young flushed reddish-brown, petiole to 4 cm; **Inf** axillary, spicate, pendent; **Fl** 0.5–2 cm apart, greenish, 8–10 mm Ø; **Fr** 3.5–4.5 cm, alate; **Se** not described.

Unique in the large genus for its thickened succulent perennial stems. Propagated by division, probably also by rooting sections of individual stems. The original publication notes the surprising similarity of the stems with those of *Smilax papyracea* Poiret (*Smilacaceae*), also native to Brazil, as well as with those of *Neoalsomitra schefferiana* ssp. *podagrica* (*Cucurbitaceae*). The stem spines are not just epidermal outgrowths, but include cortex components (Tenorio & al. 2017). — [U. Eggli].

**D. elephantipes** (L'Héritier) Engler (Veg. Erde 9(2): 267, 1908). — **Lit:** Sparshott (1935: morphology). **Distr:** RSA (Western Cape, Eastern Cape); dry rocky slopes, 250–1250 m. **I:** Rowley (1987: 2, 11, 43–45, 47); Hartl (2016: flowers, fruits & seeds). — Figs. 2 and 3.

≡ *Tamus elephantipes* L'Héritier (1788) ≡ *Testudinaria elephantipes* (L'Héritier) Lindley (1825); **incl.** *Testudinaria montana* Burchell (1824) ≡ *Testudinaria elephantipes* var. *montana* (Burchell) G. D. Rowley (1953) ≡ *Testudinaria*



*elephantipes* fa. *montana* (Burchell) G. D. Rowley (1973); **incl.** *Dioscorea elephantopus* Sprengel (1827).

Caudex  $\pm$  completely above-ground with marginal fibrous **R**, massive, 60 (–100)  $\times$  60 cm in age with 1 or more irregular domed growing points, covered in hard grey corky bark divided



**Fig. 3** *Dioscorea elephantipes*. (Copyright: U. Eggli)

into irregularly polygonal (4- to 7-sided) plates 8  $\times$  3–6 cm; stems few, stiffly erect, basally woody, spineless, partly deciduous, with spirally set horizontal **Br** that twine at the tips; **L** broadly ovate to reniform with acute tip, 2–2.5  $\times$  2–6 cm, grass-green, petiole 0.5–1 cm; **Fl**  $\pm$  4 mm  $\varnothing$ ; **Fr** to 2  $\times$  1.8 cm, obovoid, with 3 wings; **Se** lenticular, 5 mm  $\varnothing$  with a one-sided wing 10  $\times$  7 mm, dark brown to black.

The massive tubercled caudex is shared with *D. strydomiana*. The branch system is notable, and as already Darwin noted, only the lateral shoots twine. The characteristic polygonally fissured bark starts to develop after some years; caudices of seedlings are  $\pm$  smooth. The tubers are said to be edible and have been used as emergency food. Vernacular names: “Elephant’s Foot”, “Turtleback Plant”, “Hottentot Bread”. — [G. D. Rowley].

**D. fastigiata** Gay (Fl. Chil. 6: 54, 1853). **Type:** Chile, Atacama (Gay s.n. [P]). — **Distr:** Chile (from Antofagasta to Talca); dry coastal regions, often in sand. **I:** Navas B. and Erba V. (1968: t. 2: a-c); Ewest (2002). — Fig. 4.

**Incl.** *Dioscorea axilliflora* Philippi (1896); **incl.** *Dioscorea gayi* Philippi (1896); **incl.** *Dioscorea geissei* Philippi (1896); **incl.** *Dioscorea paupera* Philippi (1896); **incl.** *Dioscorea thinophila* Philippi (1896); **incl.** *Dioscorea cylindrostachya* I. M. Johnston (1929).

Caudex underground, semiglobose with flat sometimes lobed bottom, 2–4 cm  $\varnothing$ , bark pale

**Fig. 4** *Dioscorea fastigiata*. (Copyright: U. Eggli)



brown, smooth or slightly fissured; stem 1 to few, short-lived and completely deciduous, creeping, contracted, 5–20 cm, herbaceous, spineless; **L** few,  $\pm$  cordate, to  $2 \times 2$  cm, dark green, slightly thickish, petiole to 2 cm; **Inf** paniculate, 1–2 cm; **male Fl** numerous in fascicles, 1.5 mm  $\varnothing$ , whitish, **St** 6; **female Fl** 3–4 only; **Fr** roundish to obovate, 1–1.5 cm  $\varnothing$ . — [U. Eggli].

**D. hemicypta** Burkill (J. South Afr. Bot. 18: 187, 1952). — **Distr:** Namibia, RSA (Northern Cape, Western Cape); dry stony slopes, 350–1450 m. **I:** Rowley (1987: 48–49). — Fig. 5.

**Incl.** *Testudinaria glauca* Marloth (s.a.) (*nom. inval.*, Art. 32).

Caudex half-underground, dome-shaped and taller than wide, underground part amorphously lobed like molten lava, above-ground part with thick corky irregular ridges and plates; stems few,  $\pm$  completely deciduous or basally woody, spineless, side branches only twining; **L** to  $6 \times 4$  cm, always longer than broad, bluish-green; **Fl** to

6 mm  $\varnothing$ ; otherwise similar to *D. elephantipes*. — [G. D. Rowley].

**D. mexicana** Scheidweiler (Hort. Belge 4: 99, 1837). — **Distr:** S Mexico (Jalisco, Colima, Michoacán, Guerrero, Veracruz, Oaxaca, Chiapas), Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama; slopes and rocky ravines in tropical evergreen to deciduous forests and thorn forests, to 2000 m. **I:** Rowley (1987: 49, as *D. macrostachya*).

**Incl.** *Dioscorea macrostachya* Benth (1841)  $\equiv$  *Testudinaria macrostachya* (Benth) G. D. Rowley (1973); **incl.** *Dioscorea macrophylla* Martius & Galeotti (1842); **incl.** *Dioscorea deppei* Schiede ex Schlechtendal (1843); **incl.** *Dioscorea billbergiana* Kunth (1850); **incl.** *Dioscorea leiboldiana* Kunth (1850); **incl.** *Dioscorea composita* Hemsley (1884); **incl.** *Testudinaria cocolmecca* Procopp (1892); **incl.** *Dioscorea astrostigma* Uline (1896); **incl.** *Dioscorea palmeri* R. Knuth (1917)  $\equiv$  *Dioscorea macrostachya* var. *palmeri* (R. Knuth) Morton (1936); **incl.** *Dioscorea tuerckheimii* R. Knuth (1917); **incl.** *Dioscorea deamii* Matuda (1953).

Caudex  $\pm$  half-underground, semiglobose, to 1 m  $\varnothing$ , upper surface with polygonally fissured corky bark much like *D. elephantipes*, polygonal tubercles to  $5 \times 6$  cm; stems few, to 6 m,  $\pm$  completely deciduous, twining, spineless or with **Sp** to 1 cm from persistent petiole bases; **L** broadly rounded-cordate, long-acuminate,  $10\text{--}18.5 \times 8\text{--}16$  cm, much smaller on flowering shoots, bright green, petiole 4–11 cm; **male Inf** narrow spikes to 25 cm, sometimes fascicled; **female Inf** always simple; **Fl** in groups of 2–5, dark purple, 2.5–3.5 mm  $\varnothing$ ; **Fr** oblong-ellipsoid,  $2\text{--}3 \times 1.3\text{--}1.7$  cm; **Se**  $8\text{--}10 \times 5\text{--}6$  mm overall including  $2 \pm$  equal wings.

Despite the wide distribution ascribed to this species, it is poorly known, esp. as to its variability. *D. mexicana* var. *sessiliflora* (Uline) Matuda (based on *D. macrostachya* var. *sessiliflora* Uline) has recently been lectotypified by Téllez-Valdés & al. (2010) and is now a synonym of the non-succulent *D. spiculiflora*.

**D. strydomiana** Wilkin (Kew Bull. 65(3): 425–426, ill. (pp. 427–429), 2010). **Type:** RSA,



**Fig. 5** *Dioscorea hemicypta*. (Copyright: U. Eggli)

Mpumalanga (*Burrows & al.* 10627B [PRE, BNRH, LYD, K, NBG, PRU]). — **Distr:** RSA (Mpumalanga); grassy woodland on dolomite with quartzite intrusions, 1100–1150 m.

Similar to *D. elephantipes* but above-ground caudex to 1 × 1 m, subglobose when young to cylindrical-ovoid with age and then with up to 6 low domed apices from which the annual shoots appear; stems non-climbing but shrubby, with short branches; **L** obtuse to cuneate at the base, acute or shortly acuminate, 1.5–4.1 × 0.6–2 cm, dull pale green; **Fl** larger than in *D. elephantipes*; **Fr** broadly obovoid with a shallowly retuse apex.

Discovered already in 1999 (see Hurter 2003), but only named much later. Only 2 populations with ± 200 individuals are known to exist, making it a critically endangered species. — [G. D. Rowley].

**D. sylvatica** Ecklon (South Afr. Quart. J. 1: 363, 1830). **Type** [lecto]: RSA, Eastern Cape (*Ecklon* s.n. in *Ecklon & Zeyher* 3.1 [TCD, BM]). — **Lit:** Blunden & al. (1971); Wilkin (2001: 400). **Distr:** Zambia, Zimbabwe, Moçambique, RSA; often in rocky areas, in *Brachystegia* or mopane woodland, 0–1800 m. **I:** Rowley (1987: 48).

≡ *Testudinaria sylvatica* (Ecklon) Kunth (1850); **incl.** *Dioscorea sylvatica* Ecklon (s.a.) (*nom. inval.*, Art. 61.1); **incl.** *Testudinaria montana* Ecklon & Zeyher in *schedis* (s.a.) (*nom. inval.*, Art. 29.1); **incl.** *Testudinaria sylvestris* Hort. Berol. ex Kunth (1850) (*nom. illeg.*, Art. 53.1); **incl.** *Dioscorea montana* Ecklon & Zeyher ex R. Knuth (1924); **incl.** *Dioscorea montana* var. *lobata* Weimarck (1937); **incl.** *Dioscorea montana* var. *sagittata* Suessenguth (1951).

Caudex variable, above or below ground, conical, slab-like or obconical, often amorphously lobed like lava, 30–60 (–100) cm Ø; stem 1, thin, wiry, spineless, twining, branched above; **L** triangular-cordate, 2–8 × 1.5–6 cm, green, petiole to 2.5 cm; **Fl** 5 mm Ø; **Fr** to 2.7 × 1.5 cm, obovoid; **Se** 7 × 4 mm with a 1-sided wing to 16 × 6 mm.

Readily propagated when caudex lobes can be divided. This is a variable species which can be

divided into a number of varieties. Burkill (1952) and Wilkin (2001) provided information on the complicated nomenclatural status of *D. montana* and its var. *glauca*, and on typification issues. Wilkin (2001, 2009: 136–137) does not subdivide this species into varieties and comments that further studies are needed to investigate the delimitation of *D. sylvatica* from *D. elephantipes*, “as they appear to differ only in leaf shape”. Tubers are variable in shape and outline (see Blunden & al. 1971), but the full variability and the possible systematic significance remains unknown. — [G. D. Rowley].

**D. sylvatica** var. **brevipes** (Burt Davy) Burkill (J. South Afr. Bot. 18: 189, 1952). **Type:** RSA, Limpopo (*Leendertz* 1510 [K]). — **Distr:** S Zimbabwe, E RSA (Eastern Cape, KwaZulu-Natal, Free State, Gauteng, Mpumalanga, Limpopo), Swaziland; bush or forest.

≡ *Dioscorea brevipes* Burt Davy (1924) ≡ *Testudinaria paniculata* var. *brevipes* (Burt Davy) G. D. Rowley (1953) ≡ *Testudinaria sylvatica* var. *brevipes* (Burt Davy) G. D. Rowley (1973); **incl.** *Dioscorea sylvatica* ssp. *lydenbergensis* Blunden & al. (1971) ≡ *Testudinaria sylvatica* var. *lydenbergensis* (Blunden & al.) G. D. Rowley (1974).

**L** 6–8 cm long with divergent auricles; **Ped** to 2 mm; **Fr** ± 2 cm long. — [G. D. Rowley].

**D. sylvatica** var. **multiflora** (Marloth) Burkill (J. South Afr. Bot. 18: 189, 1952). **Type:** RSA, Limpopo (*Dyke* s.n. in *Marloth* 5097 [B, BM]). — **Distr:** RSA (Mpumalanga, Limpopo); 1400–1600 m.

≡ *Testudinaria multiflora* Marloth (1913) ≡ *Testudinaria sylvatica* var. *multiflora* (Marloth) G. D. Rowley (1973); **incl.** *Dioscorea marlothii* R. Knuth (1924).

**L** thin, without divergent auricles; **Fr** 1.2–1.4 cm long. — [G. D. Rowley].

**D. sylvatica** var. **paniculata** (Dümmer) Burkill (J. South Afr. Bot. 18: 189, 1952). **Type:** RSA, KwaZulu-Natal (*Dümmer* s.n. [K]). —





**Fig. 6** *Dioscorea sylvatica* var. *sylvatica*. (Copyright: U. Eggli)

**Distr:** RSA (Eastern Cape, KwaZulu-Natal); 1000–1650 m.

≡ *Testudinaria paniculata* Dümmer (1912) ≡ *Testudinaria sylvatica* var. *paniculata* (Dummer) G. D. Rowley (1973); **incl.** *Testudinaria montana* var. *paniculata* Kuntze (1898) ≡ *Dioscorea montana* var. *paniculata* (Kuntze) R. Knuth (1924); **incl.** *Dioscorea paniculata* Dümmer (1912); **incl.** *Dioscorea montana* var. *duemmeri* R. Knuth (1924).

Caudex domed or slab-like, often convex below; **L** 6–8 cm long, reniform with divergent auricles; **Ped** to 4 mm; **Fr** ± 2 cm long. — [G. D. Rowley].

**D. sylvatica** var. **rehmannii** (Baker) Burkill (J. South Afr. Bot. 18: 189, 1952). **Type:** RSA, Limpopo (*Rehmann* 5783 [K]). — **Distr:** RSA (KwaZulu-Natal, Free State, Mpumalanga, Limpopo).

≡ *Dioscorea rehmannii* Baker (1896) ≡ *Testudinaria rehmannii* (Baker) G. D. Rowley (1953) ≡ *Testudinaria sylvatica* var. *rehmannii* (Baker) G. D. Rowley (1973).

**L** thin, with convergent auricles; **Fr** 2–2.5 cm long. — [G. D. Rowley].

**D. sylvatica** var. **sylvatica** — **Distr:** RSA (Eastern Cape); 125–1650 m. – Fig. 6.

**Incl.** *Dioscorea hederifolia* Grisebach (1842); **incl.** *Tamus sylvestris* Kunth (1850); **incl.** *Dioscorea montana* var. *glauca* R. Knuth (1924).

**L** 2 × 4 cm with divergent auricles; **Fr** ± 1.5 cm long. — [G. D. Rowley].

## References

- Archibald, E. E. A. (1967) The genus *Dioscorea* in the Cape Province west of East London. J. South Afr. Bot. 33: 1–46., ills.
- Blunden, G. [ & al. 1971], Hardman, R. & Hind, F. J. (1971) The comparative morphology and anatomy of *Dioscorea sylvatica* Eckl. from Natal and the Transvaal. Bot. J. Linn. Soc. 64(4): 431–446, ills. <https://doi.org/10.1111/j.1095-8339.1971.tb02156.x>
- Bucherer, E. (1889) Beiträge zur Morphologie und Anatomie der Dioscoreaceen. Kassel (DE): Theodor Fischer.
- Burkill, I. H. (1952) *Testudinaria* as a section of the genus *Dioscorea*. J. South Afr. Bot. 18: 177–191, maps, ills.
- Caddick, L. R. [ & al. 2002b], Wilkin, P. J., Rudall, P. J., Hedderson, T. A. J. & Chase, M. W. (2002) Yams reclassified: A recircumscription of *Dioscoreaceae* and *Dioscoreales*. Taxon 51(1): 103–114. <http://www.jstor.org/stable/1554967>
- Durst, E. (2010) Dioscoree succulente: Un'introduzione. Succulent *Dioscoreae* [sic!]: An introduction. Cactus & Co. 13(4): 20–51, ills.
- Ewest, W. (2002) *Dioscorea fastigiata* Gay — ein Geophyt aus Chile. Kakt. and. Sukk. 53(5): 135–138, ills.
- Hartl, M. (2016) Früchte an *Dioscorea elephantipes*. Kakt. and. Sukk. 67(7): 191–193, ills.
- Huber, H. (1998) *Dioscoreaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 216–235, ills., key. Berlin (DE) etc.: Springer-Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_28](https://doi.org/10.1007/978-3-662-03533-7_28)
- Hurter, J. (2003) A new pachycaul *Dioscorea* species from Mpumalanga Province, South Africa and its conservation. Aloe 40(3–4): 73–75, ills.
- Knuth, R. (1924) *Dioscoreaceae*. In: Engler, A. (ed.): Das Pflanzenreich, IV. 43 (Heft 87). Leipzig (DE): W. Engelmann. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=420>

- Marloth, R. (1908) Das Kapland, insonderheit das Reich der Kapflora, das Waldgebiet und die Karoo pflanzengeographisch dargestellt. In: Chun, C. (ed.): Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899. Zweiter Band. Dritter Teil. Jena (DE): Verlag von Gustav Fischer.
- Maurin, O. [& al. 2016], Muasya, A. M., Catalan, P., Shongwe, E. Z., Viruel, J., Wilkin, P. & Bank, M. van der (2016) Diversification into novel habitats in the Africa clade of *Dioscorea* (*Dioscoreaceae*): Erect habit and elephant's foot tubers. *BMC Evol. Biol.* 16: 238, 18 pp., maps, ills. <https://doi.org/10.1186/s12862-016-0812-z>
- Navas B., E. & Erba V., G. (1968) El género *Dioscorea* en Chile. *Revista Univ. (Santiago)* 53: 41–60, ills., key.
- Rowley, G. D. (1987) Caudiciform and pachycaul succulents. Pachycauls, bottle-, barrel- and elephant-trees and their kin: A collector's miscellany. Mill Valley (US): Strawberry Press.
- Sparshott, E. N. (1935) Observations on the formation, development, and structure of the tuber of *Testudinaria elephantipes*, and on the origin of the vegetative shoot. *J. Linn. Soc., Bot.* 49(332): 593–610, ills., t. 32. <https://doi.org/10.1111/j.1095-8339.1935.tb01341.x>
- Stevens, P. F. (2001+) Angiosperm Phylogeny Website, Version 12, July 2012 [and more or less continuously updated since]. St. Louis (US): Missouri Botanical Garden. <http://www.mobot.org/MOBOT/research/APweb/>
- Téllez-Valdés, O. [& al. 2010], Blanco Fernández De Caleyá, P. & Rico Arce, L. (2010) Tipificación y actualización nomenclatural en *Dioscorea* (*Dioscoreaceae*) descritas o relacionadas con las colecciones de Martín de Sessé y José Mariano Mociño. *Anales Jard. Bot. Madrid* 67(1): 49–63, ills. <https://doi.org/10.3989/ajbm.2137>
- Teichman und Logischen, I. von [& al. 1977], Robbertse, P. J. & Schijff, H. P. van der (1977) The subterranean intermediary organs of *Dioscorea cotinifolia* Kunth: 1. The germination, development, morphology and vegetative reproduction of the tuberous swollen and cylindrical intermediary organs. *J. South Afr. Bot.* 43 (1): 41–56, ills.
- Tenorio, V. [& al. 2017], Couto, R. S., Albuquerque, E. S. B. de, Medeiros, A. M. L., Oliveira Ferreira, R. de, Braga, J. M. A. & Vieira, R. C. (2017) Stem anatomy of neotropical *Dioscorea* L. (*Dioscoreaceae*) and its importance to the systematics of the genus. *Pl. Syst. Evol.* 303: 775–786, ills. <https://doi.org/10.1007/s00606-017-1408-9>
- Viruel, J. [& al. 2016], Segarra-Moragues, J. G., Raz, L., Forest, F., Wilkin, P., Sanmartín, I. & Catalán, P. (2016) Late Cretaceous — Early Eocene origin of yams (*Dioscorea*, *Dioscoreaceae*) in the Laurasian Palaeartic and their subsequent Oligocene—Miocene diversification. *J. Biogeogr.* 43(4): 750–762. <https://doi.org/10.1111/jbi.12678>
- Wilkin, P. (2001) *Dioscoreaceae* of south-central Africa. *Kew Bull.* 56(2): 361–404, keys. <http://www.jstor.org/stable/4110963>
- Wilkin, P. (2009) *Dioscoreaceae*. In: Timberlake, J. R. & Martins, E. S. (eds.): *Flora Zambesiaca*, 12(2): 109–140, ills., key. London (GB): Royal Botanic Gardens Kew.
- Wilkin, P. [& al. 2005], Schols, P., Chase, M. W., Chayamarit, K., Furness, C. A., Huysmans, S., Rakotonasolo, F., Smets, E. & Thapayai, C. (2005) A plastid gene phylogeny of the Yam genus, *Dioscorea*: Roots, fruits and Madagascar. *Syst. Bot.* 30(4): 736–749. <https://doi.org/10.1600/036364405775097879>



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**Part XI**

**The Family Doryanthaceae**





# Doryanthaceae

P. I. Forster and U. Eggli

Giant monocarpic **Ros** plants; stems very short; **R** thick, fleshy; **L** numerous, flat,  $\pm$  succulent, with a brown tubular tip withering to leave a ragged apex; **Inf** large scapose terminal oblong thyrses or globular compound racemes, subtended by numerous sheathing **Bra**; **Fl** bisexual, actinomorphic, 3-merous, each subtended by a conspicuous **Bra**; **Per** segments united at the base into a tube, free parts spreading; **St** 6; **Fil** linear-subulate, somewhat enlarged at the base, adnate to the tepals for  $\pm$   $\frac{1}{2}$  of their length, inserted into a pit at the base of the anthers; **Anth** longitudinally dehiscent, bilocular; **Ov** inferior, 3-locular; ovules 40–50 per locule; **Sty** 1; **Sti** 3-angled; **Fr** large ellipsoidal to ovoid loculicidal capsules, 70–100 mm, with a short apical beak 6–7 mm; **Se** winged, flattened.

**Order:** Asparagales

**Important Literature:** Pedley (1986: flora Australia); Clifford (1998: synopsis).

**Distribution:** E Australia (Queensland, New South Wales).

The family embraces a single genus with 2 species only. It was traditionally included in *Agavaceae*, *Amaryllidaceae* or *Liliaceae* s.l., or in *Hemerocallidaceae*. All recent molecular phylogenies unambiguously place the family in the Asparagales. Goldblatt & al. (2008) found *Doryanthaceae* as sister to *Iridaceae*, confirming earlier tentative placements. This near-basal position in the order was recently confirmed by Seberg & al. (2012) as well as by Chen & al. (2013), who show the family as sister to a clade embracing *Ixioliriaceae*, *Tecophilaeaceae* and *Iridaceae* (all without succulence).

Succulence is modest and is most pronounced at and near the leaf bases, which, according to Clifford (1998), primarily store starch. The species of the family have considerable horticultural potential.

[Editorial note: The texts for this family, genus and species for ed. 1 were authored by P. I. Forster, and have been updated for this revised edition by the editor, as shown in the individual authorship attributions.]

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## References

- Chen, S. [ & al. 2013], Kim, D. K., Chase, M. W. & Kim, J. H. (2013) Networks in a large-scale phylogenetic analysis: Reconstructing evolutionary history of *Asparagales* (*Lilianaes*) based on four plastid genes. *PLoS One* 8(3): 1–18, ills. <https://doi.org/10.1371/journal.pone.0059472>
- Clifford, H. T. (1998) *Doryanthaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 236–238, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_29](https://doi.org/10.1007/978-3-662-03533-7_29)
- Goldblatt, P. [ & al. 2008], Rodriguez, A., Powell, M. P., Davies, T. J., Manning, J. C., van der Bank, M. & Savolainen, V. (2008) *Iridaceae* ‘out of Australasia’? Phylogeny, biogeography, and divergence time based on plastid DNA sequences. *Syst. Bot.* 33(3): 495–508. <https://doi.org/10.1600/036364408785679806>
- Pedley, L. (1986) *Cordylinae. Doryanthes*. In: George, A. S. (ed.): *Flora of Australia*, 46: 81–88. Canberra (AU): Australian Government Publishing Service.
- Seberg, O. [ & al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the *Asparagales* based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99 (5): 875–889, ills. <https://doi.org/10.3732/ajb.1100468>



# Doryanthes DORYANTHACEAE

P. I. Forster

**Doryanthes** M. P. Corrêa (Trans. Linn. Soc. London 6: 211, 1802). **Type:** *Doryanthes excelsa* M. P. Corrêa. — **Lit:** Pedley (1986: flora Australia). **Etym:** Gr. ‘dory’, wood, trunk, lance, spear; and Gr. ‘anthos’, flower.

Description as for the family.

**D. excelsa** M. P. Corrêa (Trans. Linn. Soc. London 6: 211, 1802). **Type:** Australia, New South Wales (*Bass* s.n. [not traced]). — **Lit:** Dimech & al. (2009: population diversity). **Distr:** Australia (E New South Wales); sclerophyllous *Eucalyptus* forests near the coast, mostly sandy soils. **I:** Elliot & Jones (1984: 330); Kapitany (2007: 132–133); Delange (2008).

**Incl.** *Furcraea australis* Haworth (1812) ≡ *Agave australis* (Haworth) Steudel (1821).

**Ros** to 2 m tall and 4 m Ø; **L** numerous, spreading and recurved, ensiform, 1.5–2.5 m × 8–10 cm, tip 6–7 × 0.7–1.5 cm, brown; **Inf** peduncle 3–5 m; **Fl** 100–160 × 15–20 mm Ø, red, pink-red, or white; **Ped** 40–50 mm; **Sep** lanceolate-oblong, cucullate, 60–120 × 6–9 mm; **Pet** lanceolate-oblong, 60–120 × 6–9 mm, recurved; **Fil** 54–72 mm; **Fr** 45–50 mm Ø; **Se** 15–23 × 12–13 mm.

Widely cultivated in gardens and parks in Australia and elsewhere in temperate climates. Vernacular names (Australia): “Gynea Lily”, “Giant Lily”.

The species is increasingly valued in the floricultural industry as a promising cut-flower export crop (Burchett & al. 1989), and a tissue culture protocol was established for large-scale propagation (Dimech & al. 2007). Populations show considerable genetic variability mirroring geographical distances (Dimech & al. 2009). — [P. I. Forster & U. Eggli]

**D. palmeri** W. Hill ex Bentham (Fl. Austral. 6: 452–453, 1873). **Type** [syn]: Australia, Queensland (*Hill* s.n. [K]). — **Distr:** Australia (SE Queensland, NE New South Wales); exposed rock outcrops. **I:** Pedley (1986: 87); Forster (1995); Kapitany (2007: 134–135); Delange (2008). – Fig. 1.

≡ *Doryanthes excelsa* var. *palmeri* (W. Hill ex Bentham) F. M. Bailey (1883); **incl.** *Doryanthes larkinii* C. Moore (1885) ≡ *Doryanthes palmeri* var. *larkinii* (C. Moore) C. Moore & E. Betche (1893); **incl.** *Doryanthes guilfoylei* F. M. Bailey (1893) ≡ *Doryanthes excelsa* var. *guilfoylei* (F. M. Bailey) F. M. Bailey (1902).

**Ros** to 2.5 m tall and 3 m Ø; **L** numerous, spreading and recurved, ensiform, 2–3 m ×

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**Fig. 1** *Doryanthes palmeri*. (Copyright: P. I. Forster)

15–20 cm, tip acuminate-tubular, 8–12 × 1.5–3 cm, brown; **Inf** peduncle 2–5 m; **Fl** 50–55 × 40–50 mm Ø, scarlet-red to red-brown; **Ped** 50–57 mm; **Sep** lanceolate-oblong, cucullate, 58–62 × 14–15 mm;

**Pet** lanceolate-ovate, 50–53 × 14–15 mm, erect to slightly spreading; **Fil** 25–35 mm; **Fr** 50–60 mm Ø; **Se** 15–17 × 10–11 mm wide.

Occasionally cultivated in gardens and parks, esp. in Australia. Vernacular name (Australia): “Spear Lily”.

## References

- Burchett, M. [& al. 1989], Nash, S. & Richardson, S. (1989) *Doryanthes excelsa* as a commercial crop. *Austral. Hort.* 87(3): 36–39.
- Delange, Y. (2008) *Chronique australienne*. 2. Les *Doryanthes*. *Succulentas* 2008(3): 28–32, ill.
- Dimech, A. M. [& al. 2007], Cross, R., Ford, R. & Taylor, P. W. J. (2007) Micropropagation of Gynea Lily (*Doryanthes excelsa* Corrêa) from New South Wales, Australia.. *Pl. Cell Tissue Organ Cult.* 88(2): 157–165. <https://doi.org/10.1007/s11240-006-9184-1>
- Dimech, A. M. [& al. 2009], Ades, P. K., Taylor, P. W. J., Cross, R. & Ford, R. (2009) Population diversity of *Doryanthes excelsa* (*Doryanthaceae*) in eastern Australia. *Cunninghamia* 11(2): 213–219.
- Elliot, W. R. & Jones, D. L. (1984) *Encyclopaedia of Australian plants suitable for cultivation*. Vol. 3. Melbourne etc. (AU): Lothian Publ. Co.
- Forster, P. I. (1995) *Doryanthes palmeri* (*Doryanthaceae*): The Australian “Spear Lily”. *Cact. Succ. J. (US)* 67(6): 342–346, ill., map.
- Kapitany, A. (2007) *Australian succulent plants. An introduction*. Boronia (AU): Published by the author.
- Pedley, L. (1986) *Cordylina. Doryanthes*. In: George, A. S. (ed.): *Flora of Australia*, 46: 81–88. Canberra (AU): Australian Government Publishing Service.

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**Part XII**

**The Family Eriospermaceae**





## Eriospermaceae

E. Van Jaarsveld and U. Eggli

Perennial geophytes with solitary or stoloniferous tubers; tubers hypocotyledonary, very variable in size and shape, globose to oblong with one to several apical or lateral to basal growing points, tissue white to red; **L** synanthous or hysteroanthous, usually solitary, deciduous, petiole persistent forming a sheath through which the next season's leaf appears, lamina flat, ovate to linear, smooth, hairy or with finger-like outgrowths or dissected appendages on the upper surface; **Inf** a simple raceme, usually appearing during summer or autumn; peduncle erect, without or with minute **Bra**; **Fl** pedicellate, actinomorphic, rotate to campanulate, diurnal; **Tep** and **St** 3+3 in 2 whorls; **Tep** somewhat connate basally, white, pink or yellow; **St** basally adnate to the tepals; **Fil** filiform to lanceolate; **Anth** dorsifixed, peltate, introrse, dehiscent longitudinally; **Ov** superior, globose, sessile, 3-locular; ovules few, placentation axillary; **Sty** terete; **Sti** 3-lobed; **Fr** oblong to ovate loculicidal capsules; **Se** few (to 12), pear- to comma-shaped, densely pilose with 1-celled white **Ha**.

**Order:** Asparagales

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**Important Literature:** Dahlgren & al. (1985: 168–170, synopsis); Perry & Rudall (1998: synopsis).

**Distribution:** Africa S of the Sahara, with a concentration in the Succulent Karoo regions of the Western Cape (RSA).

*Eriospermum* (102 species) is the only genus of this monotypic family. Its affiliation in traditional classifications was, despite the presence of tubers rather than bulbs, thought to be with *Liliaceae*, where it was placed in a separate subtribe *Eriosperminae* of *Asphodeloideae* – *Asphodeleae* by Krause (1930: 290–292), or regarded as part of tribe *Bowieae* by Hutchinson (1959), i.e. in close relationship with *Bowiea* and the unrelated former genus *Schizobasis* (now part of *Drimia*) (Hyacinthaceae) — perhaps based on the essentially leafless *Eriospermum aphyllum* with a similar inflorescence serving as the only photosynthetic organ in mature plants.

APG (2003) proposed to place *Eriospermaceae* in a much expanded *Asparagaceae*, and this position was reinforced by APG (2009). A position close to *Ruscaceae* s.l. (including the former *Dracaenaceae*) has been corroborated by several molecular phylogenies (Bogler & al. 2006, Givnish & al. 2006, Graham & al. 2006), and Kim & al. (2010) found good support for a position as basal sister to *Ruscaceae* s.l. Neither the very broad concept of *Asparagaceae*, nor the inclusion in the expanded *Ruscaceae* is satisfactory or results

in a phylogenetically more correct classification (Nyffeler & Eggli 2010), and for these reasons, we continue to accept *Eriospermaceae* as distinct family. This is in line with Seberg & al. (2012) who found the *Ruscaceae* s.l. to be one of the most weakly supported areas in their phylogenetic analyses.

*Eriospermaceae* differ consistently from *Asparagaceae* s.s. and *Ruscaceae* s.l. in their herbaceous habit and the capsular fruits, and the combination of herbaceous growth and underground storage tubers is diagnostic.

## References

- APG (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399–436. <https://doi.org/10.1046/j.1095-8339.2003.t01-1-00158.x>
- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- Bogler, D. J. [& al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on *ndhF*, *rbcL*, and its sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 313–328. <https://doi.org/10.5642/aliso.20062201.26>
- Dahlgren, R. M. T. [& al. 1985], Clifford, H. T. & Yeo, P. F. (1985) *The families of the Monocotyledons. Structure, evolution, and taxonomy*. Berlin, Heidelberg (DE) etc.: Springer-Verlag. <https://doi.org/10.1007/978-3-642-61663-1>
- Givnish, T. J. [& al. 2006], Pires, J. C., Graham, S. W., McPherson, M. A., Prince, L. M., Patterson, T. B., Rai, H. S., Roalson, E. H., Evans, T. M., Hahn, W. J., Millam, K. C., Meerow, A. W., Molvray, M., Kores, P. J., O'Brien, H. E., Hall, J. C., Kress, W. J. & Sytsma, K. J. (2006) Phylogenetic relationship of *Monocots* based on the highly informative plastid gene *ndhF*: Evidence for widespread concerted convergence. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 28–51. <https://doi.org/10.5642/aliso.20062201.26>
- Graham, S. W. [& al. 2006], Zgurski, J. M., McPherson, M. A., Cherniawsky, D. M., Saarela, J. M., Horne, E. F. C., Smith, S. Y., Wong, W. A., O'Brien, H. E., Biron, V. L., Pires, J. C., Olmstead, R. G., Chase, M. W. & Rai, H. S. (2006) Robust inference of *Monocot* deep phylogeny using an expanded multigene plastid data set. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 3–21. <https://doi.org/10.5642/aliso.20062201.02>
- Hutchinson, J. (1959) *The families of flowering plants. Volume 2, Monocotyledons*. Oxford (GB): Clarendon Press.
- Kim, J.-H. [& al. 2010], Kim, D.-K., Forest, F., Fay, M. F. & Chase, M. W. (2010) Molecular phylogenetics of *Ruscaceae sensu lato* and related families (Asparagales) based on plastid and nuclear DNA sequences. *Ann. Bot. (Oxford)*, n.s. 106: 775–790. <https://doi.org/10.1093/aob/mcq167>
- Krause, K. (1930) *Liliaceae*. In: Engler, A. & Prantl, K. (eds.): *Die natürlichen Pflanzenfamilien*, ed. 2, 15a: 227–385, key, ills. Leipzig (DE): W. Engelmann.
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>
- Perry, P. L. & Rudall, P. J. (1998) *Eriospermaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 241–244, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_31](https://doi.org/10.1007/978-3-662-03533-7_31)
- Seberg, O. [& al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the *Asparagales* based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ills. <https://doi.org/10.3732/ajb.1100468>





## Eriospermum ERIOSPERMACEAE

E. Van Jaarsveld

**Eriospermum** Jacquin *ex* Willdenow (Spec. Pl. 2 (1): 110, 1799). **Type:** *Eriospermum lanceifolium* Jacquin *ex* Willdenow [lectotype, designated by Phillips, Gen. South Afr. Pl., ed. 2, 115, 1951]. — **Lit:** Perry (1994: monograph). **Distr:** Africa S of the Sahara with a diversity centre in the Western Cape (RSA). **Etym:** Gr. ‘erion’, wool; and Gr. ‘sperma’, seed; for the hairy seeds.

**Incl.** *Phylloglottis* Salisbury (1866). **Type:** *Eriospermum folioliferum* Andrews.

**Incl.** *Thaumaza* Salisbury (1866). **Type:** *Ornithogalum paradoxum* Jacquin.

Description as for the family.

The monogeneric family *Eriospermaceae* is confined to Africa S of the Sahara and shows centres of endemism in the semi-arid winter-rainfall regions of the Western Cape, RSA. Species of *Eriospermum* are  $\pm$  easily cultivated from tubers, known as “Bobbejaanui” [Baboon’s Onion] in South Africa. The tubers are eaten by various animals, including porcupines and rodents. The genus embraces 102 species, classified into 3 subgenera (and a total of 9 sections, not shown here) by Perry (1994):

- [1] Subgen. *Ligulatum* P. L. Perry 1994: **Tep** all alike or almost so, spreading to recurved and ligulate; **Fil** filiform; tuber globose or irregularly shaped (31 species, mainly from tropical and subtropical Africa).
- [2] Subgen. *Cyathiflorum* P. L. Perry 1994: **Tep** all alike or almost so, **Fl** rotate or cup-shaped; tuber irregularly shaped (17 species, widespread but more common in summer-rainfall regions of RSA, reaching Malawi and Tanzania in the N).
- [3] Subgen. *Eriospermum*: **Tep** dimorphic; tuber irregularly shaped with lateral to basal growing point (54 species, mainly in the winter-rainfall regions of the Western Cape).

In addition to the characters cited, the colour of the internal tissue of the tubers is of diagnostic value. Vosa & Perry (1999) found chromosome numbers varying from  $x = 5$  to  $x = 10$  and postulated  $x = 7$  as basal number for the genus. Karyotype data shows limited congruence with the infrageneric classification outlined above.

Because of the  $\pm$  succulent tubers present in most taxa, most *Eriospermum* species could be included here. Some species with peculiar succulent

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leaf appendages are particularly attractive and worthy of cultivation (in small containers). Since none are frequently seen in cultivation, the following few taxa must be sufficient as examples. Opel & Hammer (2001), Wagner (2005), and Wagner (2006) provided overviews of the general biology of the genus and illustrate a selection of species.

**E. armianum** P. L. Perry (Contr. Bolus Herb. 17: 238, Fig. 139, 1994). **Type:** RSA, Northern Cape (Mitchell 1179 [NBSG]). — **Distr:** RSA (Northern Cape: Namaqualand escarpment); Succulent Karoo vegetation in quartz-gravel flats.

[3] Tuber irregular-globose, 2.8 × 2.2 cm; **L** hysteranthous (in winter in habitat), solitary, erect, petiole 1.2–1.5 cm, lamina cordate, 1.8 × 1.2 cm, striate, glaucous, base of upper surface with terete linear club-shaped outgrowths to 1.5 cm, glaucous, base subpeltate, apex obtuse; **Inf** to 10 cm; **Ped** to 1 cm; **Fl** ascending, white with green midveins, to 13 mm Ø; **OTep** oblong oblanceolate, 7 × 2 mm; **ITep** widening to apex, 5.5 × 1.6 mm; **Fil** ovate to triangular-oblong; **Ov** ovoid, 2 mm Ø; **Sty** 1.8 mm.

**E. bowieanum** Baker (J. Linn. Soc., Bot. 15: 267, 1876). **Type:** RSA, Western Cape (Bowie s.n. [K [lecto – icono]]). — **Distr:** RSA (Western Cape: Robertson Karoo); semi-arid regions, autumn-flowering.

**Incl.** *Eriospermum coralliferum* Marloth (1929).

[3] Tuber irregular-globose, 5.5 × 3.8 cm; **L** hysteranthous, solitary, erect, petiole to 4 cm, lamina cordate, 1 × 1 cm, glaucous, base of upper surface with terete linear club-shaped outgrowths to 5 cm, base subpeltate, apex recurved; **Inf** to 3 cm, densely flowered, spicate; **Ped** to 2.5 cm; **Fl** spreading, to 7 mm Ø; **Tep** white with green midvein; **OTep** lanceolate, 5 × 1.8 mm; **ITep** widening to apex, 4 × 2.3 mm; **Fil** lanceolate; **Ov** globose, 1.3 mm Ø; **Sty** 1.5 mm.

**E. paradoxum** (Jacquin) Ker Gawler (Curtis's Bot. Mag. 1811: t. 1382, 1811). **Type:** [lecto —

icono]; Jacquin, Collectanea 5: t. 1, 1796. — **Distr:** RSA (Northern Cape, Western Cape, W Eastern Cape); semi-arid Renosterveld and Succulent Karoo vegetations, winter-rainfall regions, autumn-flowering.

≡ *Ornithogalum paradoxum* Jacquin (1797) ≡ *Thaumaza paradoxa* (Jacquin) Salisbury (1866); **incl.** *Eriospermum cylindricum* Marloth (1929); **incl.** *Eriospermum arenicola* Von Poellnitz (1943); **incl.** *Eriospermum vallisgratiae* Schlechter ex Von Poellnitz (1944).

[1] Tuber oblong, to 5 × 2.5 cm; **L** hysteranthous, solitary, erect, ovate-cordate, 7 × 6 mm, adaxial surface hairy with central-stemmed erect oblong tree-like branched appendage 11 × 3 cm; **Inf** dense, conical in outline, 9 × 3.5 cm; **Ped** to 6 mm; **Fl** spreading, to 17 mm Ø; **Tep** white with green midvein; **OTep** loriate, 12 × 2 mm; **ITep** linear-spatulate, to 10 × 2.5 mm; **Fil** 9 × 1 mm; **Ov** globose, 2 mm Ø; **Sty** to 6 mm, white.

**E. strachaniae** Van Jaarsveld (Aloe 48(3): 52–53, ills., 2011). **Type:** Namibia (Van Jaarsveld & al. 21,045 [WIND]). — **Distr:** S Namibia (Lüderitz: Hunsberg); dolomite cliffs, Succulent Karoo vegetation, autumn-flowering.

[2] Tuber first globose, 1.5–3 cm Ø, proliferating and forming small clusters; **R** white, fleshy, tapering, 2.5 mm Ø at the base; **L** appearing towards the end of April after flowering, 1–3 from the top of the tuber, flattened on the ground, orbicular and deeply cordate, 1.5–2.5 × 1.8–2.5 cm, sometimes basally produced on erect leaf sheaths 0.5–1 cm long, dark green, glabrous, fleshy, lower surface paler, apex obtuse; **Inf** erect, 5.5–10 cm, raceme triangular, laxly 6- to 12-flowered, 4.5–6 × 3.5–4.5 cm; **Bra** triangular-subulate, 0.7 mm, appressed to the pedicels, light green; **Ped** arcuate-ascending, the lower 10 mm; **Fl** small, to 10 mm Ø; **Tep** yellowish with greenish midvein, oblanceolate, spreading, 5 × 1.5 mm; **Fil** flat, tapering towards the apex; **Ov** tapering, grooved, yellow, 4 × 1.2 mm; **Sty** 0.6 mm, yellowish.

**E. titanopsoides** P. L. Perry (Contr. Bolus Herb. 17: 281, Fig. 163, 1994). **Type:** RSA,

Western Cape (*Bruyns* 3151 [NBG]). — **Distr:** RSA (Western Cape: Knersvlakte); Succulent Karoo vegetation in quartz gravel flats. **I:** Desmet (2000); Opel & Hammer (2001).

[3] Tuber oblong, to  $1.5 \times 1$  cm; **L** hysteroanthous (in winter in habitat), solitary, prostrate, ovate, lamina  $0.9 \times 0.5$  cm, folded, succulent, glaucous, margin conspicuously undulate and wrinkled, epidermis papillate, base subpeltate, apex obtuse; **Inf** 2.5 cm; **Ped** to 12 mm; **Fl** ascending, to 9 mm  $\varnothing$ ; **Tep** white with green midvein; **OTep** elliptic,  $5 \times 1.5$  mm; **ITep** widening to the apex,  $5 \times 2$  mm; **Fil** ovate to triangular-oblong; **Ov** ovoid, 2 mm  $\varnothing$ ; **Sty** to 1.8 mm.

## References

- Desmet, P. (2000) Namaqualand. Journey of discovery. *Veld Fl.* (1975+) 86(2): 62–66, ills.
- Opel, M. R. & Hammer, S. (2001) Elusive *Eriospermum*s. *Cact. Succ. J. (US)* 73(4): 187–193, ills.
- Perry, P. L. (1994) A revision of the genus *Eriospermum* (*Eriospermaceae*). *Contr. Bolus Herb.* 17: 320 pp., maps, ills., key.
- Vosa, C. G. & Perry, P. L. (1999) On the cytotaxonomy of the genus *Eriospermum* Jacq. ex Willd. (*Eriospermaceae*). *Caryologia* 52(3–4): 117–125, ills. <https://doi.org/10.1080/00087114.1998.10589161>.
- Wagner, G. F. (2005) Seltsame *Eriospermum*-Species aus dem westlichen Südafrika. *Avonia* 23(1): 1–7, ills.
- Wagner, G. F. (2006) Seltsame *Eriospermum*-Species aus dem westlichen Südafrika (2). *Avonia* 24(1): 1–7, ills.



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**Part XIII**

**The Family Hyacinthaceae**







# Hyacinthaceae

E. Van Jaarsveld and U. Eggli

**Including** *Eucomidaceae* Salisbury.

**Including** *Lachenaliaceae* Salisbury.

**Including** *Ornithogalaceae* Salisbury.

**Including** *Scillaceae* Vest.

Perennial bulbous herbs, rarely rhizomatous, bulbs geophytic or rarely above-ground, bulb scales rarely separate from each other and strongly succulent; **R** fleshy, contractile, rarely thickened storage roots (*Ledebouria* p.p.); **L** basal, numerous or few or rarely solitary, rarely early deciduous, rarely absent in adult plants (*Bowiea*, *Drimia* p.p. [former *Schizobasis*]), lamina linear to oblong, mostly flat, strap-shaped, occasionally softly succulent, sometimes broadly ovate or tapering; **Inf** racemose, paniculate or spicate, rarely climbing if the only assimilating organ of the plant, bracteate; **Ped** not articulated; **Fl** bisexual, actinomorphic or rarely zygomorphic (*Lachenalia* p.p.), 3-merous; **Tep** in 2 whorls of 3, free or basally connate, sometimes forming a tube, often white but colour variable; **St** 6 but sometimes only 3 fertile, free or often basally adnate to the tepals; **Fil** flat, often lanceolate; **Anth** dorsifixed,

introrse, dehiscent longitudinally or rarely with an apical pore (*Drimia* p.p. [*Sagittanthera*]); **Ov** superior (semi-inferior in *Bowiea*), 3-locular; ovules few, placentation axillary; **Sty** terete; **Fr** loculicidal capsules; **Se** variable, often ovoid to orbicular, sometimes winged.

**Order:** Asparagales

**Important Literature:** Dahlgren & al. (1985: 168–170, synopsis); Speta (1998a: synopsis); Pfosser & al. (2003: phylogeny); Manning & al. (2004: classification); Manning & al. (2009: phylogeny & classification); Martínez-Azorín & al. (2011a: phylogeny & classification); Lebrun & Stork (2014: 63–104, synopsis tropical Africa).

**Distribution:** Africa, Mediterranean to Europe, SW, C and E Asia, South America, but concentrated in RSA.

A large family belonging to the core Asparagales, with some 920 species in 45 (–70?) genera, with a concentration of diversity in the winter rainfall regions of RSA. APG (2009) and Chase & al. (2009) included *Hyacinthaceae* as subfamily *Scilloideae* in a much broadened concept of *Asparagaceae*, but the resulting classification is phylogenetically not more correct than the traditional circumscriptions of *Hyacinthaceae* and other families (Nyffeler & Eggli 2010), and the traditional concepts are therefore retained here, which is congruent, e.g., with the textbook of Judd & al. (2016).

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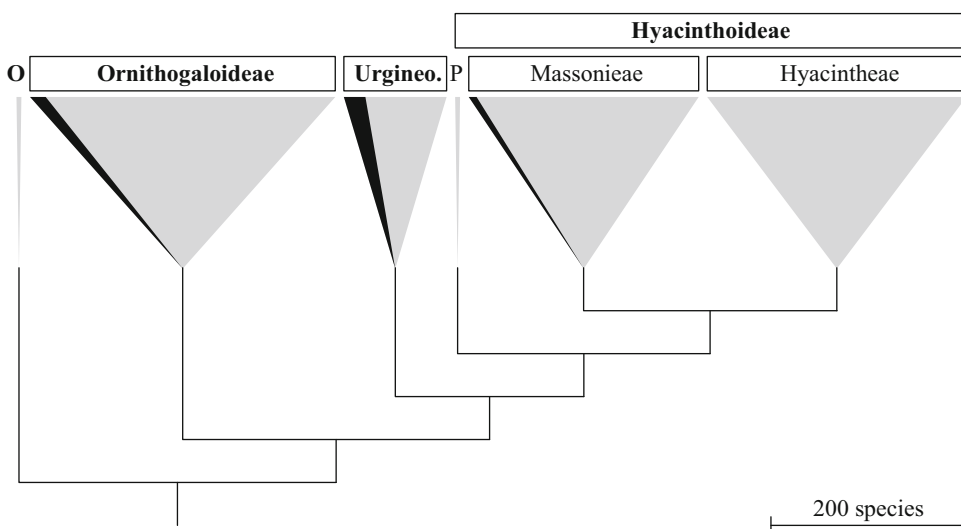
The family occupies a position between the more basal *Asparagaceae* s.s. and the highly derived *Agavaceae* and *Anthericaceae*.

**Classification:** Speta (1998a) divides the family in 5 subfamilies, of which the *Chlorogaloideae* (4 genera, 17 species, New World only, no succulents) have since been removed to *Agavaceae* s.l. Of the remaining subfamilies, *Oziroeoideae* (*Oziroë* only, 5 species, S America, no succulents) is sister to the three more speciose subfamilies *Ornithogaloideae*, *Urgineoideae* and *Hyacinthoideae* (Manning & al. 2004; Pfosser 2007; Ali & al. 2012). These 3 subfamilies have a “bimodal” distribution pattern, involving primary centres of diversity in sub-Saharan Africa, and a secondary centre in the Mediterranean (Pfosser 2007; Ali & al. 2012) (Fig. 1). The origin of the family as a whole is postulated to have been in sub-Saharan Africa with early dispersal events to the Mediterranean region and subsequent further dispersal events and radiations (Pfosser 2007; Ali & al. 2012). Its biogeography and radiation thus conforms to an “out of Africa” scenario. Pfosser (2007: 384) hypothesizes that long-distance dispersals are unlikely, and that the present distribution patterns should be explained by vicariance events.

The break-down of the family into numerous small genera by Speta (1998a) and Speta (1998b) has met with considerable criticism in two closely similar contributions by Stedje (2001) and Stedje (2002), and this author especially notes that the two classifications proposed by Speta in 1998 are not completely identical. Stedje (l.c.) argues for broad circumscriptions of genera such as *Drimia*, *Ornithogalum* or *Scilla*, and this is the classification preferred for this handbook.

The subfamilies are characterized as follows:

- *Oziroeoideae* Speta 1998: **Fl** often 2 (–3) from each bract; **Sti** inconspicuous; **Se** pyriform.
- *Urgineoideae* Speta 1998: Floral **Bra** conspicuously spurred; **Se** flat or winged with fragile, loosely adhering testa. In addition, the subfamily is also diagnostically characterized by the presence of bufadienolides (a group of cardiac-active steroidal glycosides) (Pfosser & Speta 2001).
- *Ornithogaloideae* Speta 1998: **Sti** 3-lobed to capitate; **Se** flat to angular with firmly adhering testa. The subfamily is chemically characterized by the presence of cardenolides (Pfosser & Speta 2004: 246).



**Fig. 1** Summary phylogeny of *Hyacinthaceae* based on Manning (2004) and Ali & al. 2012 (922 species total). O = *Oziroeoideae*, P = *Pseudoprosperae*, Urgineo. = *Urgineoideae*. (Copyright: U. Eggli)

- *Hyacinthoideae*: **Sti** feathery; **Se** ellipsoid to globose or pyriform. Some additional seed characters are potentially useful to delimit genera or groups of genera (Jessop 1975; Pfosser & al. 2003), but the sampling is inadequate for a complete picture. According to the study of Lynch & al. (2006), the presence of mucilage is possibly a synapomorphy for the subfamily, and mucilage is esp. prevalent in the genera of tribe *Massonieae*. Chemically, this subfamily is characterized by the presence of homoisoflavonones (Pfosser & Speta 2004: 246).

The taxonomy of the *Ornithogaloideae* is in continued dispute, and different authors arrive at incompatible classifications: Speta (1998a) recognized no less than 14 genera for the subfamily (and was criticized for this by Stedje (2002)), while Manning & al. (2004) proposed significant lumping, esp. resulting in a much enlarged *Ornithogalum* s.l. These radical approaches appear unsatisfactory, and with increased molecular sampling, Manning & al. (2009) concluded that the four genera *Albuca*, *Dipcadi*, *Ornithogalum* and *Pseudogaltonia* should be recognized in this basically African subfamily. These authors subdivided the subfamily into tribes *Albuceae* (monogeneric), *Dipcadieae* and *Ornithogaleae* (monogeneric). Martínez-Azorín & al. (2011a) also accept these 3 tribes, but according to their phylogeny, no less than 19 genera should be accepted. Here, we follow the classification proposed by Manning & al. (2009), which is also supported e.g., by Buerki & al. (2012).

Subfamily *Hyacinthoideae* is divided into 3 tribes by Ali & al. (2012), of which only the *Massonieae* have succulent representatives. Müller-Doblies & Müller-Doblies (1997) propose to subdivide the *Massonieae* into 3 separate subtribes *Lachenaliinae*, *Ledebouriinae* and *Massoniinae*.

**Succulence:** Succulence is notoriously difficult to define for bulbous plants, and arguably, geophytic bulbs of taxa from semi-arid and arid sites exhibit some degree of water storage, which allows flowering towards the end of the dry season. Volkens (1887: 145) found that the fleshy tunics of the bulbs of several species of *Ornithogalum* and *Drimia* store mainly water,

rather than starch. The bulb scales of the widespread Mediterranean *Drimia maritima* are formed by abundant large-celled parenchyma with scattered mucilage cells, and the stored water is used to produce the inflorescence in the autumn near the end of the dry season, while foliage leaves are produced in response to seasonal rain (Al-Tardeh & al. 2008).

In some species, the grossly enlarged scales of the above-ground or semi-underground bulbs are almost or completely separate from each other, and this is a special case of leaf succulence where water storage is not in the main photosynthetically active leaf part (e.g., *Drimia haworthioides*, *D. mzimvubuensis*). A small number of species has evolved truly succulent deciduous leaves (e.g., *Ornithogalum naviculum*, *Albuca unifoliata*) and ecologically resemble some species of *Bulbine* (*Asphodelaceae*).

Species of *Bowiea* and *Drimia* p.p. (former *Schizobasis*) do not produce foliage leaves once they have reached maturity, and the bulbs (above-ground or semi-underground) are strongly succulent, covered by thin translucent outer tunics to allow some photosynthesis. *Bowiea* species in addition have somewhat succulent inflorescence axes and branches and thus weakly qualify as a special form of stem succulents.

**Ethnobotany:** *Drimia maritima* is used against dropsy since earliest times, and scattered species of *Albuca* and *Ledebouria* are known to have local ethnobotanical uses. Several species of S African genera are known to be poisonous to grazing cattle, esp. species of *Ledebouria*, while a couple of other taxa have edible bulbs (Speta 1998a).

**Horticulture:** Several genera have considerable horticultural importance, e.g., *Ornithogalum*, *Hyacinthus*, *Lachenalia*, *Veltheimia* and *Eucomis*, and species of *Hyacinthoides* and *Muscari* are popular hardy spring-flowering bulbs in N hemisphere gardens. Some species of *Ornithogalum* are popular in the cut-flower trade. Succulents from several genera are occasionally cultivated; most of these are from the semi-arid winter-rainfall regions of RSA and should be kept dry during summer. Most are readily propagated from seeds or daughter bulbs, some also from bulb scales.

**Key to genera with succulents (adopted from Dyer 1975–1976)**

<b>1a</b>	Adult plants without <b>L</b> ; <b>Inf</b> erect or twining, richly branched, green	2
<b>1b</b>	Adult plants with <b>L</b> in various shapes; <b>Inf</b> racemes or capitate	3
<b>2a</b>	<b>Inf</b> twining-climbing, succulent	<i>Bowiea</i>
<b>2b</b>	<b>Inf</b> erect, wiry-sturdy to wiry-filiform	<i>Drimia</i> ( <i>Schizobasis</i> )
<b>3a</b>	Lower <b>Bra</b> spurred, early deciduous; <b>Fr</b> circumscissile below; <b>Se</b> flattened	4
<b>3b</b>	<b>Bra</b> not spurred, persistent; <b>Se</b> globose, angular or flat; <b>L</b> normally synanthous	8
<b>4a</b>	Plants 10–150 cm tall; <b>St</b> exerted	5
<b>4b</b>	Plants to 6 cm tall; <b>Fl</b> solitary; <b>St</b> not exerted	<i>Drimia</i> ( <i>Litanthus</i> )
<b>5a</b>	<b>Tep</b> usually free or fused only near the base; <b>St</b> spreading	<i>Drimia</i> ( <i>Urginea</i> )
<b>5b</b>	<b>Tep</b> usually fused and forming a tube	6
<b>6a</b>	<b>Tep</b> lobes reflexed	<i>Drimia s.s.</i>
<b>6b</b>	<b>Tep</b> lobes spreading and <b>Fl</b> campanulate	7
<b>7a</b>	<b>Tep</b> lobes fused for ½ of their length, thin-textured	<i>Drimia</i> ( <i>Rhadamanthus</i> )
<b>7b</b>	<b>Tep</b> lobes fused for > ⅓ of their length, ± thick-textured	<i>Drimia</i> ( <i>Rhodocodon</i> )
<b>8a</b>	<b>Tep</b> free or fused only near the base; <b>Fl</b> neither tubular nor campanulate	9
<b>8b</b>	<b>Tep</b> distinctly fused; <b>Fl</b> tubular or campanulate; <b>L</b> in <b>Ros</b> or only 2 large basal <b>L</b>	11
<b>9a</b>	<b>OTep</b> spreading, <b>ITep</b> erect and cucullate; <b>St</b> often 3 fertile and 3 sterile	<i>Albuca</i>
<b>9b</b>	All <b>Tep</b> spreading	10
<b>10a</b>	<b>Inf</b> apparently terminal; ovules many; <b>L</b> always unspotted	<i>Ornithogalum</i>
<b>10b</b>	<b>Inf</b> axillary; <b>Tep</b> tips reflexed; ovules 2 per locule; <b>L</b> often blotched with different colours	<i>Ledebouria</i>
<b>11a</b>	<b>OTep</b> shorter than <b>ITep</b> , with distinct appendage; <b>Se</b> flat, discoid	<i>Dipcadi</i>
<b>11b</b>	If <b>OTep</b> shorter than <b>ITep</b> then without appendage; <b>Se</b> globose to pear-shaped	12
<b>12a</b>	Upper <b>Fl</b> of each <b>Inf</b> rudimentary; <b>OTep</b> shorter than the <b>ITep</b>	<i>Lachenalia</i>
<b>12b</b>	Upper <b>Fl</b> normally developed; all <b>Tep</b> of ± the same length; <b>L</b> usually only 2	13
<b>13a</b>	<b>Inf</b> racemose and clearly held above the leaves, with sterile <b>Bra</b> at the tip	14
<b>13b</b>	<b>Inf</b> subcapitate, ± held between the leaves, without sterile <b>Bra</b> at the tip	15
<b>14a</b>	<b>Bra</b> papillose on both faces; <b>Fl</b> subcampanulate; <b>Sty</b> straight	<i>Massonia</i> ( <i>Desertia</i> )
<b>14b</b>	<b>Bra</b> glabrous; <b>Fl</b> subrotate; <b>Sty</b> hooked	<i>Massonia</i> ( <i>Whiteheadia</i> )
<b>15a</b>	<b>Tep</b> not distinctly caudate; <b>Fr</b> exposed from the dry perianth at maturity	<i>Massonia</i>
<b>15b</b>	<b>Tep</b> distinctly caudate; <b>Fr</b> enclosed by the fleshy perianth at maturity	<i>Namophila</i>

**References**

- Al-Tardeh, S. [ & al. 2008], Sawidis, T., Diannelidis, B.-E. & Delivopoulos, S. (2008) Water content and reserve allocation patterns within the bulb of the perennial geophyte Red Squill (*Liliaceae*) in relation to the Mediterranean climate. *Botany* 86: 291–299, ills. <https://doi.org/10.1139/B07-130>
- Ali, S. S. [ & al. 2012], Yu, Y., Pfosser, M. F. & Wetschnig, W. (2012) Inferences of biogeographical histories within subfamily *Hyacinthoideae* using S-DIVA and



- Bayesian binary MCMC analysis implemented in RASP (Reconstruct Ancestral State in Phylogenies). *Ann. Bot. (Oxford)*, n.s. 109(1): 95–107, maps, keys. <https://doi.org/10.1093/aob/mcr274>
- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- Buerki, S. [ & al. 2012], Jose, S., Yadav, S. R., Goldblatt, P., Manning, J. C. & Forest, F. (2012) Contrasting biogeographic and diversification patterns in two Mediterranean-type ecosystems. *PLoS One* 7(6): e39377 (11 pp.). <https://doi.org/10.1371/journal.pone.0039377>
- Chase, M. W. [ & al. 2009], Reveal, J. L. & Fay, M. F. (2009) A subfamilial classification for the expanded Asparagalean families *Amaryllidaceae*, *Asparagaceae* and *Xanthorrhoeaceae*. *Bot. J. Linn. Soc.* 161(2): 132–136. <https://doi.org/10.1111/j.1095-8339.2009.00999.x>
- Dahlgren, R. M. T. [ & al. 1985], Clifford, H. T. & Yeo, P. F. (1985) The families of the Monocotyledons. Structure, evolution, and taxonomy. Berlin, Heidelberg (DE) etc.: Springer-Verlag. <https://doi.org/10.1007/978-3-642-61663-1>
- Dyer, R. A. (1975–1976) The genera of Southern African flowering plants. Vol. I: Dicotyledons; Vol. II: Gymnosperms and Monocotyledons. Pretoria (ZA): Department of Agricultural Technical Services.
- Jessop, J. P. (1975) Studies in the bulbous *Liliaceae* in South Africa. 5. Seed surface characters and generic groupings. *J. South Afr. Bot.* 41: 67–85.
- Judd, W. S. [ & al. 2016], Campbell, C. S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J. (2016) Plant systematics: A phylogenetic approach. Ed. 4. Sunderland (US): Sinauer Associates.
- Lebrun, J.-P. & Stork, A. L. (2014) Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (*Anthericaceae* – *Palmae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Lynch, A. H. [ & al. 2006], Rudall, P. J. & Cutler, D. F. (2006) Leaf anatomy and systematics of *Hyacinthaceae*. *Kew Bull.* 61(2): 145–159, ills. <http://www.jstor.org/stable/20443254>
- Manning, J. C. [ & al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperaeae*. *Edinburgh J. Bot.* 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>
- Manning, J. C. [ & al. 2009], Forest, F., Devey, D. S., Fay, M. F. & Goldblatt, P. (2009) A molecular phylogeny and a revised classification of *Ornithogaloideae* (*Hyacinthaceae*) based on an analysis of four plastid DNA regions. *Taxon* 58(1): 77–107, ills., key. <http://www.jstor.org/stable/27756826>
- Martínez-Azorín, M. [ & al. 2011a], Crespo, M. B., Juan, A. & Fay, M. F. (2011) Molecular phylogenetics of subfamily *Ornithogaloideae* (*Hyacinthaceae*) based on nuclear and plastid DNA regions, including a new taxonomic arrangement. *Ann. Bot. (Oxford)*, n.s. 107: 1–37, ills. key. <https://doi.org/10.1093/aob/mcq207>
- Müller-Doblies, U. & Müller-Doblies, D. (1997) A partial revision of the tribe *Massonieae* (*Hyacinthaceae*). 1. Survey, including three novelties from Namibia: A new genus, a second species in the monotypic *Whiteheadia* and a new combination in *Massonia*. *Feddes Repert.* 108(1–2): 49–96, ills., keys. <https://doi.org/10.1002/fedr.19971080106>
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>
- Pfossler, M. F. (2007) Migration durch Dispersionsverbreitung und Vikarianz bei Pflanzen — eine Analyse evolutionärer Mechanismen anhand molekularer Daten am Beispiel der Pflanzenfamilie *Hyacinthaceae*. *Denisia* 20: 379–393, maps, ills.
- Pfossler, M. F. & Speta, F. (2001) Bufadienolide und DNA-Sequenzen: Über Zusammenhalt und Aufteilung der *Urgineoideae* (*Hyacinthaceae*). *Stapfia* 75: 177–250.
- Pfossler, M. F. & Speta, F. (2004) From *Scilla* to *Charybdis* — is our voyage safer now? *Pl. Syst. Evol.* 246(3–4): 245–263, maps. <https://doi.org/10.1007/s00606-004-0153-z>
- Pfossler, M. F. [ & al. 2003], Wetschnig, W., Ungar, S. & Prenner, G. (2003) Phylogenetic relationships among genera of *Massonieae* (*Hyacinthaceae*) inferred from plastid DNA and seed morphology. *J. Pl. Res.* 116: 115–132, ills. <https://doi.org/10.1007/s10265-003-0076-8>
- Speta, F. (1998a) *Hyacinthaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 261–285, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_35](https://doi.org/10.1007/978-3-662-03533-7_35)
- Speta, F. (1998b) Systematische Analyse der Gattung *Scilla* L. (*Hyacinthaceae*). *Phyton (Horn)* 38(1): 1–141, ills.
- Stedje, B. (2001) Notes on African plants. *Hyacinthaceae*. The generic delimitation within *Hyacinthaceae*, a comment on works by F. Speta. *Bothalia* 31(2): 192–195. <https://doi.org/10.4102/abc.v31i2.519>
- Stedje, B. (2002) Generic delimitation of *Hyacinthaceae*, with special emphasis on sub-Saharan genera. *Syst. & Geogr. Pl.* 71(2): 449–454.
- Volkens, G. (1887) Die Flora der ägyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen. Berlin (DE): Gebrüder Borntraeger.



## Albuca HYACINTHACEAE

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- Albuca** Linné (Spec. Pl., ed. 2, 438, 1762). **Type:** *Albuca major* Linné [according to J. C. Manning & Goldblatt, Edinburgh J. Bot. 60: 544, 2004]. — **Ornithogaloideae—Albucaeae** — **Lit:** Müller-Doblies (1994: partial synopsis); Müller-Doblies (1995: partial synopsis); Müller-Doblies (2006: partial synopsis); **Distr:** S Africa to Arabia, centred in RSA. **Etym:** Lat. ‘albus’, “Asphodel” (*Asphodelus sp.*, from Lat. ‘albus’, white, for the white flowers); for the similarity of some species to Asphodel.
- Incl.** *Stellarioides* Medikus (1790). **Type:** *Stellarioides canaliculata* Medikus.
- Incl.** *Fenelonias* Rafinesque (1832). **Type:** *Ornithogalum bracteatum* Thunberg.
- Incl.** *Coilonox* Rafinesque (1837). **Type:** *Anthericum albucoides* Aiton.
- Incl.** *Tomoxis* Rafinesque (1837). **Type:** *Ornithogalum virens* Lindley [lectotype, designated by Speta, Stapfia 75: 173, 2001].
- Incl.** *Trimelopter* Rafinesque (1837). **Type:** *Ornithogalum fuscatum* Jacquin.
- Incl.** *Adernia* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum fuscatum* Jacquin.
- Incl.** *Ardernia* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum fuscatum* Jacquin.
- [type according to Manning & al., Taxon 58: 92, 2009].
- Incl.** *Branciona* Salisbury (1866). **Type:** *Albuca setosa* Jacquin.
- Incl.** *Falconera* Salisbury (1866). **Type:** *Albuca viscosa* Linné *fil.* [lectotype, designated by Müller-Doblies, Feddes Repert. 106: 355, 1995].
- Incl.** *Monotassa* Salisbury (1866). **Type:** *Ornithogalum secundum* Jacquin.
- Incl.** *Osmyne* Salisbury (1866). **Type:** *Ornithogalum odoratum* Jacquin.
- Incl.** *Pallastema* Salisbury (1866). **Type:** *Albuca abyssinica* Jacquin.
- Incl.** *Taeniola* Salisbury (1866) (*nom. illeg.*, Art. 53.1). **Type:** *Albuca vittata* Ker Gawler.
- Incl.** *Urophyllon* Salisbury (1866). **Type:** *Ornithogalum caudatum* Jacquin [lectotype, designated by Speta, Stapfia 75: 173, 2001].
- Incl.** *Battandiera* Maire (1926). **Type:** *Ornithogalum amoenum* Battandier.
- Incl.** *Igidia* Speta (1998). **Type:** *Urginea volubilis* H. Perrier.

Perennial bulbous plants; bulbs variable, tunicate, underground or above-ground, mostly globose, rarely depressed, tunics fleshy, imbricate; **L** very variable, deciduous and hysteroanthous, rarely evergreen, rosulate, straight or curved or spiralling, terete to flattened; **Inf** racemose; **Bra** acuminate; **Ped** erect, variable in length; **Fl** actinomorphic, erect or drooping; **Tep** 6, fleshy,

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lorate, green, white or yellow with green to brown midstripe and 3–5 veins aggregated along the middle; **OTep** 3, free and spreading; **ITep** covering stamens and ovary and cucullate with large apical gland, or  $\pm$  stellately spreading-ascending; **St** 6, all fertile or the outer 3 sterile; **Fil** dilated at the base and covering the ovary; **Anth** introrse, versatile, oblong; **Ov** superior, 3-locular, oblong; **Sty** obconical-prismatic; **Sti** capitate or conical with 3 deltoid fimbriate lobes; **Fr** 3-locular loculicidal capsules, ovoid to trigonous; **Se** flat, black, shiny.

A genus of  $\pm$  125 species occurring in Africa and Arabia with its main centre in RSA. About 70 species are native to RSA, and are widespread in grassland, savanna, Albany Thicket, Succulent Karoo, Nama Karoo and Fynbos vegetations. A few species are cremnophytes. Many have xeromorphic features, and some are slightly to distinctly succulent. The few species covered below are horticultural curiosities sometimes cultivated. *Albuca* are easily grown from seed.

**Classification and History:** The genus is thought to have originated in S Africa. In the traditional sense, *Albuca* was easily recognized by the markedly dissimilar outer and inner tepal whorls. Based on molecular data, Manning & al. (2004) adopted a broad view of the ornithogaloid genera, and only the single genus *Ornithogalum* was recognized, relegating *Albuca* to synonymy. In a later paper, based on additional evidence, *Albuca* was again accepted at generic level, though in a redefined and enlarged circumscription (Manning & al. 2009). *Albuca* now includes *Ornithogalum* subgen. *Osmyne* and most members of *Ornithogalum* subgen. *Urophyllon*. This new view defines *Albuca* by its succulent-textured oblong tepals and a broad longitudinal central green to brown band on the adaxial side, and 3–5 veins aggregated along the middle (Manning & Goldblatt 2011).

**Infrageneric classification:** The genus has been divided into 5 subgenera, of which subgen. *Albuca* is by far the largest (Manning & al. 2009):

[1] Subgen. *Albuca*: Plants small to large, bulbs above-ground or underground; **L** 1 to several, terete to lanceolate; raceme subspicate,

racemose or corymbose; **Fl** spreading, erect or pendulous, diurnal, whitish or yellowish, fragrant; **St** whorls dimorphic, inner **Fil** constricted near the base; **Ov** with septal crests; **Sty** prismatic; **Fr** ovoid to oblong, acute to obtuse; **Se** angular, semi-lunate or discoid, colliculate. — Sub-Saharan Africa (1 species in Ethiopia), winter-rainfall regions. The subgenus can be divided into 4 sections (c. 70 species in total, of which 13 are succulent).

[2] Subgen. *Monarchos* (U. & D. Müller-Doblies) J. C. Manning & Goldblatt 2009 ( $\equiv$  *Ornithogalum* sect. *Monarchos* U. & D. Müller-Doblies 1996): **L** ovate to elliptic; racemes pyramidal; **Fl** diurnal, yellow; **Ov** with a prominent bilobed keel on each locule; **Fr** globose, prominently keeled; **Se** discoid. — Mainly from winter-rainfall arid W parts of RSA and Namibia (10 species, none succulent).

[3] Subgen. *Namibiogalum* (U. & D. Müller-Doblies) J. C. Manning & Goldblatt 2009 ( $\equiv$  *Ornithogalum* sect. *Namibiogalum* U. & D. Müller-Doblies 1996): **L** canaliculate; racemes pyramidal; **Fl** white; **Ov** stipitate; **Fr** 3-lobed, apically retuse. — This group is recognized as separate genus *Battandiera* by Martínez-Azorín & al. (2011a) and Martínez-Azorín & Crespo (2014). Mainly from the summer-rainfall E parts of RSA (11 species, of which 1 is succulent).

[4] Subgen. *Osmyne* (Salisbury) J. C. Manning & Goldblatt 2009 ( $\equiv$  *Osmyne* Salisbury 1866): Plants small to medium, bulbs underground; **L** 1 to several, terete to lanceolate; raceme subspicate to racemose; **Fl** spreading to somewhat pendent, diurnal, yellowish (rarely white), fragrant; **Fr** ovoid or oblong, acute; **Se** angular, semi-lunate, colliculate. — Winter-rainfall parts of RSA and Namibia. The subgenus can be divided in 2 sections and 2 series (29 species in total, of which 4 are succulent).

[5] Subgen. *Urophyllon* (Salisbury) J. C. Manning & Goldblatt 2009 ( $\equiv$  *Urophyllon* Salisbury 1866): Bulbs moderate to large, above-ground or underground; **L** linear to

lanceolate; raceme subspicate to narrowly cylindrical; **Fl** white; **Ov** ovoid; **Fr** subglobose; **Se** semi-lunate. — Temperate and subtropical Africa (N-wards to Ethiopia) and Madagascar (4 species, of which 2 are succulent).

**Succulence:** Most species are adapted to seasonally dry conditions, but only some exhibit distinctly succulent leaves; many others have merely somewhat fleshy leaves and are not included here.

**Ecology:** The pollination ecology of the non-succulent South African *A. canadensis* and *A. setosa* has been studied in detail by Johnson & al. (2012): Flowers are visited predominantly by megachilid (leafcutter) bees, which deposit pollen on the papillate tips of the inner tepals. The pollen germinates while still on the tepal tip, and the pollen tubes penetrate the style when the perianth is wilting. Pollen capture by the inner tepals increases the accuracy of pollen transfer.

The curly leaves of *A. spiralis* are probably an adaptation to trap water from dew and fog (Vogel & Müller-Doblies 2011).

**A. batteniana** Hilliard & B. L. Burt (Notes Roy. Bot. Gard. Edinburgh 42(2): 247–249, Fig. 1, 1985). **Type:** RSA, Eastern Cape (Hilliard & Burt 12454 [E, NU, PRE]). — **Distr:** RSA (Eastern Cape); Eastern Valley Bushveld vegetation, sheer cliff faces, flowers spring to autumn.

≡ *Ornithogalum battenianum* (Hilliard & B. L. Burt) J. C. Manning & Goldblatt (2004).

[1] Evergreen, bulbs above-ground (rarely underground), solitary, ovoid, 5 × 3 cm, tunics fleshy, truncate at the top, green; **R** fleshy, white, to 2 mm Ø; **L** 12–30 × 2–3 cm, oblong, linear-attenuate, soft, succulent, canaliculate, dark green, faintly lineate, glabrous, apex acute; **Inf** spreading to 80 cm, racemose, scape to 25 cm, basally 6–10 mm Ø; **Bra** acuminate, 4 × 1.3 cm, green with white, margin translucent; **Ped** erect, to 12 cm for the lowest flowers, becoming shorter (to 3.5 cm) further up; **Fl** erect; **Tep** white with green midstripes, oblong, cucullate; **OTep** 30–42 × 7 mm; **ITep** 25–30 × 7 mm; **Fl** 15–20 mm, white, flattened at the base; **Anth**

oblong, versatile, outer 4 × 1 mm, inner 7 × 2.5 mm; **Ov** 8–12 mm, obtusely trigonous; **Sty** 10–13 mm; **Sti** trilobate, white; **Se** flat, shiny.

An attractive, robust, evergreen species easily cultivated.

**A. bracteata** (Thunberg) J. C. Manning & Goldblatt (Taxon 58(1): 93, 2009). **Type:** RSA, Eastern Cape (Thunberg 8277 [UPS]). — **Lit:** Smith & al. (2003: as *Ornithogalum longibracteatum*). **Distr:** RSA (Eastern Cape, KwaZulu-Natal); rocky, well-drained terrain, mainly in Albany Thicket biome and Eastern Valley Bushveld vegetations (savanna biome); neophyte in Australia (Glanzign & Kessal 2004) and Spain (Roselló Gimeno & al. 2013). – Fig. 1.

≡ *Ornithogalum bracteatum* Thunberg (1794) ≡ *Fenelonina bracteata* (Thunberg) Rafinesque (1832); **incl.** *Ornithogalum longibracteatum* Jacquin (1776) ≡ *Stellarioides longibracteata* (Jacquin) Speta (2001); **incl.** *Ornithogalum caudatum* Aiton (1789) (*nom. illeg.*, Art. 53.1); **incl.** *Stellarioides canaliculata* Medikus (1790); **incl.** *Ornithogalum massonii* J. F. Gmelin (1791); **incl.** *Ornithogalum scilloides* Jacquin (1797); **incl.** *Eliokarmos caudatum* Rafinesque (1837);



**Fig. 1** *Albuca bracteata*. (Copyright: U. Eggli)



**incl.** *Urginea mouretii* Battandier & Trabut (1921).

[5] Bulbs above-ground and cluster-forming, globose, to 8 cm Ø, bulbiferous, tunics succulent, green, withering grey, exposing green live tissue; **R** white, terete, succulent; **L** synanthous, 20–100 × 2–5 cm, ascending to curving, linear, flaccidly succulent, channelled, withering from the apex; **Inf** to 1 m, racemose, densely flowered, scape terete, erect; **Bra** to 4 cm, filiform, broadening at the base; **Ped** to 5 mm (lengthening to 15 mm in fruit); **Per** stellate; **Tep** linear-elliptic, 9 × 2.5 mm, green with white margins; **Ov** globose; **Fr** trigonous, 10 × 6 mm; **Se** oblong, angular, 4 × 1.5 mm.

Frequently cultivated and colloquially known as “Pregnant Onion” or “False Sea Onion”, and in the past sometimes confused with the true “Sea Onion”, *Drimia maritima* (Speta 2001). Unfortunately, the well-known specific epithet *longibracteatum* is pre-occupied because of *Albuca longibracteata* Engler, and the next younger name (*Ornithogalum bracteatum* Thunberg) has to be taken up. Smith & al. (2003) discuss the available evidence for the often-cited toxicity of the species. At least in RSA, feeding experiments have not shown toxic effects, but toxicity is probably dependent on plant part and time of the year, and the species is reported as being toxic in Kenya. The exact distribution outside of RSA is insufficiently known (Smith & al. 2003), and reports from Mozambique and Zambia are probably due to confusion with other taxa of the genus (Lebrun & Stork 2014: 64). Material cultivated in Morocco was described as *Urginea mouretii* (Lebrun & Stork 2014: 64). Xu & al. (2000: as *Ornithogalum caudatum*) report three steroidal saponins for this species.

**A. buffelspoortensis** Van Jaarsveld (Aloe 52 (1): 15–17, ill., 2016). **Type:** RSA, Western Cape (*Van Jaarsveld* 17667 [PRE]). — **Distr:** RSA (Western Cape: Buffelspoort, Little Karoo); Succulent Karoo vegetation.

[1] Evergreen geophyte, bulbs shallow, globose, 2–3 cm, proliferating from the base, outer tunics fleshy, imbricate, truncate at the top exposing the green tissue, clasping; **R** white, 1 mm Ø,

fleshy; **L** solitary (rarely 2), linear, succulent, inrolled with margins often touching and then appearing terete, 6–15 × 0.15–0.3 cm, glabrous, green, tip terete, acute; **Inf** ascending, horizontally curved in the upper ½, 10–27 cm, scape 9–12 cm, terete, 2–3 mm Ø at the base, glaucous-green due to a waxy covering, raceme placed horizontally, 5.5–14 cm, flowers 5–18, secund; **Bra** clasping, translucent greenish-white, the lower ones 15 × 2.5 mm, linear-lanceolate, becoming shorter upwards; **Ped** 10–15 mm; **Fl** ascending; **Tep** white with a broad green midstripe; **OTep** spreading, oblong-ovate, 12 × 4 mm, obtuse, incurved, hooded, with a crest of glandular hairs; **ITep** cohering and enclosing stamens and ovary, 10 × 7 mm, oblong-ovate, tip with a yellow hood, incurved; **Fil** white, the outer 7 × 2 mm, the inner abruptly constricted, broadening to 2 mm and canalicate at the base, translucent; **Ov** 3 × 3 mm, green, grooved, 3-angled, tapering towards the base; **Sty** 4–5 × 2 mm, 3-angled, yellow, papillate; **Sti** 3-lobed, obtuse, 2 mm, green; **Fr** and **Se** not seen.

**A. clanwilliamae-gloria** U. Müller-Doblies (Feddes Repert. 105(5–8): 358, 1996). **Type:** RSA, Western Cape (*Müller-Doblies* 75062 [PRE, B, BTU, K]). — **Distr:** RSA (Western Cape: NW of Clanwilliam); in deep sand in Leipoldtville Sand Fynbos vegetation. **I:** Manning & al. (1999).

≡ *Ornithogalum clanwilliamae-gloria* (U. Müller-Doblies) J. C. Manning & Goldblatt (2004).

[1] Summer-deciduous solitary geophytes 1.2–2.5 m tall; bulbs turbinate, compressed, 3–5 cm Ø, occasionally bulbiferous, tunics white, papery; **L** 3, succulent, linear-lanceolate, 52–134 cm, involute, 12–15 mm Ø; **Inf** erect, elongate, 1.2–2.5 m, scape 5–7 mm Ø; **Bra** lanceolate-attenuate; **Ped** spreading, distally recurved, 12–22 mm, elongating to 55 mm, becoming erect in fruit; **Fl** nodding, golden-yellow; **OTep** oblong, 25–36 × 8–10 mm, apex truncate, rolled inwards, **ITep** 20–32 × 8–10 mm; **St** fertile in both whorls; **Fil** 13–22 mm; **Anth** 2.6–5 mm; inner **Fil** adnate to the tepal bases, 13–20 × 1.5 mm; **Ov** oblong-trigonous, 7–10 mm;

**Sty** cylindrical-trigonous, 10–17 mm, abruptly tapering; **Fr** erect, oblong to ovoid-trigonous, tapering, apically rounded, 20–28 × 10–15 mm; **Se** discoid, 4.5 mm.

Best grown in sandy soil and to be kept dry during summer. It has the tallest inflorescence found in the genus.

**A. cremnophila** Van Jaarsveld & A. E. van Wyk (Aloe 36(4): 72–73, ill., 2000). **Type:** RSA, Eastern Cape (*Van Jaarsveld* 12171 [NBG]). — **Distr:** RSA (Eastern Cape); Valley Bushveld vegetation, on sheer cliff faces, in summer- and winter-rainfall regions. **I:** Jaarsveld & al. (2007).

≡ *Ornithogalum cremnophilum* (Van Jaarsveld & A. E. van Wyk) J. C. Manning & Goldblatt (2004).

[1] Evergreen; bulbs above-ground (rarely underground), solitary or dividing to form small clusters, ovoid, 9 × 5–6 cm, tunics fleshy, imbricate, truncate at the top, green-grey; **R** fleshy, white, to 3 mm Ø; **L** 30–70 × 2–3 cm, linear-attenuate, firm and succulent, canaliculate, drooping, dark green, glabrous, tips acute; **Inf** pendulous, to 2 m, racemose, scape to 25 cm; **Bra** acuminate, membranous, margin translucent, lower **Bra** to 45 × 5 mm, diminishing in size further up to 15 × 3 mm; lower **Ped** 6 mm becoming shorter further up; **Fl** erect; **Tep** white with green midstripes; **OTep** linear-obovate, 20 × 8 mm; **ITep** ovate with hooded yellowish apex, 18 × 10 mm; **Fil** 13 mm, 2.5 mm Ø at the base, all fertile; **Ov** 6 mm, stipitate for 1 mm, 4 mm Ø at the base narrowing to 3 mm, triangular, basally each angle with a raised twin tubercle; **Sty** linear, trigonous, 10 × 2 mm; **Fr** 15 × 9 mm, grey-brown; **Se** flat, 4 × 3 mm, shiny.

Summer-active, and easily grown from seed or divisions.

**A. crudenii** Archibald (Bothalia 6: 542–544, ill., 1956). **Type:** RSA, Eastern Cape (*Cruden* 14a [AMH]). — **Distr:** RSA (Eastern Cape: near Grahamstown); S-facing sandstone cliffs in Albany Thicket vegetation.

≡ *Ornithogalum crudenii* (Archibald) J. C. Manning & Goldblatt (2004).

[1] Summer-deciduous, bulbs halfway above-ground (rarely underground), offsetting from the base, forming small clusters to 8 cm Ø; bulb globose, to 3 cm Ø, outer tunics thin, papery, grey-green, clasping, withering and exposing green tissue; **L** 1, rarely 2, green, flaccid, slightly fleshy, glandular-hairy, linear-lanceolate, to 45 × 1.9 cm; **Inf** to 45 cm, scape to 28 cm, to 3 mm Ø, sparsely glandular-hairy, raceme secund, 7–14 cm; **Bra** puberulous, deltoid, apiculate, to 9 mm, 8 mm broad at the base; **Ped** cernuous, becoming erect at fruiting time; **Fl** 3–10, pendulous, faintly vanilla-scented; **OTep** 15 × 6 mm, patent, oblong, bright yellow; **ITep** to 12 × 5 mm, erect, connivent, ovate, pale yellow; **Fr** 13 mm; **Se** 3 × 1.5 mm.

The only member of sect. *Falconera* with glandular-hairy leaves. Easily grown in well-drained, sandy, mineral-poor soil. Regarded as vulnerable (Raimondo & al. 2009).

**A. deaconii** Van Jaarsveld (Herbertia [ser. 3], 66: 146–154, ill., 2013). **Type:** RSA, Eastern Cape (*Deacon* 1336 [NBG]). — **Distr:** RSA (Eastern Cape: Groot Winterhoek, SE Drakensberg); cliffs in Amatole Mountain Grassland vegetation, 1400 m.

[1] Evergreen, bulbs above-ground (rarely underground), 10–12 × 6–8 cm, solitary or dividing and forming small clusters with up to 5 heads, tunics fleshy, green, imbricate, withering and becoming grey, leaf remnants persistent; **R** fleshy, white; **L** 53–113 × 3–4 cm, in a rosette, firm and leathery, succulent, oblong, canaliculate, linear-attenuate, drooping, grey-green (like a leek), glabrous, becoming almost terete at the apex and with an obtuse yellowish end; **Inf** 32–85 cm, spreading but soon becoming pendent, scape 1 cm Ø at the base; raceme 13–17 cm; **Bra** triangular, acuminate, clasping the pedicels; **Fl** 30 mm long, erect, yellowish-green; **OTep** linear-obovate, 30 × 10 mm, yellow with green median part, apex hooded; **ITep** 25 × 14 mm, ovate with a fleshy yellow hinged apical appendage; **Fil** white, translucent, tapering, outer 16 mm, 4 mm Ø at the base, with a constriction in the lower 1/3, inner 15 mm, 2.5 mm Ø at the base; **Anth** of inner filaments 6 × 2 mm, of the outer

filaments  $4 \times 1$  mm; **Ov** green, stipitate for 1 mm,  $10 \times 4.5$  mm  $\emptyset$ , angular; **Sty** yellow, linear, trigonous,  $11 \times 3$  mm; **Sti** green, trilobate; **Fr** oblong,  $18 \times 9$  mm.

**A. dilucula** (Obermeyer) J. C. Manning & Goldblatt (Taxon 58(1): 95, 2009). **Type:** RSA, Western Cape (*Mauve & Oliver* s.n. in *PRE* 57046 [PRE]). — **Distr:** RSA (Northern Cape, Western Cape: S of Touwsrivier); Succulent Karoo. **I:** Obermeyer (1978: 371, Fig. 54).

≡ *Ornithogalum diluculum* Obermeyer (1978)  
 ≡ *Coilonox diluculum* (Obermeyer) Speta (2001).

[4] Bulb underground, globose,  $\pm 3$  cm  $\emptyset$ ; **L** solitary, hysteroanthous, narrowly oblong,  $8 \times 1.5$  cm, canaliculate, succulent and leathery, glaucous, margin swollen, white; **Inf** 25 cm, racemose with up to 10 slightly nodding flowers, scape 5 mm  $\emptyset$ , glaucous; **Bra** narrowly ovate-acuminate, to 15 mm, striate; **Ped** 20 mm; **Tep** linear,  $15 \times 5$  mm, glaucous-green with narrow yellow margin; **St** 8 mm; **Ov** narrowly oblong, 6 mm, shallowly 3-grooved, green; **Sty** elongate-clavate; **Sti** globose-penicillate; **Fr** oblong-globose, 7–10 mm, 3 mm  $\emptyset$ ; **Se** ovate, 3 mm  $\emptyset$ , papillate.

**A. garipeensis** J. C. Manning & Goldblatt (Bothalia 41(2): 315–317, ill., 2011). **Type:** RSA, Northern Cape (*Manning* 3294 [NBG, MO, PRE]). — **Distr:** RSA (Northern Cape); Bushmanland Arid Grassland vegetation; flowers mid-summer to autumn.

[3] Bulbs underground, pear-shaped, to 1–2.5 cm  $\emptyset$ , solitary, outer tunics dry and somewhat leathery, brownish and finely transversely barred, inner tunics succulent, tightly overlapping, white; **L** 4–9, ascending-spreading, not clasping below, linear,  $7\text{--}20$  cm  $\times$   $1\text{--}4$  mm, succulent, dull bluish-green, slightly coiled or twisted apically, canaliculate, lower face rounded; **Inf** solitary (sometimes up to 3), subpyramidal, densely 8- to 25-flowered, 3–8 cm, elongating slightly during anthesis; **Bra** lanceolate-aristate, lowermost  $20 \times 3$  mm, often slightly coiled; **Ped** spreading, 5–15 mm; **Fl** held horizontally, rotate, 14–20 mm  $\emptyset$ , faintly lemon-coconut-scented; **OTep** overlapping, oblong-elliptic,  $7\text{--}10 \times$

$2.5\text{--}3$  mm, slightly keeled apically; **ITep** elliptic,  $7\text{--}10 \times 3\text{--}3.5$  mm, concave apically and penicillate; **St** free, erect; **Fil** 4–5 mm, verruculose, both series with a square expansion in the basal 1.5 mm; **Anth** versatile, 2 mm, pale cream-yellow; **Ov** ovoid, shortly stipitate,  $\pm 3$  mm, 3-angled, green; **Sty** erect, tapering, 3-angled,  $\pm 3$  mm, acute; **Sti** trigonous, papillate, green in the lower  $\frac{1}{2}$ , distally white; **Fr** depressed-cordate in outline, deeply 3-lobed,  $10\text{--}12 \times 15\text{--}20$  mm; **Se** discoid,  $5 \times 8$  mm, colliculate, glossy black.

Martínez-Azorín & Crespo (2014: 216) consider this taxon as belonging to *Battandiera* (= *Albuca* subgen. *Namibiogalum*), and argue that it could be conspecific with *B. stapfii* (= *Ornithogalum stapfii*), a variable taxon that is not considered to be succulent.

**A. gildenhuisii** (Van Jaarsveld) Van Jaarsveld (Bradleya 34: 142, 2016). **Type:** RSA, Northern Cape (*Van Jaarsveld & al.* 21110 [NBG]). — **Distr:** RSA (Northern Cape: S of Steinkopf); sandstone cliffs in Succulent Karoo, spring-flowering.

≡ *Ornithogalum gildenhuisii* Van Jaarsveld (2012).

[4] Summer-deciduous, bulbs underground, solitary or dividing forming small groups, globose-ovoid,  $2.5\text{--}6 \times 2.5\text{--}7$  cm, tunics thin, greyish-green; **L** 3–7, synanthous,  $25\text{--}100 \times 1\text{--}4.2$  cm, clasping at the base, ascending to horizontally spreading, becoming pendent, lorate-lanceolate, dark green, softly semi-succulent, smooth, faintly striate, margins entire, apex acute, mucronate; juvenile leaves linear, subterete, softly succulent; **Inf** 20–45 cm, 1 per bulb, scape ascending, terete, 11–23 cm,  $3\text{--}4.5$  mm  $\emptyset$  at the base, raceme 8–22 cm, 9- to 15-flowered; **Bra** ascending, linear-lanceolate, acuminate,  $8\text{--}10 \times 1\text{--}1.5$  mm, becoming smaller further up; **Ped** to 15 mm, ascending, becoming shorter further up; **Fl** nodding,  $15\text{--}18$  mm  $\emptyset$ ; **Tep** reflexed, yellow, narrowly elliptic,  $10\text{--}12 \times 3\text{--}4$  mm; **St** 7–8 mm; **Fil** yellow, subulate, inner filaments expanded below; **Anth** 2 mm; **Ov** oblong, abruptly tapering at the apex,  $8 \times 2$  mm; **Sty** erect, 7.5 mm, yellow; **Sti** capitate; **Fr** ovoid,  $10 \times 13$  mm; **Se** flat, crescent-shaped,  $3 \times 2$  mm.

Easy to grow when kept completely dry during summer.

**A. juncifolia** Baker (Gard. Chron., ser. nov. 5: 534, 1876). **Type:** RSA, Western Cape (*Hutton* s.n. [K]). — **Distr:** RSA (Western Cape); coastal Renosterbosveld vegetation, flowers in late spring. — Fig. 2.

**Incl.** *Albuca imbricata* F. M. Leighton (1947) ≡ *Ornithogalum imbricatum* (F. M. Leighton) J. C. Manning & Goldblatt (2004).

[1] Bulbs partly above-ground, depressed-globose, to  $4.5 \times 3$  cm, solitary or dividing to form small groups, tunics succulent, brownish-green, drying to grey-white; **R** fleshy, white, to 3 mm  $\varnothing$ ; **L** 2–5, ascending to spreading, 5.5–20 cm  $\times$  1–5 mm, linear-attenuate, succulent, appearing terete but with strongly inrolled margins, base flat and channelled, apex acute; **Inf** 1–2, erect, to 28 cm, racemose, scape 3 mm  $\varnothing$  at the base, sterile for the lower  $\frac{1}{2}$ ; lower **Bra** lanceolate-acuminate,  $25 \times 7$  mm, becoming smaller further up, white, soon becoming brown; lower **Ped** to 7 cm; **Fl** erect; **Tep** yellow with broad green midstripe; **OTep**  $25 \times 7$  mm, erectly spreading, oblong, lorate, apex cucullate; **ITep**  $20 \times 7$  mm,



**Fig. 2** *Albuca juncifolia*. (Copyright: U. Eggli)

elliptic-ovate, cymbiform, apex cucullate and notched, truncate; **Fil** 12–14 mm, white, flat and 3 mm broad at the base, inner **Fil** basally constricted; **Anth** oblong,  $3 \times 1.2$  mm, versatile; outer **Fil** and **Anth** smaller; **Ov** 6–7 mm, obtusely trigonous; **Sty** prismatic, 7 mm, slightly widening at the tip, yellowish; **Sti** trilobate, yellow.

**A. karachabpoortensis** (U. & D. Müller-Doblies) J. C. Manning & Goldblatt (Taxon 58 (1): 95, 2009). **Type:** RSA, Northern Cape (*Müller-Doblies* 88103c [PRE, B, BTU, K, NBG, WIND]). — **Distr:** RSA (Northern Cape: Richtersveld); in Succulent Karoo. **I:** Müller-Doblies & Müller-Doblies (1996: 368, t. 4a–b).

≡ *Ornithogalum karachabpoortense* U. & D. Müller-Doblies (1996).

[4] Bulbs solitary or in groups, underground, ovoid, 1.5–2 cm  $\varnothing$ , white with thin, dry, greyish-white, papery tunics; **L** solitary, appressed to the ground, ovate to elliptic, flat to slightly navicular towards the tip,  $3.5\text{--}5.5 \times 0.9\text{--}1.3$  cm, leathery-succulent, dark green, densely covered by hyaline longitudinal ribs; **Inf** racemose with 2–5 flowers, scape  $\pm 10$  cm, raceme 2.5–6.5 cm; **Bra** 8–11 mm; lower **Ped** 10–15 mm; **Fl** nodding, stellate; **Tep** reflexed, 11–13 mm, yellow with green median stripe; **OTep** 3.2 mm broad; **ITep** 3.5–4.5 mm broad; **Fil** 7–8 mm, scabrid; **Ov** cylindrical, 3–4 mm, 1.7 mm  $\varnothing$ ; **Sty** green, 7 mm; **Fr** and **Se** unknown.

*A. scabrocostata* has similar longitudinally ridged but more succulent leaves.

**A. kirstenii** (J. C. Manning & Goldblatt) J. C. Manning & Goldblatt (Taxon 58(1): 97, 2009). **Type:** RSA, Western Cape (*Manning* 2942 [NBG, K, MO]). — **Distr:** RSA (Western Cape: Gouritz and Breede Rivers); shale cliffs in Albany Thicket vegetation, flowers in autumn. **I:** Manning & Goldblatt (2006: 88).

≡ *Ornithogalum kirstenii* J. C. Manning & Goldblatt (2006).

[1] Bulbs above-ground (rarely underground), globose to ovoid, to  $2 \times 1.8$  cm, forming small clusters, summer-deciduous, outer tunics thin, papery, grey-green, clasping, withering, exposing green tissue; **L** 1 or 2, linear, succulent, inrolled

and appearing terete, 5–10 cm, 1.5–2 mm  $\varnothing$ , smooth, glaucous, apex acute; **Inf** ascending, to 14 cm, scape smooth, glaucous; raceme to 5 cm; **Bra** ovate-acuminate, thin, papery, 7  $\times$  3 mm, base clasping; **Ped** 3 mm, bending down; **Fl** pendent, yellow; **OTep** spreading, linear-obovate, 12  $\times$  3 mm, pale yellow with green median part; **ITep** 11  $\times$  5 mm, ovate, with hooded apex; **Fil** 9 mm, canaliculate at the base, white; **Anth** 1.5 mm, oblong, white, pollen yellowish; **Ov** stipitate for 1 mm, 4–6 mm, 2–3 mm  $\varnothing$ , green, grooved, trigonous; **Sty** trigonous, 6  $\times$  1 mm, yellowish; **Sti** capitate; **Fr** 12–16  $\times$  6.5 mm; **Se** 2–3  $\times$  1–2 mm.

**A. lebaensis** (Van Jaarsveld) J. C. Manning & Goldblatt (Bothalia 41(2): 297, 2011). **Type:** Angola, Benguella (*Van Jaarsveld* 22611 [LUB, NBG, WIND]). — **Distr:** SW Angola (Benguella: W escarpment W of Lubango); sheer sandstone cliffs, 1800–2000 m. **I:** Jaarsveld (2010: 95).

≡ *Ornithogalum lebaense* Van Jaarsveld (2010) ≡ *Stellarioides lebaensis* (Van Jaarsveld) Martínez-Azorín & M. B. Crespo (2012).

[5] Plants bulbous, winter-deciduous; bulb underground, solitary or dividing and forming small clusters to 10 cm  $\varnothing$ , globose-ovoid, 3–4  $\times$  2–3 cm, tunics white; **L** 4–5, synanthous, 70–82  $\times$  2.5–3.5 cm, spreading to pendent, spirally curved, semi-succulent, soft and flaccid, lorate, linear-acuminate and channelled, terete at the apex, surface glaucous; juvenile **L** linear, subterete, softly succulent; **Inf** 20–30 cm, pendent, 1–2 per bulb, raceme conical, 8–14 cm, 35- to 50-flowered, scape terete, 12–15 cm, 5 mm  $\varnothing$  at the base, inflating to 10–15 mm  $\varnothing$  further up and tapering again in the upper  $\frac{1}{2}$ ; **Bra** conspicuous, attenuate-lanceolate, cymbiform, white with a median green stripe; lower **Ped** 12–17 mm, becoming shorter further up, the lower **Ped** lengthening in fruit to  $\pm$  30 mm; **Fl** densely arranged, sweet-scented; **Per** stellate, white, 20 mm  $\varnothing$ ; **Tep** spreading, with a greenish median band, ovate-elliptic, 8–11  $\times$  4–5 mm; **St** 8 mm; **Fil** white, linear and with abrupt lateral extensions in the lower  $\frac{1}{2}$ , 1.5–2 mm broad; **Anth** 2 mm; **Ov** yellowish-green, trigonous, ridged, abruptly tapering at the apex, 4.5  $\times$  4.5 mm; **Sty** 3 mm,

extending to 5 mm during anthesis, yellow; **Sti** white; **Fr** 7–9  $\times$  7–9 mm, trilobate; **Se** flattened, angular, semi-lunate, 4  $\times$  2 mm.

Flowering in late autumn to winter, and then becoming dormant.

**A. nelsonii** N. E. Brown (Gard. Chron., ser. nov. 14: 198, t. 41 (p. 199), 1880). **Type:** RSA, KwaZulu-Natal (*Nelson* s.n. [K]). — **Distr:** RSA (Eastern Cape, Free State, KwaZulu-Natal); Bushveld, summer-rainfall regions, flowers mid-summer to autumn.

≡ *Ornithogalum nelsonii* (N. E. Brown) J. C. Manning & Goldblatt (2004).

[1] Bulbs pear-shaped, to 12  $\times$  9.5 cm, above-ground, solitary or dividing to form small groups, tunics succulent, green, imbricate and truncate at the apex, becoming shorter towards the base; **R** fleshy, white, to 5 mm  $\varnothing$ ; **L** 4–6, 20–100  $\times$  1.7–5 cm, ascending, curved, oblong, linear-attenuate, succulent, firm, dark green, glabrous and shiny, channelled for most of the length, apex acute; **Inf** erect, to 1.2 m, racemose, scape 75 cm, 1.5 cm  $\varnothing$  at the base; **Bra** lanceolate-acuminate, 4–15 cm, green with white translucent margin; **Ped** erect, 8–16 cm; **Fl** erect, to 35 mm long; **Tep** white with green midstripes; **OTep** 33–35  $\times$  9 mm, oblong to ovate, cucullate; **ITep** 30  $\times$  13 mm, elliptic-oblong, cucullate, truncate; **Fil** white, outer 24  $\times$  1 mm, inner 28 mm  $\times$  basally 3.5 mm; outer **Anth** 4  $\times$  1 mm, inner 6–7  $\times$  2.5 mm, all fertile; **Ov** 8–12 mm, obtusely trigonous; **Sty** prismatic, 5 mm; **Sti** trilobate, white.

Often grown in RSA because of the striking large white flowers.

**A. pendula** B. Mathew (Kew Bull. 49(1): 125–128, ill., 1994). **Type:** Saudi Arabia, Jizan (*Collenette* 7855 [K]). — **Distr:** SW Saudi Arabia (Jizan: Jabel Qahar); cliff-ledges, 1670 m, spring-flowering.

≡ *Ornithogalum pendulum* (B. Mathew) J. C. Manning & Goldblatt (2004).

[1] Bulb subglobose, underground (?), to 6 cm  $\varnothing$ , with tapering neck, outer tunics thinly membranous, white to light brown, inner tunics fleshy; **L** up to 8, linear-lanceolate, 14  $\times$  6 cm (5 cm at the



base), pendent, glabrous, bright mid-green, slightly glaucous, canaliculate near the base, margin narrowly hyaline and undulating, apex subulate; **Inf** pendent, raceme curving upwards, to 30 cm, scape stout, 8 mm  $\varnothing$  at the base; **Bra** linear-lanceolate, the lowest 6.8 cm, upper ones smaller; **Ped** suberect, the lower 8 mm; **Fl**  $\pm$  40–45, suberect, to horizontal in bud, pendent at anthesis; **Tep** free, glabrous, yellow with a green median stripe, cucullate; **OTep** spreading, oblong, 27–28  $\times$  6 mm; **ITep** oblanceolate, 26  $\times$  10 mm; **St** free, all fertile; **Fil** 17–20 mm, flattened, expanded in the lower  $\frac{1}{2}$  to 2–2.5 mm, constricted above the ovary; **Anth** oblong, 3 mm; **Ov** 4  $\times$  5 mm, subconical, base with three triangular depressions; **Sty** subulate, 1.8–1.9 mm; **Sti** obscurely 3-partite, yellow, papillate; **Fr** broadly ovoid, 11–12  $\times$  10 mm; **Se** black, flat, suborbicular, 5 mm.

**A. scabrocostata** (U. & D. Müller-Doblies) J. C. Manning & Goldblatt (Taxon 58(1): 95, 2009). **Type:** RSA, Northern Cape (*Müller-Doblies* 79176k [PRE, B, BOL, BR, BTU, G, K, LI, M, MO, NBG, S, WIND, Z]). — **Distr:** RSA (Northern Cape: Richtersveld); shallow bedrock, winter-growing. **I:** Williamson (1998).

$\equiv$  *Ornithogalum scabrocostatum* U. & D. Müller-Doblies (1996)  $\equiv$  *Coilonox scabrocostatum* (U. & D. Müller-Doblies) Speta (2001).

[4] Similar to *A. unifoliata*, but the single **L** spreading at an angle (instead of erect), to 6  $\times$  0.6 cm, subclavate, upper face flat or slightly canaliculate, lower face convex, margins hyaline, surface covered with ribs with rough raised rounded projections; **Inf** to 12 cm; **Tep** canary-yellow with a deep green midvein.

**A. shawii** Baker (J. Bot. 12: 367, 1874). **Type** [lecto]: RSA, Northern Cape (*Shaw* s.n. [K]). — **Distr:** RSA (Northern Cape, Eastern Cape, Mpumalanga, Free State, KwaZulu-Natal), Lesotho; grassland and savanna, spring-flowering.

$\equiv$  *Ornithogalum shawii* (Baker) J. C. Manning & Goldblatt (2004); **incl.** *Albuca elliotii* Baker (1881); **incl.** *Albuca trichophylla* Baker (1889); **incl.** *Albuca minima* Baker (1897); **incl.** *Albuca granulata* Baker (1904).

[1] Evergreen or deciduous, proliferating from the base, forming small clusters to 12 cm  $\varnothing$ ; bulb globose to ovoid, to 2  $\times$  1.8 cm, underground (?), outer tunics thin, papery; **L** up to 12, ascending to drooping, linear-lanceolate, succulent, 15–40 cm  $\times$  1.5–6 mm, surface green, slightly hairy, margins ciliate, apex acuminate, young leaves terete; **Inf** ascending, 20 cm, scape 3 mm  $\varnothing$  at the base, green, raceme to 8–10 cm; **Bra** ovate-acuminate, thin, papery, 16  $\times$  4 mm, base clasping; **Ped** 20 mm, ascending; **Fl** nodding, yellow, 18 mm  $\varnothing$ ; **OTep** spreading, linear-lanceolate, 7  $\times$  3.5 mm, pale yellow, tips obtuse, incurved; **ITep** 11  $\times$  4 mm, linear-ovate, with hooded incurved tip; **Fil** 9 mm, white, hyaline, outer 1.5 mm broad at the canaliculate base; **Anth** 15  $\times$  1 mm, oblong, white, pollen yellowish; **Ov** stipitate for 1 mm, 4  $\times$  2 mm, green, grooved, trigonous; **Sty** 5 mm, obpyramidate, 1 mm  $\varnothing$  expanding to 2 mm, yellow; **Sti** 3-lobed, truncate.

Müller-Doblies (2012) placed this taxon in the synonymy of *Albuca tenuifolia*, but Martínez-Azorín & al. (2012) show that this interpretation is unwarranted, and that the two taxa are distinct.

This is the only summer-growing member of sect. *Falconera*. The obpyramidate style is also diagnostic. Very variable in leaf size and hairiness.

**A. spiralis** Linné (Suppl. Pl., 196, 1782). **Type** [lecto]: RSA, Western Cape (*Thunberg* 7242 [UPS]). — **Distr:** RSA (Northern Cape, Western Cape); Renosterveld vegetation, mainly winter-rainfall regions, spring-flowering.

$\equiv$  *Falconera spiralis* (Linné *fil.*) Salisbury ex B. D. Jackson (1895); **incl.** *Albuca viridiflora* Jacquin (1797); **incl.** *Ornithogalum circinatum* J. C. Manning & Goldblatt (2004) (*nom. illeg.*, Art. 53.1); **incl.** *Ornithogalum volutare* J. C. Manning & Goldblatt (2006).

[1] Dwarf winter-growing geophytes with the top of the bulbs exposed, solitary or dividing to form small groups; bulb ovoid, 0.8–2.5  $\times$  0.5–2.5 cm  $\varnothing$ , tunics green and fleshy, withering grey and membranous; **L** 15–20, densely arranged, 3–11 cm  $\times$  1 mm, terete, green, glandular-pubescent, withering in summer, erect and spirally curved at the tip, upper face slightly channelled at the base; **Inf** 4–5 cm with 1–5

drooping flowers; **Bra** linear-lanceolate, to  $18 \times 4$  mm, glandular-hairy; **Ped** cernuous, 20–25 mm; **Tep** to 18 mm, yellow; **St** all fertile; **Sty** prismatic, as long as the ovary; **Sti** tricuspidate; **Ov** obovoid-ellipsoid to globose, 6-grooved, with light green tubercles along the middle part.

Belongs to sect. *Albuca* characterized by nodding, scented flowers. Easily cultivated, to be kept dry during summer. Vogel & Müller-Doblies (2011) interpret the spiralling leaves as an adaptation for dew collection.

**A. tenuifolia** Baker (Refug. Bot. 5: t. 335 + text, 1872). **Type:** [lecto — icono]: l.c. t. 335. — **Lit:** Martínez-Azorín & al. (2011b); Martínez-Azorín & al. (2012). **Distr:** RSA (Eastern Cape, Mpumalanga: S Drakensberg); mainly on dolerite and basalt escarpment cliffs.

≡ *Ornithogalum nematophyllum* J. C. Manning & Goldblatt (2004).

[1] Bulb underground,  $1.5\text{--}4 \times 0.5\text{--}2$  cm, ovoid to oblong, proliferous from the base forming small groups, tunics membranous, white to brown; **R** somewhat fleshy; **L** 4–9, filiform, to  $25 \text{ cm} \times 1\text{--}1.2$  mm, ascending to spreading, terete, minutely papillose, bright green, slightly channelled adaxially, rounded abaxially; **Inf** 40–70 cm, 3- to 4- (to 5-) flowered, corymbiform; **Ped** 3–7 cm, lowermost much longer; **Bra** lanceolate to triangular, acuminate,  $5\text{--}25 \times 3\text{--}7$  mm; **Fl** erect; **Tep** yellow, white below; **OTep**  $17\text{--}21 \times 5\text{--}7$  mm, lanceolate-oblong, apex slightly cucullate; **ITep**  $13\text{--}17 \times 6\text{--}8$  mm, ovate, apex cucullate; **St** all fertile; **Ov**  $\pm 4 \times 2.5\text{--}3$  mm, subglobose to obovoid, green, stipitate, with 3 prominent tuberculate ridges; **Sty** 8–10 mm, yellow, narrowly obpyramidal or clavate, trigonous; **Sti** yellow to orange, trigonous; **Fr**  $13\text{--}15 \times 10\text{--}11$  mm, ovoid, trigonous to subglobose; **Se**  $3\text{--}5 \times 2\text{--}3$  mm, dark brown to black, flattened and semicircular in outline.

**A. thermarum** Van Jaarsveld (Bothalia 33(1): 116, ill., 2003). **Type:** RSA, Western Cape (*Van Jaarsveld* 14152 [NBG]). — **Distr:** RSA

(Western Cape: Badspoort near Calitzdorp); sheer rock faces in thickets, spring-flowering.

≡ *Ornithogalum thermarum* (Van Jaarsveld) J. C. Manning & Goldblatt (2004).

[1] Evergreen; bulbs underground (rarely above-ground), solitary or dividing to form small groups, ovoid,  $7 \times 5.5$  cm, tunics fleshy, imbricate and truncate at the top; **L** oblong, linear-attenuate,  $30\text{--}55 \times 2\text{--}3$  cm, drooping, succulent, firm, dark green, glabrous, channelled for most of their length, apex acute; **Inf** spreading to pendulous; scape to 26 cm, raceme 40–60 cm; **Bra** acuminate,  $4.5 \times 0.8$  cm; **Ped** ascending to erect, lowest to 10.5 cm, becoming shorter further up, uppermost to 3.5 cm; **Fl** erect; **Tep** yellowish-green; **OTep**  $25 \times 7$  mm, strap-shaped, apex cucullate; **ITep** ovate,  $20 \times 12$  mm; outer **Fil**  $15 \times 2$  mm, inner **Fil** 13 mm, with a distinct, short, channelled constriction 4.5 mm from the base, basal  $\frac{1}{3}$  broadly triangular-ovate, 3 mm wide at the base; **Anth** oblong, versatile, outer  $2.5 \times 1.5$  mm, inner  $3.5 \times 2.5$  mm; **Ov** oblong, 3-angled,  $7 \times 4$  mm, stipitate for 1.5 mm; **Sty** linear-trigonous, clavate,  $9 \times 2$  mm; **Sti** yellowish-green; **Fr**  $18 \times 10$  mm; **Se** flat,  $6 \times 3$  mm, angular.

Regarded as critically rare (Raimondo & al. 2009). Easily grown and suitable for hanging baskets.

**A. unifoliata** G. D. Rowley (Ashingtonia 2: 55–56, 1975). **Type:** RSA, Northern Cape (*Hall & Rowley* 329 [K]). — **Distr:** RSA (Northern Cape); Succulent Karoo, spring-flowering. **I:** Obermeyer (1978: 370, as *Ornithogalum*). — Fig. 3.

≡ *Ornithogalum unifoliatum* (G. D. Rowley) Obermeyer (1978) ≡ *Coilonox unifoliatum* (G. D. Rowley) Speta (2001).

[4] Dwarf hysteroanthous solitary geophytes; bulbs globose, to 2 cm  $\varnothing$ , yellow; **L** solitary, terete, club-shaped,  $4 \times 1$  cm; **Inf** racemose, to 12 cm, erect, 5- to 9-flowered; **Bra** deltoid-acuminate, 1 cm; **Ped** 10 mm, ascending; **Per** stellate, yellow; **Tep**  $15 \times 4$  mm, elliptic; **St** 5 mm, **Fil** filiform; **Sty** erect; **Sti** capitate; **Se** flat, semi-orbicular, black.



**Fig. 3** *Albuca unifoliata*. (Copyright: U. Eggli)

## References

- Glanzng, A. & Kessal, O. (2004) Invasive plants of national importance and their legal status by state and territory. Sydney (AU): WWF Australia.
- Jaarsveld, E. J. van (2010) *Ornithogalum lebaense*, a new cliff dwelling *Ornithogalum* (*Hyacinthaceae*) from southwest Angola (Benguela Province). *Herbertia* [ser. 3], 64: 91–103, ills., map.
- Jaarsveld, E. J. van [ & al. 2007], Wyk, A. E. (B.) van & Blake, T. (2007) *Ornithogalum cremnophilum*. *Flow. Pl. Afr.* 60: 8–13, map, t. 2222.
- Johnson, S. D. [ & al. 2012], Jürgens, A. & Kuhlmann, M. (2012) Pollination function transferred: Modified tepals of *Albuca* (*Hyacinthaceae*) serve as secondary stigmas. *Ann. Bot. (Oxford)*, n.s. 110: 565–572, ills. <https://doi.org/10.1093/aob/mcs114>
- Lebrun, J.-P. & Stork, A. L. (2014) Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (*Anthericaceae* – *Palmae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Manning, J. C. & Goldblatt, P. (2006) Notes on African plants. *Hyacinthaceae*. *Ornithogalum kirstenii* (*Albuca* group), a new species from Western Cape, South Africa, and new combinations in the group. *Bothalia* 36(1): 86–89, ills., map. <https://doi.org/10.4102/abc.v36i1.347>
- Manning, J. C. & Goldblatt, P. (2011) Notes on African plants. *Hyacinthaceae*. *Ornithogalum lebaense* transferred to *Albuca*. *Bothalia* 41(2): 297. <https://doi.org/10.4102/abc.v41i2.64>
- Manning, J. C. [ & al. 1999], Goldblatt, P. & Anderson, F. (1999) *Albuca clawilliamigloria*. *Flow. Pl. Afr.* 56: 8–12, t. 2142, map.
- Manning, J. C. [ & al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperae*. *Edinburgh J. Bot.* 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>
- Manning, J. C. [ & al. 2009], Forest, F., Devey, D. S., Fay, M. F. & Goldblatt, P. (2009) A molecular phylogeny and a revised classification of *Ornithogaloideae* (*Hyacinthaceae*) based on an analysis of four plastid DNA regions. *Taxon* 58(1): 77–107, ills., key. <https://www.jstor.org/stable/27756826>
- Martínez-Azorín, M. & Crespo, M. B. (2014) Nomenclatural novelties and taxonomic notes in *Battandiera* Maire (*Ornithogaloideae*, *Hyacinthaceae*). *Pl. Biosystems* 148(2): 213–216, ills. <https://doi.org/10.1080/11263504.2012.761291>
- Martínez-Azorín, M. [ & al. 2011a], Crespo, M. B., Juan, A. & Fay, M. F. (2011a) Molecular phylogenetics of subfamily *Ornithogaloideae* (*Hyacinthaceae*) based on nuclear and plastid DNA regions, including a new taxonomic arrangement. *Ann. Bot. (Oxford)*, n.s. 107: 1–37, ills. key. <https://doi.org/10.1093/aob/mcq207>
- Martínez-Azorín, M. [ & al. 2011b], Clark, V. R., Crespo, M. B., Dold, A. P. & Barker, N. P. (2011b) The rediscovery of *Albuca tenuifolia*, an orophilous species from the eastern Great Escarpment in South Africa. *Nordic J. Bot.* 29: 465–470. <https://doi.org/10.1111/j.1756-1051.2011.00944.x>
- Martínez-Azorín, M. [ & al. 2012], Crespo, M. B. & Dold, A. P. (2012) Notes on African plants. *Hyacinthaceae*. *Albuca tenuifolia* and *A. shawii* (*Ornithogaloideae*), two distinct species from South Africa. *Bothalia* 42 (2): 193–196, ills. <https://doi.org/10.4102/abc.v42i2.17>
- Müller-Doblies, U. (1994) Enumeratio Albucaarum (*Hyacinthaceae*) Austro-Africanarum adhuc cognitarum. 1. Subgenus *Albuca*. *Feddes Repert.* 105(5–6): 365–368. <https://doi.org/10.1002/fedr.19941050515>
- Müller-Doblies, U. (1995) Enumeratio Albucaarum (*Hyacinthaceae*) Austro-Africanarum adhuc cognitarum. 2. Subgenus *Falconera* (Salisb.) Baker emend. U. M.-D. 1987. *Feddes Repert.* 106(5–8): 353–370, ills. <https://doi.org/10.1002/fedr.19961060506>
- Müller-Doblies, U. (2006) Enumeratio Albucaarum (*Hyacinthaceae*) Austro-Africanarum adhuc cognitarum. 3. Additions and additional notes to *Albuca* subgenus *Falconera* and *A.* subgenus *Albuca*. *Feddes Repert.* 117 (1–2): 96–138, ills., maps. <https://doi.org/10.1002/fedr.200611089>
- Müller-Doblies, U. (2012) The enigma of *Albuca tenuifolia* Baker resolved. *Feddes Repert.* 121(7–8):

- 285–298, ills., map. <https://doi.org/10.1002/fedr.201000030>
- Müller-Doblies, U. & Müller-Doblies, D. (1996) Revisionula incompleta Ornithogalorum austro-africanorum (*Hyacinthaceae*). Feddes Repert. 107 (5–6): 361–548, ills., key. <https://doi.org/10.1002/fedr.19961070511>
- Obermeyer, A. A. (1978) *Ornithogalum*: A revision of the southern African species. Bothalia 12(3): 323–376, ills., key. <https://doi.org/10.4102/abc.v12i3.1793>
- Raimondo, D. [& al. 2009], von Staden, L., Foden, W., Victor, J. E., Helme, N. A., Turner, R. C., Kamundi, D. A. & Manyama, P. A. (eds.) (2009) Red List of South African plants 2009. Pretoria (ZA): South African National Biodiversity Institute SANBI (= Strelitzia No. 25).
- Roselló Gimeno, R. [& al. 2013], Laguna Lumbreras, E. & Guillot Ortiz, D. (2013) Sobre algunas especies capenses asilvestradas en tierras valencianas. Bouteloua 13: 11–15, ills.
- Smith, G. F. [& al. 2003], Steyn, E. M. A., Crouch, N. & Condy, G. (2003) *Ornithogalum longibracteatum*. Flow. Pl. Afr. 58: 22–29, t. 2185, map.
- Speta, F. (2001) Die Echte und die Falsche Meerzwiebel: *Charybdis* Speta und *Stellarioides* Medicus (*Hyacinthaceae*), mit Neubeschreibungen und Neukombinationen im Anhang. Stapfia 75: 139–176.
- Vogel, S. & Müller-Doblies, U. (2011) Desert geophytes under dew and fog: The “curly-whirlies” of Namaqualand (South Africa). Flora (Jena) 206(1): 3–31, ills. <https://doi.org/10.1016/j.flora.2010.01.006>
- Williamson, G. (1998) *Ornithogalum scabrocostatum* U. & D. Müller-Doblies, a recently described succulent species from the Richtersveld. Aloe 35(1): 25–26, ills., map.
- Xu, T. H. [& al. 2000], Xu, Y. J., Liu, D. Y. & Xu, D. M. (2000) Studies on the chemical constituents from *Ornithogalum caudatum* Ait. Yaoxue Xuebao 35(1): 32–36.



## Bowiea HYACINTHACEAE

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**Bowiea** Harvey ex Hooker *fil.* (Curtis's Bot. Mag. 43: t. 5619 + text, 1867). **Type:** *Bowiea volubilis* Harvey ex Hooker *fil.* — **Urgineoideae** — **Lit:** Jessop (1977: 312–314, systematics); Bruyns & Vosa (1987: systematics & cytology); Jaarsveld (1992: ill. synopsis). **Distr:** Tropical E Africa to S Africa. **Etym:** For James Bowie (1789–1869), English horticulturist and botanical collector in S Africa.

**Incl.** *Ophiobostrix* Skeels (1911) (*nom. illeg.*, Art. 52.1). **Type:** *Bowiea volubilis* Harvey ex Hooker *fil.*

**Incl.** *Schizobasopsis* J. F. Macbride (1918). **Type:** *Bowiea volubilis* Hooker *fil.*

Perennial bulbous geophytes; **R** fleshy, white, to 5 mm Ø; bulbs depressed-globose, subterranean to almost fully exposed, exposed parts green, tunics thickly fleshy withering to paper-like; **L** only present in immature young plants, fleshy, linear-lanceolate, canaliculate, short-lived; stem (= inflorescence) annual, scandent, twining or scrambling, much branched, softly succulent, green or glaucous, branchlets subulate; **Bra** lanceolate, spurred; **Ped** arched; **Fl** diurnal, scented; **Te** 6, equal, free to the base, white or green to yellowish-green, patent

to reflexed, oblong to lanceolate, margins revolute towards the base, apex subacute; **St** 6; **Fil** suberect; **Ov** 3-locular, broadly conical, light green, glutinous on the upper surface; **Sty** terete; **Sti** apical, 3-lobed; **Fr** 3-locular erect capsules with emarginate to acuminate valves, dehiscent longitudinally; **Se** black, angular-oblong, shiny.

*Bowiea* is regarded as sister group of the expanded genus *Drimia*, and differs through long-lived flowers, completely free tepals, and a persistent perianth attached to the base of the developing fruits (Goldblatt & Manning 2000: 710–711). The habit (largely leaf-less bulbs with photosynthetic inflorescence axes) is a parallel development to that of the former *Schizobasis* species now placed in the expanded genus *Drimia*, disproving the close relationships between the two taxa assumed by Jessop (1975) and others.

Irmisch (1879) has investigated the germination and bulb formation, which starts immediately after the cotyledon has expanded, usually followed by a second linear leaf. In the second vegetation period, a few linear leaves are first formed, followed by the first inflorescence stem with rudimentary scale leaves. Subsequently, no further laminar leaves are produced. The bulb has a sympodial construction, with an arrested innovation shoot from the base of the innermost bulb scale, and this shoot forms both the new bulb as well as one to several inflorescence stem primordia. The bulb scales show few stomata on the outer surface, and their bulk volume is made up by a large-celled parenchymatic water-storage tissue (Figdor 1928).

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Propagation is by seed or daughter bulbs. According to Figdor (1928), detached bulb scale fragments can be rooted and produce daughter bulbs from the cut surface. Seeds show high germination rates without any special treatment (Mofokeng & al. 2012).

**B. gariensis** Van Jaarsveld (J. South Afr. Bot. 49(4): 343–346, ill., 1983). **Type:** RSA, Northern Cape (Van Jaarsveld 6650 [NBG, PRE]). — **Distr:** S Namibia, RSA (W Northern Cape); mainly in Eastern Gariiep Rocky Desert vegetation, along cool S-facing screes in the Orange River valley, autumn- and winter-growing/flowering. **I:** Reid & al. (1990); Jaarsveld (1992). – Fig. 1.

≡ *Bowiea volubilis* ssp. *gariensis* (Van Jaarsveld) Bruyns (1987).

Bulb to 14 cm Ø; stem (= **Inf**) to 1.2 m, glaucous to glaucous-green, branchlets subulate, to 7 cm × 2–5 mm Ø; **Bra** lanceolate, spurred, 3–5 mm; **Fl** 14–23 mm Ø; **Tep** 12 × 3.5 mm, white, patent to somewhat reflexed, oblong to lanceolate, apex subacute; **Fr** globose, depressed, 4–6 mm with emarginate valves; **Se** 4–5 mm.



**Fig. 1** *Bowiea gariensis*. (Copyright: U. Eggli)

Bruyns & Vosa (1987) suggest to treat this taxon merely as a subspecies of the wide-spread *B. volubilis*, but the widely disjunct range and the morphological differences are overwhelming.

**B. volubilis** Harvey ex Hooker fil. (Curtis's Bot. Mag. 43: t. 5619 + text, 1867). **Type:** RSA, KwaZulu-Natal (Cooper 3263 [K]). — **Distr:** Tropical E Africa (Kenya, Tanzania, Uganda) to Moçambique, Zimbabwe, Malawi, Angola and SE RSA (Eastern Cape, KwaZulu-Natal, Mpumalanga, Gauteng, Limpopo); dry to moist savanna and Afrotropical forest, spring- and summer-growing/flowering. **I:** Jaarsveld (1992).

≡ *Ophiobolus volubilis* (Harvey ex Hooker fil.) Skeels (1911) (*incorrect name*, Art. 11.4) ≡ *Schizobasopsis volubilis* (Harvey ex Hooker fil.) J. F. Macbride (1918) (*incorrect name*, Art. 11.4) ≡ *Schizobasis volubilis* (Harvey ex Hooker fil.) Van Jaarsveld (1992) (*nom. inval.*, Art. 34.1c); **incl.** *Bowiea kilimandscharica* Mildbraed (1936) ≡ *Schizobasopsis kilimandscharica* (Mildbraed) Bartsch (1954) (*incorrect name*, Art. 11.4).

Bulb to 16 cm Ø; stem (= **Inf**) 3–4 (–10) m, green, branchlets subulate, to 7 cm × 2–5 mm Ø; **Bra** lanceolate, spurred, 3–5 mm; **Fl** 10–16 mm Ø; **Tep** 12 × 3.5 mm, green to yellowish-green, reflexed, oblong to lanceolate, apex acute to subacute; **Ov** broadly conical, 5 mm Ø, light green; **Fr** conical, 8–30 mm with acuminate valves; **Se** 5–10 mm.

*Bowiea volubilis* is the 14. most-traded medicinal plant in RSA (Masondo & al. 2013). It is used against a number of ailments, e.g., against sore eyes and to treat dropsy, to help pregnant women with delivery, and as a body wash (Zukulu & al. 2012: 43; Masondo & al. 2013; Aremu & al. 2015). Wild populations are becoming increasingly decimated because of indiscriminate collecting. Propagation is by bulb scales or seeds, and garden-grown bulbs have similar biological activities as wild-collected plants (Masondo & al. 2013).

## References

- Aremu, A. O. [ & al. 2015], Moyo, M., Amoo, S. O. & van Staden, J. (2015) Ethnobotany, therapeutic value, phytochemistry and conservation status of *Bowiea*

- volubilis*: A widely used bulbous plant in southern Africa. J. Ethnopharmacol. 174: 308–316, map, ills. <https://doi.org/10.1016/j.jep.2015.08.009>
- Bruyns, P. V. & Vosa, C. G. (1987) Taxonomic and cytological notes on *Bowiea* Hook. f. and allied genera (*Liliaceae*). Caryologia 40(4): 287–297, fig., map, chromosome ills. <https://doi.org/10.1080/00087114.1987.10797831>
- Figdor, W. (1928) Über den Einfluss des Lichtes auf die Gestaltung der *Bowiea volubilis* sowie über die Vermehrung und den Bau ihrer Zwiebel. Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 137: 45–54, ills.
- Goldblatt, P. & Manning, J. (2000) Cape plants. A conspectus of the Cape Flora of South Africa. Pretoria (ZA): National Botanical Institute of South Africa / St. Louis (US): Missouri Botanical Garden. = Strelitzia 9.
- Irmisch, T. (1879) Die Wachstumsverhältnisse von *Bowiea volubilis* Hkr. fil. Abh. Naturwiss. Vereine Bremen 6: 433–440, 1 t. <http://www.biodiversitylibrary.org/page/33504368>
- Jaarsveld, E. J. van (1992) *Bowiea gariensis* and *Bowiea volubilis*. Brit. Cact. Succ. J. 10(4): 96–98, ills., key.
- Jessop, J. P. (1975) Studies in the bulbous *Liliaceae* in South Africa. 5. Seed surface characters and generic groupings. J. South Afr. Bot. 41: 67–85.
- Jessop, J. P. (1977) Studies in the bulbous *Liliaceae* in South Africa. 7. The taxonomy of *Drimia* and certain allied genera. J. South Afr. Bot. 43(4): 265–319, keys.
- Masondo, N. A. [et al. 2013], Ndhala, A. R., Aremu, A. O., van Staden, J. & Finnie, J. F. (2013) A comparison of the pharmacological properties of garden cultivated and muthi market-sold *Bowiea volubilis*. South Afr. J. Bot. 86: 135–138. <https://doi.org/10.1016/j.sajb.2013.02.169>
- Mofokeng, M. [et al. 2012], Prinsloo, G. & Kritzing, Q. (2012) Germination response of four South African medicinal plants to a range of temperatures and treatments. Seed Sci. Technol. 40(1): 123–128.
- Reid, C. [et al. 1990], Müller-Doblies, D. & Müller-Doblies, U. (1990) *Bowiea gariensis*. Flow. Pl. Afr. 51(1): t. 2007 + text, map.
- Zukulu, S. [et al. 2012], Dold, T., Abbott, T. & Raimondo, D. (2012) Medicinal and charm plants of Pondoland. Pretoria (ZA): South African National Biodiversity Institute SANBI.





## Dipcadi HYACINTHACEAE

U. Eggli

**Dipcadi** Medikus (Hist. & Comment. Acad. Elect. Sci. Theod.-Palat. 6: 431, 1790). **Type:** *Hyacinthus serotinus* Linné. — **Ornithogaloideae**—**Dipcadieae** — **Lit:** Obermeyer (1964: revision RSA); Pinter (2012: phylogeny). **Distr:** Africa, Madagascar, Socotra, Mediterranean region to India. **Etym:** Perhaps the ancient oriental name for some species today classified as *Muscari* (“Grape Hyacinth”).

**Incl.** *Zuccagnia* Thunberg (1798) (*nomen rejiciendum*, Art. 56.1). **Type:** *Hyacinthus viridis* Linné.

**Incl.** *Uropetalon* Burchell ex Ker Gawler (1816). **Type:** *Hyacinthus viridis* Linné.

**Incl.** *Uropetalum* Burchell (1822) (*nom. inval.*, Art. 61.1). **Type:** *Hyacinthus viridis* Linné.

**Incl.** *Polemannia* P. J. Bergius ex Schlechtendal (1826) (*nomen rejiciendum*, Art. 56.1). **Type:** *Polemannia hyacinthiflora* Schlechtendal.

**Incl.** *Tricharis* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Hyacinthus serotinus* Linné

Small to large perennial bulbous geophytes; bulbs with papery or subfleshy tunics; **L** synanthous or hysteranthous, linear to lorate or lanceolate, rarely  $\pm$  succulent; **Inf** usually

solitary, with a long scape and pyramidal to subspicate racemes with  $\pm$  unilaterally arranged nodding flowers; **Bra** membranous, bracteoles present or absent; **Fl** nocturnal, scented; **Per** green, greenish, yellowish or brownish, often glaucous; **Tep** in 2 distinct series, basally united to form a short to long tube; tips of **OTep** spreading-ascending, with or without an apical appendage; **ITep** continuing the perianth tube, tips ascending or spreading; **Fil** inserted at the mouth of the perianth tube, thin-textured, appressed to the perianth; **Ov** sessile, ovoid, with numerous ovules; **Fr** flattened, deeply 3-lobed acute or retuse membranous capsules; **Se** compressed, oblong to discoid.

The genus is widely distributed esp. in Africa and Arabia and counts  $\pm$  26 species (Manning & al. 2009: 98–99). Centres of diversity are in S Africa and in India. The genus is closely related to the monotypic S African genus *Pseudogaltonia* and Manning & al. (2009) and Martínez-Azorín & al. (2011a) place the two genera in tribe *Dipcadieae*. Species of *Dipcadi* are easily recognizable on the base of the continuation of the perianth tube formed by the inner tepals, and the usually long-appendiculate tips of the outer tepals. Many taxa are notable for their glaucous dark green or brownish flowers. According to Manning & al. (2009: 98), *Dipcadi* can be divided into 2 series, ser. *Dipcadi* (outer tepals without apical appendage) and ser. *Uropetalon* (Burchell ex Ker-Gawler) J. C. Manning & Goldblatt (outer tepals with short to long apical appendage). In

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contrast, Pinter (2012: 99) found little evidence for such a division in his DNA-derived phylogeny and favours the recognition of 2 infrageneric taxa based on style length.

Moderate leaf succulence is found in the following species (of ser. *Dipcadi*) only:

**D. brevifolium** (Thunberg) Fourcade (Trans. Roy. Soc. South Africa 21: 78, 1932). **Type:** RSA, Eastern Cape (*Thunberg* s.n. [UPS, PRE [photo]]). — **Distr:** Namibia, throughout RSA, Moçambique, SW coastal Madagascar.

≡ *Hyacinthus brevifolius* Thunberg (1794) ≡ *Scilla brevifolia* (Thunberg) Ker Gawler (1812) ≡ *Periboea brevifolia* (Thunberg) Kunth (1843) ≡ *Baeoterpe brevifolia* (Thunberg) Salisbury (1866) (*nom. inval.*, ICN Art. 35.2); **incl.** *Polemannia hyacinthoides* P. J. Bergius ex Schlechtendal (1826) ≡ *Uropetalon hyacinthoides* (P. J. Bergius ex Schlechtendal) Sprengel (1827) ≡ *Dipcadi hyacinthoides* (P. J. Bergius ex Schlechtendal) Baker (1871) ≡ *Ornithogalum hyacinthoides* (Baker) J. C. Manning & Goldblatt (2004) (*nom. inval.*, Art. 33.6, Ex. 11); **incl.** *Lachenalia graminifolia* Solander ex Baker (1870); **incl.** *Dipcadi spirale* Baker (1892).

Bulbs shallowly seated or at ground-level, ovoid, ± 1.5 cm Ø; **L** 3–10, semi-erect or spreading, strap-shaped, 15–40 × 0.4–1 cm, succulent and coriaceous, slightly roughened, with parallel narrow channels, margins finely white-toothed; **Inf** 1–2, 25–35 cm, scape ± ⅓ of overall inflorescence length, naked; **Bra** all fertile, papery, 4–12 mm, longer than the pedicel; **Ped**

2–10 mm, elongating at fruiting time; **Fl** pendent; **Per** 16–25 mm, brownish-grey, slightly glaucous; appendix of **OTep** short and thick, 3–4 mm; tube of **ITep** 6 mm longer than the outer tube; free part of **Fil** ± 0.5 mm, flattened; **Ov** basally narrowed.

Manning & al. (2012) report that the flowers produce a sour/acrid nocturnal scent and that they are pollinated by the nocturnal moth *Syngrapha circumflexa*.

## References

- Manning, J. C. [ & al. 2009], Forest, F., Devey, D. S., Fay, M. F. & Goldblatt, P. (2009) A molecular phylogeny and a revised classification of *Ornithogaloideae* (*Hyacinthaceae*) based on an analysis of four plastid DNA regions. *Taxon* 58(1): 77–107, ill., key. <http://www.jstor.org/stable/27756826>
- Manning, J. C. [ & al. 2012], Goldblatt, P., Parker, E. & Kaiser, R. (2012) First record of pollination in the Afro-Eurasian *Dipcadi* Medik. (*Hyacinthaceae*): Pollination of *D. brevifolium* by the owlet moth *Syngrapha circumflexa* (*Noctuidae*). *South Afr. J. Bot.* 81(1): 15–18, ill. <https://doi.org/10.1016/j.sajb.2012.03.012>
- Martínez-Azorín, M. [ & al. 2011a], Crespo, M. B., Juan, A. & Fay, M. F. (2011) Molecular phylogenetics of subfamily *Ornithogaloideae* (*Hyacinthaceae*) based on nuclear and plastid DNA regions, including a new taxonomic arrangement. *Ann. Bot. (Oxford)*, n.s. 107: 1–37, ill. key. <https://doi.org/10.1093/aob/mcq207>
- Obermeyer, A. A. (1964) The South African species of *Dipcadi*. *Bothalia* 8(2): 117–137, key. <https://doi.org/10.4102/abc.v8i2.1615>
- Pinter, M. (2012) *Taxonomie und Phylogenie ausgewählter Vertreter der Gattung Dipcadi (Asparagaceae, Scilloideae, Ornithogaleae)*. Saarbrücken (DE): Akademikerverlag.





## Drimia HYACINTHACEAE

E. Van Jaarsveld and U. Eggli

**Drimia** Jacquin (Collectaneorum Suppl., 39, 1797). **Type:** *Drimia elata* Jacquin ex Willdenow [lectotype, designated by E. Phillips, Gen. South Afr. Pl., ed. 2, 190, 1951]. — **Urgineoideae** — **Lit:** Nordenstam (1970: monograph *Rhadamanthus* group); Jessop (1977: monograph s.s. S Africa); Stearn (1978: synopsis Mediterranean, India); Stedje (1987: Flora E Africa); Pfosser & Speta (2004: classification); Jaarsveld & Wyk (2006: key to cliff-dwelling taxa); Manning & al. (2014b: monograph *Schizobasis* group); Lebrun & Stork (2014: 77–84, synopsis tropical Africa); Knirsch & al. (2015: monograph *Rhodocodon* group). **Distr:** Africa, Madagascar, Mediterranean, SW Asia and extending to India, Vietnam and Myanmar. **Etym:** Gr. ‘drimys’, acute, biting; for the bitter acrid taste of the roots of *D. elata* (and not for the pointed capsules as suggested by some older sources).

**Incl.** *Urginea* Steinheil (1834). **Type:** *Urginea fugax* Steinheil [lectotype, designated by Adamson, J. South Afr. Bot. 8: 237, 1942].

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**Incl.** *Squilla* Steinheil (1836) (*nom. illeg.*, Art. 53.1). **Type:** *Scilla maritima* Linné.

**Incl.** *Fusifilum* Rafinesque (1837). **Type:** *Anthericum physodes* Jacquin [lectotype, designated by Deb & Dasgupta, J. Econ. Tax. Bot. 3: 823, 1982].

**Incl.** *Pilasia* Rafinesque (1837). **Type:** *Anthericum filifolium* Jacquin [lectotype, designated by Deb & Dasgupta, J. Econ. Tax. Bot. 3: 823, 1982].

**Incl.** *Strepsiphylla* Rafinesque (1837). **Type:** *Drimia villosa* Lindley.

**Incl.** *Tenicroa* Rafinesque (1837). **Type:** *Anthericum fragrans* Jacquin.

**Incl.** *Idothea* Kunth (1843). **Type:** *Drimia elata* Jacquin [lectotype, designated by Stearn, Ann. Mus. Goulandris 4: 203, 1978].

**Incl.** *Urginia* Kunth (1843) (*nom. inval.*, Art. 61.1). **Type:** *Urginea fugax* Steinheil.

**Incl.** *Drimya* Lemaire (1845) (*nom. inval.*, Art. 61.1). **Type:** *Drimia elata* Jacquin.

**Incl.** *Idothearia* Presl (1845). **Type:** not typified.

**Incl.** *Physodia* Salisbury (1866). **Type:** *Anthericum pusillum* Jacquin [lectotype, designated by Deb & Dasgupta, J. Econ. Tax. Bot. 3: 823, 1982].

**Incl.** *Rhadamanthus* Salisbury (1866). **Type:** *Hyacinthus convallarioides* Linné fil.

**Incl.** *Sypharissa* Salisbury (1866). **Type:** *Anthericum exuviatum* Jacquin [lectotype, designated by Obermeyer, Bothalia 13: 111, 1980].

- Incl.** *Schizobasis* Baker (1873). **Type:** *Schizobasis macowanii* Baker.
- Incl.** *Rhodocodon* Baker (1881). **Type:** *Rhodocodon madagascariensis* Baker [typification by inference, only element included].
- Incl.** *Litanthus* Harvey (1884). **Type:** *Litanthus pusillus* Harvey.
- Incl.** *Thuranthos* C. H. Wright (1916). **Type:** *Ornithogalum macranthum* Baker.
- Incl.** *Urgineopsis* Compton (1930). **Type:** *Urgineopsis salteri* Compton.
- Incl.** *Charybdis* Speta (1998). **Type:** *Scilla maritima* Linné.
- Incl.** *Ebertia* Speta (1998). **Type:** *Urginea nana* Oeyewole.
- Incl.** *Rhadamanthopsis* (Obermeyer) Speta (1998). **Type:** *Rhadamanthus namibensis* Obermeyer.
- Incl.** *Urginavia* Speta (1998). **Type:** *Scilla micrantha* A. Richard.
- Incl.** *Boosia* Speta (2001). **Type:** *Urginea macrocentra* Baker.
- Incl.** *Duthiea* Speta (2001) (*nom. illeg.*, Art. 53.1). **Type:** *Urginea senegalense* Kunth.
- Incl.** *Geschollia* Speta (2001). **Type:** *Ornithogalum anomalum* Baker.
- Incl.** *Indurgia* Speta (2001). **Type:** *Scilla indica* Roxburgh.
- Incl.** *Ledurgia* Speta (2001). **Type:** *Ledurgia guineensis* Speta.
- Incl.** *Sekanama* Speta (2001). **Type:** *Urginea sanguinea* Schinz.
- Incl.** *Mucinaea* M. Pinter & al. (2013). **Type:** *Tenicroa nana* Snijman.
- Incl.** *Sagittanthera* Martinez-Azorín & al. (2013). **Type:** *Rhadamanthus cyanelloides* Baker.
- Incl.** *Vera-duthiea* Speta (2016). **Type:** *Urginea senegalense* Kunth.

Perennial bulbous geophytes, usually hysteroanthous, with fleshy tunics forming a lax to compact bulb, solitary or proliferating to form groups; **L** strap-shaped, flat, variable, usually withering during the dry season, rarely completely absent in adult plants (*Schizobasis* group); **Inf** racemose, with glabrous and usually erect scape; **Per** campanulate; **Tep** spreading, recurved or reflexed, almost free or distinctly united at the base; **St** inserted at the throat of the perianth

tube, spreading or erect to erect-connivent; **Fil** terete to flat; **Anth** versatile, introrse; **Ov** sessile, ovoid to pyramidal, 3-locular with many ovules; **Sty** terete; **Sti** capitate; **Fr** 3-angled ovoid loculicidal capsules; **Se** black, angled.

The circumscription of *Drimia* has been controversially discussed in the past, and some authors (e.g. Speta (1998b) and later papers) have suggested accepting a number of segregate genera. This was heavily criticized by Stedje (2001) and Stedje (2002). In the traditional sense, *Drimia* consisted of  $\pm 15$  species, and was diagnostically separated by free tepals from the much larger genus *Urginea* (some 100 species) with fused tepals. Jessop (1975) and Jessop (1977) (subsequently followed by Stearn (1978)) argued that this and other allegedly important differences are quantitative and gradual, and cannot serve to discriminate between the two genera, and that *Urginea* should be treated as synonym of an expanded *Drimia*. This was subsequently corroborated by Stedje (1987), who also commented on the variability of flower architecture, and describes three main types differing in the arrangement of tepals (stellate-spreading, stellate-recurved, or reflexed) and stamens (spreading or erect). Goldblatt & Manning (2000: 710–712) accepted this change and concluded that a number of additional genera that showed similarities with *Drimia* but were treated as separate taxa should also be included: *Rhadamanthus* was separated from *Urginea* by having short filaments and anthers that dehisce by an apical pore, or tardily with a longitudinal slit almost to the base, and is therefore transitional (Nordenstam 1970, Snijman & al. 1999, Goldblatt & Manning 2000: 710). *Litanthus* and *Schizobasis* were separated from *Drimia* by having scabrid scapes, but this character also occurs in some former *Rhadamanthus*, as well as in some smaller species of *Drimia* (Goldblatt & Manning 2000: 710). The wiry inflorescence of the former *Schizobasis* species is a parallel development to the fleshier twining inflorescence of *Bowiea*, and there is no close relationship between the two. *Rhodocodon*, finally, differs in its nodding urceolate flowers with the tepals fused for most of their length; it was already treated as synonym of *Rhadamanthus* by Speta

(1998). Here, we follow the wide concept, and *Litanthus*, *Rhadamanthus*, *Rhodocodon* and *Schizobasis*, accepted at generic rank in the first edition of this Handbook, are now treated here as synonyms. *Drimia* now embraces some 100 species. It is characterized by short-lived flowers and tepals basally fused, and a caducous perianth abscising at the base and remaining as dry cap on the developing fruit (vs. long-lived flowers with persistent perianth attached to the fruit base, and free tepals in the sister genus *Bowiea*) (Goldblatt & Manning 2000: 710–711).

Only a couple of *Drimia* species are succulent, including some with bulbs almost completely desintegrated into separate, loosely arranged but grossly thickened outer tunics, such as the highly specialized *D. mzimvubuensis*. These can be easily propagated by detaching and rooting the individual still turgid tunics, which form an adventive bulb along the margin (Aditya 2013).

**D. acarophylla** E. Brink & A. P. Dold (South Afr. J. Bot. 69(3): 396–397, ills., 2003). **Type:** RSA, Eastern Cape (*Brink* 788 [GRA, BOL]). — **Distr:** RSA (Eastern Cape); blue-grey shale gravel patches.

Plants dwarf, inconspicuous, to 4 cm tall, in small colonies; bulbs underground, globose to irregularly ovoid, 1.4–2.5 × 1.1–2.4 cm; **R** numerous, white, fleshy, contractile, tunics clothing the upper ½ of the bulbs, thin, flaking, papery, not forming a neck; **L** 1–2, present or absent at anthesis, deciduous, underground part semiterete, white, lamina succulent, clavate, 9–24 × 5–8 mm at the broadest point, surfaces smooth, becoming wrinkled, dark grey-green with dull whitish bloom, adaxial surface shallowly channelled; **Inf** single, racemose, subcapitate, scape slender, erect, smooth, 1.1–2.7 cm, 1–3 mm Ø; **Bra** deltoid, 1.6–2 × 1–1.2 mm, loosely clasping, attenuate, saccate, keeled, occasionally with a spur; **Ped** 1–9 mm; **Fl** 6–17, opening 1 per day; **Per** spreading-erect, shallowly cup-shaped; **OTep** ovate, 4–5 × 1.8–2 mm, outer face purple-brown, inner face white flushed pink, apex obtusely pointed; **ITep** broadly elliptic, 4–4.4 × 1–1.5 mm, apex truncate; **St** erect; **Fil** lanceolate, 1.8–2 × 0.6–0.8 mm, white;

**Anth** ovoid, bilobed, 1.6 × 0.8 mm; **Ov** ovoid, 1.5–2.2 × 1.6 mm, shallowly 3-lobed, pale yellow; **Sty** terete, 1.6–2 mm, white; **Sti** swollen; **Fr** globose, 4.5–6.4 × 3–6.2 mm, campanulate at dehiscence; **Se** 2–2.4 × 1–2.2 mm, glossy, narrowly winged along the angles. — [E. Van Jaarsveld]

**D. albiflora** (B. Nordenstam) J. C. Manning & Goldblatt (*Strelitzia* 9: 711, 2000). **Type:** RSA, Western Cape (*Acocks* 23242 [PRE]). — **Distr:** RSA (Western Cape); Fynbos vegetation, mid-summer-flowering.

≡ *Rhadamanthus albiflorus* B. Nordenstam (1970).

Bulb underground, ovoid to pear-shaped, to 3 × 2.5 cm Ø, tunics papery, grey; **L** unknown; **Inf** to 25 cm, scape reddish-brown, erect, raceme lax, to 6 cm, to 15-flowered; **Bra** membranous, ovate-deltoid, to 2 mm, acuminate, spurred; **Ped** to 9 mm; **Fl** campanulate, drooping, to 6 mm; **Tep** white, oblong, basally connate for 1.5 mm, obtuse; free part of **Fil** flat; **Anth** to 2.7 mm, introrse; **Ov** ovoid, to 2 mm; **Fr** and **Se** unknown. — [E. Van Jaarsveld]

**D. altissima** (Linné *fil.*) Ker Gawler (*Curtis's Bot. Mag.* 27: t. 1074 + text, 1808). **Type:** RSA, “Cape Prov.” (*Thunberg* s.n. [UPS]). — **Distr:** Tropical and S Africa, from Senegal to E Africa (N-wards to Ethiopia) and to RSA and Namibia; widespread, often in grassland, bushlands, or open woodland. **I:** Sebsebe Demissew & Nordal (2010: 199–200). — Fig. 1.

≡ *Ornithogalum altissimum* Linné *fil.* (1782) ≡ *Urginea altissima* (Linné *fil.*) Baker (1873) ≡ *Idothea altissima* (Linné *fil.*) Kuntze (1891) ≡ *Urginavia altissima* (Linné *fil.*) Speta (1998); **incl.** *Ornithogalum giganteum* Jacquin (1797) ≡ *Drimia gigantea* (Jacquin) Oyewole (1975) ≡ *Urginea gigantea* (Jacquin) Oyewole (1975); **incl.** *Drimia uitenhagensis* Ecklon (1830); **incl.** *Scilla micrantha* A. Richard (1850) ≡ *Urginea micrantha* (A. Richard) Solms (1867) ≡ *Urginavia micrantha* (A. Richard) Speta (1998); **incl.** *Drimia barteri* Baker (1870) ≡ *Idothea barteri* (Baker) Kuntze (1891); **incl.** *Urginea brevipes* Baker (1874); **incl.** *Urginea forsteri* Baker (1897); **incl.** *Urginea kniphofioides* Baker



**Fig. 1** *Drimia altissima*. (*Urginea epigea*). (Copyright: E. Van Jaarsveld)

(1897); **incl.** *Urginea viridula* Baker (1898)  $\equiv$  *Urginavia viridula* (Baker) Speta (1998); **incl.** *Drimia paolii* Chiovenda (1916); **incl.** *Drimia incerta* A. Chevalier (1920) (*nom. inval.*, Art. 32.1d); **incl.** *Urginea epigea* R. A. Dyer (1947)  $\equiv$  *Urginavia epigea* (R. A. Dyer) Speta (2001).

Bulbs above or below ground, solitary or dividing to form small groups of up to four bulbs, globose, to 15 cm  $\varnothing$ , bulb scales fleshy, tightly imbricate, to 7 cm wide, withering from the tip; **L** hysteroanthous, 15–30  $\times$  2–3 cm, linear-lanceolate, tough, ascending, green and shiny; **Inf** racemose, erect, to 1 m, up to 100-flowered, scape terete, to 15 mm  $\varnothing$  at the base; **Fl** in the upper  $\frac{1}{2}$  of the inflorescence only; lower **Bra** linear-lanceolate, to 8 mm, basally spurred; **Ped** to 25 mm; **Fl** stellate; **OTep** linear-lanceolate, 6  $\times$  2.5 mm; **ITep** 6  $\times$  3 mm, white with green keel; **St** 5 mm; **Fil** tapering; **Ov** greenish, 4 mm,

oblong-ovoid; **Sty** erect, 3 mm; **Fr** 10  $\times$  10 mm, 3-angled; **Se** black, winged.

Variable with several distinct forms. Used medicinally by the inhabitants of Sekukuniland (RSA), and known to be very poisonous to livestock.

The synonymization of *Urginea epigea* here by Jessop (1977: 288) is not supported by Pfosser & Speta (2001: 219), since the epigeous bulbs appear to be genetically fixed.

**D. anomala** (Baker) Baker (in Thiselton-Dyer, Fl. Cap. 6: 442, 1897). **Type:** RSA, “Cape Prov.” (*Cooper* s.n. [not preserved]). — **Distr:** RSA (Western Cape, Eastern Cape, KwaZulu-Natal); Succulent Karoo and Bushveld vegetations.

$\equiv$  *Ornithogalum anomalum* Baker (1870)  $\equiv$  *Geschollia anomala* (Baker) Speta (2001); **incl.** *Urginea eriospermoides* Baker (1887).

Bulbs above-ground, solitary, globose to pear-shaped, 5–8  $\times$  5–8 cm  $\varnothing$ , with fleshy green tunics, withering grey-translucent; **R** fleshy, 2 mm  $\varnothing$ , terete; **L** 1 (occasionally 2), synanthous, dark green, ascending to spreading, firmly succulent, terete, to 30 cm, 4–6 mm  $\varnothing$ , surrounded by grey papery sheaths at the base, withering from the tip; **Inf** to 60 cm, up to 80-flowered, erect; lower **Bra** broadly ovate, 1 cm, spurred; upper **Bra** 1 mm, early deciduous; **Ped** to 8 mm; **Fl** spreading, yellowish-green; **Tep** reflexed,  $\pm$  5 mm, fused at the base; **OTep** 1 mm broad; **ITep** 2 mm broad; **St** to 4 mm; **Ov** 2 mm, ovoid; **Sty** erect, 1.5–2 mm; **Fr** ellipsoid, 4–6 mm, oblong; **Se** 1.5–2 mm. — [E. Van Jaarsveld]

**D. arenicola** (B. Nordenstam) J. C. Manning & Goldblatt (*Strelitzia* 9: 711, 2000). **Type:** RSA, Northern Cape (*Pillans* s.n. [BOL 18253]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo; late spring- and early summer-flowering. **I:** Nordenstam (1970: 169, as *Rhadamanthus*).

$\equiv$  *Rhadamanthus arenicola* B. Nordenstam (1970).

Bulb underground, fleshy, 2.5–5 cm  $\varnothing$ , tunics fleshy, somewhat loosely imbricate, ovate-



lanceolate, 1–3 × 0.5–1.5 cm, tips acuminate; **L** erect, filiform; **Inf** 5–15 cm, erect, lax; **Bra** membranous, ovate-deltoid, to 2 × 1.5 mm, acuminate; **Fl** campanulate, to 4 mm; **Tep** elliptic, connate, 4 × 2 mm, dirty white, obtuse; **Anth** to 1 mm; **Ov** ovoid, to 2.5 mm; **Fr** ovoid-globose, to 5 mm; **Se** oblong, to 4 mm, shiny black, rugose. — [E. Van Jaarsveld]

**D. chalumnensis** A. P. Dold & E. Brink (South Afr. J. Bot. 70(4): 631–634, ill., 2004). **Type:** RSA, Eastern Cape (*Dold* 4619 [GRA]). — **Distr:** RSA (Eastern Cape); shallow shale gravel flats, Valley Bushveld vegetation.

Bulbs underground, dwarf, winter-deciduous, formig colonies of up to 40 plants, globose to subglobose, 1–1.5 × 1.5–1.8 cm, tunics loose, separate, turgid, petiolate, each bearing a leaf, becoming truncate when the lamina is shed; **L** 2–8, present or absent at anthesis, prostrate, linear-lanceolate, 1.5–3.2 cm × 2–2.5 mm, stiffly coriaceous, subterranean part white, erect, adaxially channelled, acute, glabrous, margins light brown, cartilaginous, thickened; **Inf** single, subcapitate-racemose, scape erect, to 1.9 cm; **Bra** deltoid, 1.2–1.4 × 0.6 mm, attenuate, saccate, occasionally producing a short rounded spur to 0.4 mm; lowest **Ped** to 4 mm, decreasing in length further up; **Fl** spreading-erect, stellate; **Tep** fused for 0.8 mm at the base, recurved at the apex; **OTep** white flushed pale golden-brown above, 3–3.4 × 1.6–2 mm; **ITep** ovate, 3–3.2 × 1.4–1.6 mm, apices truncate; **St** erect, inserted at the base of the tepals; **Fil** 1.8–2 × 0.6–0.8 mm broad at the base, basally contiguous and forming a cup around the ovary, white; **Anth** globose, 0.6 × 0.6 mm; **Ov** ovoid, 1–1.4 × 1 mm, shallowly 3-lobed, pale green; **Sty** terete, 1–1.2 mm, white; **Sti** trigonous, papillate; **Fr** 3-lobed, 4–5 × 4–4.5 mm, subglobose, leathery, pale pinkish-brown; **Se** ± 24 per capsule, lightly winged along the angles, 1.6–1.9 × 1–1.6 mm, glossy, shallowly reticulate. — [E. Van Jaarsveld]

**D. cochlearis** Martínez-Azorín & al. (Taxon 39(6): 1239, 2014). **Type:** RSA, Western Cape

(*Martínez-Azorín & al.* MMA941 [GRA]). — **Distr:** RSA (Western Cape, Eastern Cape); deep sandy soils, or rocky soils on ledges, in shrubby Succulent Karoo vegetation, 150–900 m.

Bulb halfway above-ground, ovoid to globose, flattened at the top, 1.6–2.5 × 1.5–2.3 cm, dividing to form dense groups, tunics membranous; **R** fleshy, ± 2 mm Ø; **L** 4–9 in a basal rosette, mostly withered at flowering time, ascending-spreading, 1.9–4.5 × 0.7–0.9 cm, obovate-oblong, firm, leathery and slightly succulent, dark glossy green, smooth, concave with cucullate apex, margins membranous, 0.7–1 mm wide, erose, translucent and sometimes undulate; **Inf** ascending, to 23 cm, with 12–32 (–41) flowers; scape 5–10 cm, pale green, papillate in the basal part; **Bra** ovate-lanceolate to triangular, acuminate, to 1 mm, inconspicuous, lowermost with an evident basal spur; **Ped** (13-) 15–20 mm, patent or suberect; **Fl** (sub-) erect; **Tep** white with a pale green mid-stripe, ovate-oblong, 4–6 × 1.5–2 mm, shortly fused at the base for ± 0.4 mm, outer strongly reflexed, inner subpatent; **St** subpatent and spreading; **Fil** subcylindrical, white, smooth, 1.9–2.5 mm; **Ov** ovoid, white with pale green longitudinal stripes, 1.1–1.5 × 1–1.3 mm, sessile; **Sty** filiform, white, 2 mm, usually bent; **Sti** white, trigonous and inconspicuous; **Fr** ovoid, ± 5 × 4 mm, trigonous to subglobose. — [E. Van Jaarsveld]

**D. convallarioides** (Linné *fil.*) J. C. Manning & Goldblatt (*Strelitzia* 9: 711, 2000). **Type:** RSA, Northern Cape (*Thunberg* s.n. [UPS [Herb. Thunberg 8519]]). — **Distr:** RSA (Northern Cape, Western Cape); Fynbos vegetation, quartzitic sandstone rock crevices, midsummer-flowering. **I:** Nordenstam (1970: 161, as *Rhadamanthus*).

≡ *Hyacinthus convallarioides* Linné *fil.* (1782) ≡ *Rhadamanthus convallarioides* (Linné *fil.*) Baker (1871); **incl.** *Rhadamanthus montanus* B. Nordenstam (1970).

Bulb underground, ovoid to pear-shaped, to 5 cm Ø, tunics papery, grey-brown, translucent; **L** to 24, filiform, to 10 cm; **Inf** to 40 cm, scape reddish-brown, erect, raceme to 22 cm, to 50-flowered; **Bra** ovate-deltoid, to 2 mm, spurred;



**Ped** to 18 mm; **Fl** campanulate, drooping, to 8 mm; **Tep** white to pale yellow, to 8 × 3 mm, oblong; **Fil** basally connate, free parts flat; **Anth** yellowish-green, to 1.6 mm; **Ov** oblong-ovoid, to 3 mm; **Fr** subglobose; **Se** numerous. — [E. Van Jaarsveld]

**D. cryptopoda** (Baker) Pfosser & al. (Linzer Biol. Beitr. 38(2): 1736, ills. (p. 1735), 2006). **Type:** Madagascar (*Baron* 2164 [K 00009871 p. p.]). — **Lit:** Pfosser & al. (2006); Knirsch & al. (2015); both with ills. **Distr:** C Madagascar (Antananarivo: Ankaratra, Ibity); open grasslands, ± 1700–1800 m. **I:** Perrier (1938: 137, t. 18: 1, as *Hyacinthus*).

≡ *Hyacinthus cryptopodus* Baker (1883) ≡ *Ledebouria cryptopoda* (Baker) J. C. Manning & Goldblatt (2004) ≡ *Rhodocodon cryptopodus* (Baker) Knirsch & al. (2015).

Bulb underground, globose, 2–3 cm Ø, usually solitary, outer tunics fleshy, green, rather laxly arranged; **L** synanthous, 6–10 in a basal rosette, ascending, linear-lanceolate, 6 × 1 cm, elongating after flowering to 25 × 1 cm, somewhat fleshy, dark green, glossy; **Inf** to 5 cm, erect, sessile or with a scape to 5 cm; **Bra** lanceolate, pale rose, 2–3 mm, with a 2–3 mm long spur; **Fl** densely arranged, almost sessile, ascending-spreading; **Per** ± 7 mm long, white with pink, free lobes oblong, 2.5 × 1.5 mm; **St** attached in the middle of the short perianth tube; **Fil** filiform; **Ov** ovoid; **Sty** cylindrical, 2.5 mm; **Fr** globose-trigonal, 4 × 4.5 mm; **Se** few, ovoid, irregularly angled, black.

This taxon was previously treated as a member of *Hyacinthus*, and was tentatively placed in *Ledebouria* by Manning & al. (2004) on account of seed characters and bulb scales that produce fibres when torn. The molecular analysis of Pfosser & al. (2006) unambiguously placed the taxon amongst species of *Drimia*, with which it shares the strongly spurred bracts typical for *Urgineoideae* (Pfosser 2007). — [U. Eggli]

**D. cyanelloides** (Baker) J. C. Manning & Goldblatt (Strelitzia 9: 711, 2000). **Type:** RSA, Eastern Cape (*Flanagan* 573 [K, BOL, PRE]). —

**Lit:** Martínez-Azorín & al. (2013: as *Sagittanthera*, with ills.). **Distr:** RSA (Eastern Cape); Eastern Valley Bushveld vegetation, mainly on cliffs, flowering during late spring.

≡ *Rhadamanthus cyanelloides* Baker (1897) ≡ *Sagittanthera cyanelloides* (Baker) Martínez-Azorín & al. (2013); **incl.** *Drimia cremnophila* Van Jaarsveld (2006).

Bulbs solitary or cluster forming, halfway above-ground, 3 cm tall and to 8 cm Ø, bulb tunics loose, thick, succulent, oblong-clavate with emergent tips, 1.5–4.5 × 0.5–1.2 cm, with a flattened stalk to 2 × 0.4 cm, distal part ovate-depressed, upper face flat, lower face cymbiform to convex, apex obtuse or truncate, surface dark purplish-green; **R** white, fleshy, 2 mm Ø; **L** deciduous, linear, dorsiventrally compressed, amplexicaul at the base, 10–20 cm × 3–8 mm, dark green, margin entire, lower face with a distinct midrib; **Inf** spreading, ascending, racemose, 25–30 cm, scape dark green, terete, glabrous, racemes 5–8 cm with 4–12 nodding flowers; **Bra** 3.5–5 mm, white, the lowermost with a spur ± 6 mm long, linear-lanceolate, caudate, white, spur appressed to the scape; **Ped** 7–8 mm; **Fl** opening in the morning and lasting 2 days; **Per** white, 15–16 mm Ø; **Tep** oblanceolate-oblong, 7–9 × 2 mm, tips obtuse to acute; **St** appressed to the ovary into an erect cone-like structure, 11 mm long; **Fil** free, short, 1.5 × 0.5 mm; **Anth** linear-lanceolate, 5–6 mm, erectly projected, apex acute, opening by means of an apical pore; **Ov** ovoid, 3–4 × 1–2 mm, 6-grooved, green, shortly stipitate, stipe black; **Sty** 3 mm; **Sti** capitate; **Fr** not described; **Se** oblong, ± flattened, black. — [E. Van Jaarsveld]

**D. delagoensis** (Baker) Jessop (J. South Afr. Bot. 43(4): 294, 1977). **Type:** Moçambique (*Bolus* 7627 [K, BOL]). — **Lit:** Crouch & Martínez-Azorín (2015: with ills.). **Distr:** RSA (Mpumalanga, KwaZulu-Natal), border areas with Moçambique and Swaziland; dry savannah on the Lebombo Mts., spring- and early summer-flowering. **I:** Dyer (1942).

≡ *Urginea delagoensis* Baker (1897) ≡ *Sekanama delagoensis* (Baker) Speta (2001);

**incl.** *Urginea lydenburgensis* R. A. Dyer (1942);  
**incl.** *Urginea ubomboensis* R. A. Dyer (1942)  
 (*nom. inval.*, Art. 61.1).

Bulbs above-ground, solitary or dividing to form small groups of up to 5 plants, globose, 7–10 cm Ø, tunics large, imbricate, loose, succulent, globose, purplish-green, 3.5 × 3.5 cm, dry parts brown, older tunics becoming brownish and truncate at the top, ultimately withering; **R** fleshy, 3 mm Ø, terete; **L** 5–10, synanthous, green to glaucous, ascending, linear-acuminate, 14–50 cm, upper face channelled, lower face convex; **Inf** racemose, 45–50 cm, up to 50-flowered in the upper 1/3, erect, scape terete; floral **Bra** inconspicuous, triangular-lanceolate, white, 2 mm, withering before flowers mature; **Ped** 5–6 mm; **Fl** 5–10 mm apart, spreading to drooping; **Per** stellate above the cup-like base, ± 6 mm Ø; **Tep** linear-obovate, 6 × 2 mm, erectly spreading, white with purplish median stripes, tips obtuse; **St** 3 mm; **Fil** filiform; **Anth** 0.5 mm; **Ov** greenish, 2 mm, globose-obovoid; **Sty** erect, 3 mm; **Fr** oblong-ovoid, 10–12 × 4–5 mm; **Se** oblong, winged, 7 × 1.5 mm.

Crouch & Martínez-Azorín (2015) prefer to accept *Urginea lydenburgensis* as separate species, but a combination under *Drimia* is not yet available, pending the resolution of the classification of the group at genus level. These authors report *D. delagoensis* as non-toxic, while *U. lydenburgensis* is toxic to livestock. — [E. Van Jaarsveld]

**D. edwardsii** N. R. Crouch & Martínez-Azorín (Phytotaxa 195(2): 137, ill. (pp. 138–139), 2015). **Type:** RSA, KwaZulu-Natal (*Crouch* 1280 [BNRH, HSMC]). — **Distr:** RSA (S KwaZulu-Natal); shrubby vegetation on shale outcrops, 380–400 m, early spring-flowering.

Bulbs underground, solitary, angular-ovoid, 7 × 5 cm bearing 6–10 cucullate pedicellate loose grey-white bulb scales with obtuse apices; **R** contractile; **L** solitary, synanthous, 7–36 cm × 0.6–2 mm, ascending, filiform, sometimes flexuous, dark green, upper face shallowly grooved, lower face single- to multi-faceted, denticulate along the facet edges, apex acute; **Inf** 1 per bulb,

30–62 cm, ascending, up to 56-flowered; peduncle 15–32 cm, 1.4–2 mm Ø, base hirtellous; lowermost **Bra** weakly spurred, caducous, navicular, 0.7 mm; **Ped** 2.6–5.2 mm at anthesis, erectly spreading; **Fl** campanulate, 1 to 4 open at a time, pale brownish with darker keels; **Tep** oblong, ± 4.5–6 × 1 mm, canaliculate, apices obtuse, base fused for ± 0.3 mm, with overlapping margins forming a cup 2–2.5 mm long; **St** adnate to the tepals for ± 0.5 mm; **Fil** erect, subterete and tapering, ± 2.5 mm; **Anth** dehiscing by longitudinal slits, to 0.5 mm, yellow with yellow pollen; **Ov** ellipsoid, 1.5 × 1.3 mm, truncate; **Sty** columnar, ± 2.5 mm, white, truncate; **Sti** minutely papillate **Fr** (immature) prolate, ± 7.5 × 3 mm, 4–5 mm pedicellate; **Se** narrowly lanceolate, flattened, ± 5 × 1.5 mm.

The bulbs of *D. edwardsii* are very similar to those of *D. haworthioides*, which is part of *Drimia* s.s., however, with strongly reflexed tepals, and different foliage leaves. *D. mzimvubuensis* also has a similar bulb architecture but differs in stellate flowers and connivent sagittate anthers. — [E. Van Jaarsveld]

**D. fasciata** (B. Nordenstam) J. C. Manning & Goldblatt (Strelitzia 9: 711, 2000). **Type:** RSA, Northern Cape (*Leistner* 1983 [PRE, LD]). — **Distr:** Namibia, RSA (Northern Cape); arid savanna, spring-flowering. **I:** Nordenstam (1970: 177, as *Rhadamanthus*).

≡ *Rhadamanthus fasciatus* B. Nordenstam (1970).

Bulb ovoid to pear-shaped, underground, to 4 × 3 cm Ø, tunics papery, grey-brown; basal **L** sheath cross-banded; **L** filiform, solitary; **Inf** to 25 cm, scape brownish, erect, raceme lax, to 11 cm, to 30-flowered; **Bra** ovate-deltoid, to 1.5 mm, spurred; **Ped** to 11 mm; **Fl** campanulate, drooping, to 5.5 mm; **Tep** white to pale yellow, oblong; **Fil** free; **Anth** green to yellowish-green, to 2.3 mm; **Ov** globose-ovoid, to 2 mm; **Fr** and **Se** unknown. — [E. Van Jaarsveld]

**D. flagellaris** T. J. Edwards & al. (South Afr. J. Bot. 71(1): 122–126, ill., 2005). **Type:** RSA, KwaZulu-Natal (*Crouch* 1023 [NU, K, NH,

PRE]). — **Distr:** RSA (Eastern Cape, KwaZulu-Natal); quartzitic sandstone cliffs in Valley Bushveld vegetation.

Evergreen; bulbs above-ground, proliferating from the base to form tight clusters, angular-ovoid,  $3\text{--}7 \times 2.5\text{--}5.5$  cm, tunics keeled, imbricate, green to reddish, truncate; **L** 1–5, terete,  $10\text{--}80$  cm  $\times$   $2.5\text{--}7$  mm, flaccid, green to glaucous, sheathing basal part with membranous margin, apex acute, becoming truncate due to abscission; **Inf** 1–6 per bulb, racemose, 20–65 cm, 20- to 90-flowered; lower **Bra** caudate, upper **Bra** weakly spurred, naviculate; **Ped** 17–25 mm; **Fl** stellate; **Tep**  $5\text{--}8 \times 2\text{--}3$  mm, fused below for 0.2–0.5 mm; **OTep** narrowly obovate; **ITep** narrowly elliptic, obtuse; **St** ascending; **Fil** lanceolate; **Anth** versatile; **Ov** obovoid, 3-lobed,  $2.5\text{--}4 \times 1.7\text{--}2.5$  mm; **Sty** erect, 1–3.5 mm; **Fr** erect, ovoid, 6–7.5 mm, apex acute; **Se** elongate, wrinkled. — [E. Van Jaarsveld]

**D. haworthioides** Baker (Gard. Chron., ser. nov. 3: 366, 1875). **Type:** RSA, Eastern Cape (*Bolus* 40 [K]). — **Distr:** RSA (Western Cape, Eastern Cape); Succulent Karoo vegetation and arid savanna, usually in the shade of shrubs, midsummer-flowering. — Figs. 2 and 3.

Bulbs solitary or forming small groups, with loose, incurved, succulent, pink-purplish, club-shaped tunics, outer tunics 0.5–2.5 cm petiolate, flat with a swollen, semiglobose apical part  $1.5 \times 1.2$  cm, inner tunics becoming smaller towards the centre, ovate-attenuate, 2.5 cm; **R** succulent, spreading, to 3 mm  $\varnothing$ , white; **L** linear-lanceolate,  $3.5\text{--}5 \times 0.6\text{--}1$  cm, ciliate, spreading and appressed against the ground (in autumn and winter), green, channelled and tubular at the base; **Inf** 20–24 cm; scape erect, purple, 1 mm  $\varnothing$ ; **Bra**  $4 \times 1$  mm, basally spurred for 2 mm; **Fl** horizontally spreading; closed **Per** 7–13 mm, ventricose in the lower part and 3 mm  $\varnothing$  at the base; **Tep** free for 7–9 mm, distinctly reflexed, whitish, green towards the apex; **Fil** 7–8 mm, white, flat and broadening towards the base, appressed against the style; **Anth** 0.5 mm, dorsifixed, versatile, dirty brown; **Ov** conical, green,  $2 \times 2$  mm; **Sty** 10 mm, elongating to 11 mm after anthesis; **Fr**



**Fig. 2** *Drimia haworthioides*. (Copyright: U. Eggli)

3-angled,  $8 \times 4$  mm; **Se** oblong,  $5 \times 2$  mm, shiny. — [E. Van Jaarsveld]

**D. intricata** (Baker) J. C. Manning & Goldblatt (*Strelitzia* 9: 712, 2000). **Type** [lecto]: RSA (*Zeyher* 4284 [K, SAM]). — **Distr:** Ethiopia, Zimbabwe, Zambia, Moçambique, Angola, Tanzania, Namibia, Botswana, Swaziland, RSA (widespread).

≡ *Anthericum intricatum* Baker (1872) ≡ *Schizobasis intricata* (Baker) Baker (1874).

Widespread throughout the summer rainfall regions of tropical and S Africa. Distinguished from the closely related *D. sigmoidea* from winter rainfall regions of RSA by suberect to spreading pedicels that become geniculate in fruit. — [E. Van Jaarsveld]

**D. intricata** var. **intricata** — **Lit:** Manning & al. (2014b: with ills.). **Distr:** Ethiopia, Zimbabwe,



**Fig. 3** *Drimia haworthioides*.  
(Copyright: E. Van Jaarsveld)



**Fig. 4** *Drimia intricata*  
var. *intricata*. (Copyright:  
U. Eggli)



Zambia, Moçambique, Angola, Tanzania, Namibia, Botswana, Swaziland, RSA (widespread); well-drained rock-crevices, to 1500 m. **I:** Stedje (1996: 29, as *Schizobasis*); Maule (2010: as *Schizobasis*, ills. of variability). – Figs. 4 and 5.

**Incl.** *Schizobasis macowanii* Baker (1873); **incl.** *Asparagus cuscutoides* Burchell ex Baker (1875)  $\equiv$  *Schizobasis cuscutoides* (Burchell ex Baker) Bentham & Hooker (1883)  $\equiv$  *Drimia cuscutoides* (Burchell ex Baker) J. C. Manning

& Goldblatt (2000); **incl.** *Schizobasis angolensis* Baker (1878); **incl.** *Schizobasis schlechteri* Baker (1901); **incl.** *Schizobasis dinteri* Krause (1912); **incl.** *Schizobasis gracilis* R. E. Fries (1916); **incl.** *Schizobasis buchbergensis* Dinter (1932); **incl.** *Asparagus micranthus* Thunberg ex Jessop (1977) (*nom. inval.*, Art. 34.1a).

Bulbs deciduous, globose, below or above ground, 1–5 cm  $\varnothing$ , outer tunics papery, whitish, the inner overlapping, green or pink; L only

**Fig. 5** *Drimia intricata* var. *intricata*. (Copyright: U. Eggli)



present at the seedling stage, filiform, to  $40 \times 0.3$  mm; **Inf** persistent, 1–3, deflexed at the base then suberect, sprawling to twining, 5–20 cm long, wiry, purplish below, sparingly to richly branched, lower **Br** subopposite or ternate, **Br** suberect or divaricate, straight or flexuose; **Bra** 2–3 mm, lanceolate, spurred; **Ped** 10–20 mm, suberect to spreading, arcuate-ascending or apically deflexed at flowering, geniculate in fruit; **Fl** campanulate, spreading to pendent; **Tep** white to pale yellow, 3–4 mm, connate at the base, lobes spreading or apically recurved, elliptic to obovate  $2.5\text{--}3 \times 1\text{--}1.5$  mm, penicillate; **St** adnate to the tepals, inserted at the top of the tube, connivent around the style; **Fil** filiform, suberect or apically inflexed,  $\pm 2$  mm; **Anth** spreading or connivent around the style, dorsifixed, connective  $\pm 0.1$  mm; **Ov** subglobose,  $\pm 1$  mm  $\varnothing$ ; **Sty** columnar, 1.5 mm, slightly longer than the ovary, erect or spreading; **Fr** subglobose to narrowly ellipsoid,  $3\text{--}5 \times 2\text{--}5$  mm; **Se** ellipsoid with peripheral wing,  $1.5\text{--}2 \times 1\text{--}1.5$  mm, glossy black. — [E. Van Jaarsveld]

**D. intricata** var. **visagieae** Van Jaarsveld (Bradleya 32: 78–79, ill., 2014). **Type:** Angola, Benguella (Van Jaarsveld & Harrower 23119

[LUB, NBG]). — **Distr:** SW Angola (Lubango); NE-facing quartzitic vertical cliffs, 2000 m.

Differs from var. *intricata*: Bulbs broadly ovate, yellowish-green,  $3.5\text{--}5 \times 4.5\text{--}5.5$  cm; **Inf** only 10–14 cm long and broad; **Tep** white,  $6\text{--}7 \times 2\text{--}2.5$  mm. — [E. Van Jaarsveld]

**D. karooica** (Obermeyer) J. C. Manning & Goldblatt (Strelitzia 9: 712, 2000). **Type:** RSA, Western Cape (Van Zanten s.n. [PRE 45560]). — **Distr:** RSA (Northern Cape, Western Cape: Little and S Great Karoo); in rock crevices, midsummer-flowering.

$\equiv$  *Rhadamanthus karooicus* Obermeyer (1980)  
 $\equiv$  *Rhadamanthopsis karooicus* (Obermeyer) Speta (1998).

Bulbs clustering, underground, oblong-globose to 3 cm  $\varnothing$ , with exposed green fleshy tunics withering grey at the tips; **R** terete, succulent, to 2 mm  $\varnothing$ ; **L** to 6, lorate-lanceolate, spreading, to  $8 \times 2$  cm, green, glabrous and shiny, apex acute, mucronate; **Inf** to 20 cm, scape erect, to 30-flowered in the upper part; **Bra** membranous; **Ped** to 8 mm; **Fl** campanulate,  $\pm 9$  mm, mauve, free **Tep** part  $\pm 5$  mm; **Fil** basally connate, connivent; **Anth** 1 mm; **Ov** ovoid; **Fr** narrowly ellipsoid, 5–7 mm, apiculate; **Se** semi-discoid to



narrowly obovoid, 4–5 mm, black, shiny. — [E. Van Jaarsveld]

**D. loedolffiae** Van Jaarsveld (Aloe 43(2–3): 50, ill., 2006). **Type:** RSA, Eastern Cape (Van Jaarsveld & Voigt 17914 [NBG]). — **Distr:** RSA (Eastern Cape: Kei River); shale cliffs in Valley Bushveld vegetation.

Evergreen, bulbs above-ground, proliferating from the base to form tight clusters, ovoid to globose, 4–4.5 × 2.5–5 cm, outer tunics greyish-white, papery, exposing the purplish-green inner tunics; **L** 2–4, flaccid, linear, terete, tapering towards the apex, 20–26 cm × 1–4 mm, surface striate, bright green, withering from the tip; **Inf** racemose, 35–40 cm; racemes 60- to 65-flowered, 12–15 cm, flowers 1–3 mm apart, densely arranged in the distal ¼; **Bra** deltoid-cymbiform, 2 × 0.5 mm, purplish-white, slightly translucent, basal bracts caudate, spur to 4 × 1 mm; **Ped** 1.5–2.5 mm, lengthening to 4–5 mm at fruiting time; **Fl** stellate, cream-coloured, to 12 mm Ø; **Tep** linear-elliptic to linear-obovate; **OTep** 5.5 × 1.75 mm; **ITep** 5 × 1.5 mm; **St** 2.5 mm; **Fil** linear, inner slightly shorter; **Anth** 1 mm, versatile, pollen yellow; **Ov** ovoid, 3-lobed, tapering towards the apex, 1.5–2 × 1.5 mm, green, shortly stipitate; **Sty** erect, 2 mm; **Sti** minute, truncate; **Fr** ovoid, 5 × 2.5–4 mm; **Se** flattened, falcate, 2.5–3 × 1–1.8 mm. — [E. Van Jaarsveld]

**D. maritima** (Linné) Stearn (Ann. Mus. Goulandris 4: 204, 1978). **Type:** not typified. — **Lit:** Stearn (1978: classification); Speta (1980: cytology); Speta (2001: classification). **Distr:** Mediterranean from Portugal to Turkey and Israel, also Canary Islands, N Africa (Morocco, Tunisia, Libya); autumn-flowering.

≡ *Scilla maritima* Linné (1753) ≡ *Ornithogalum maritimum* (Linné) Lamarck (1779) ≡ *Squilla maritima* (Linné) Steinheil (1836) (*incorrect name*, Art. 11.4) ≡ *Urginea maritima* (Linné) Baker (1872) ≡ *Charybdis maritima* (Linné) Speta (1998); **incl.** *Anthericum aphyllum* Forsskål (1775) ≡ *Urginea aphylla* (Forsskål) Speta (1980) ≡ *Charybdis aphylla* (Forsskål)

Speta (1998); **incl.** *Scilla anthericoides* Poirét (1789) ≡ *Urginea anthericoides* (Poirét) Steinheil (1834) ≡ *Squilla anthericoides* (Poirét) Jordan & Fourreau (1869) (*incorrect name*, Art. 11.4) ≡ *Urginea maritima* var. *anthericoides* (Poirét) Maire & Weiller (1958); **incl.** *Scilla undulata* Desfontaines (1798) ≡ *Urginea undulata* (Desfontaines) Steinheil (1834) ≡ *Charybdis undulata* (Desfontaines) Speta (2001); **incl.** *Anthericum fugax* Moris (1827) ≡ *Urginea fugax* (Moris) Steinheil (1834) ≡ *Scilla fugax* (Moris) Munby (1847) ≡ *Drimia fugax* (Moris) Stearn (1978); **incl.** *Urginea scilla* Steinheil (1834) (*nom. illeg.*, Art. 52.1); **incl.** *Squilla pancration* Steinheil (1836) (*incorrect name*, Art. 11.4) ≡ *Urginea pancration* (Steinheil) G. de Philippe (1863) ≡ *Urginea maritima* var. *pancracion* (Steinheil) Baker (1873) ≡ *Charybdis pancration* (Steinheil) Speta (1998); **incl.** *Urginea hesperia* Webb & Berthelot (1848) ≡ *Charybdis hesperia* (Webb & Berthelot) Speta (1998); **incl.** *Squilla insularis* Jordan & Fourreau (1869) (*incorrect name*, Art. 11.4) ≡ *Urginea insularis* (Jordan & Fourreau) Grey (1938); **incl.** *Squilla littoralis* Jordan & Fourreau (1869) (*incorrect name*, Art. 11.4) ≡ *Urginea littoralis* (Jordan & Fourreau) Grey (1938); **incl.** *Squilla numidica* Jordan & Fourreau (1869) (*incorrect name*, Art. 11.4) ≡ *Urginea numidica* (Jordan & Fourreau) Grey (1938) ≡ *Urginea maritima* var. *numidica* (Jordan & Fourreau) Maire & Weiller (1958) ≡ *Charybdis numidica* (Jordan & Fourreau) Speta (1998); **incl.** *Squilla sphaeroidea* Jordan & Fourreau (1869) (*incorrect name*, Art. 11.4) ≡ *Urginea sphaeroidea* (Jordan & Fourreau) Grey (1938) ≡ *Urginea maritima* var. *sphaeroidea* (Jordan & Fourreau) Maire & Weiller (1958); **incl.** *Urginea undulata* var. *caeculi* Pau (1916) ≡ *Drimia undata* ssp. *caeculi* (Pau) Mateo & M. B. Crespo (1995) ≡ *Urginea undulata* ssp. *caeculi* (Pau) M. B. Crespo & Mateo (1997); **incl.** *Urginea maura* Maire (1923) ≡ *Urginea maritima* var. *maura* (Maire) Maire (1958) ≡ *Charybdis maura* (Maire) Speta (1998) ≡ *Drimia maritima* ssp. *maura* (Maire) Förther & Podlech (2001); **incl.** *Urginea maritima*

var. *stenophylla* Maire (1929); **incl.** *Urginea undulata* var. *tazensis* Battandier & Maire (1931)  $\equiv$  *Charybdis tazensis* (Battandier & Maire) Speta (2001)  $\equiv$  *Urginea tazensis* (Battandier & Maire) Valdés (2004); **incl.** *Urginea anthericoides* var. *secundiflora* Maire (1933); **incl.** *Urginea maritima* var. *angustifolia* Maire (1938)  $\equiv$  *Urginea maritima* fa. *angustifolia* (Maire) Maire (1958); **incl.** *Urginea maritima* fa. *latifolia* Maire & Weiller (1958) (*nom. inval.*, Art. 36.1); **incl.** *Drimia undata* Stearn (1978).

Bulbs massively voluminous, underground or just slightly emerging, to 10–15 cm  $\varnothing$ , pear-shaped, outer tunics dry; **L** deciduous, hysteroanthous, to 35  $\times$  2–7 cm, appressed to the ground, flat; **Inf** to 150 cm, scape purplish, terete, raceme dense, 50- to 100-flowered; **Bra** lanceolate-linear, 5–8 mm, conspicuously spurred; **Ped** 10–20 mm; **Fl** stellate; **Tep** whitish with greenish to pinkish midvein area, 6–8 mm; **Fil** white; **Anth** greenish; **Fr** ovoid; **Se** 20–30, 3  $\times$  6–8 mm, shiny.

Al-Tardeh & al. (2008) have convincingly shown that this taxon is a succulent, as explained by Eggli & Nyffeler (2009): Bulb water content diminishes during the dry season, and the bulk volume of the bulb scale tissue is made up by a large-celled parenchymatic tissue with high water-storage capacity. The stored water is used to produce the inflorescence during the dry season.

Pfossner & Speta (2001) and Pfossner & Speta (2004) recognize the segregate genus *Charybdis* for this species, which was also informally referred to as the *Urginea maritima* aggregate in the past. The species is cytologically variable, and includes diploids ( $2n = 20$ ), triploids, tetraploids, pentaploids and hexaploids; some cytotypes are geographically restricted, others more widespread (Stearn 1978). According to Pfossner & Speta (2001), allopolyploidization likely played a role in the evolution of this species complex, but the cytological data is not congruent with their phylogeny derived from molecular markers, although a strong geographic pattern has been found (Pfossner & Speta 2004). Some authors, e.g. Maire (1958), divide the species into many infraspecific taxa (some of them rather distinct), while Speta (1980) advocates a division into several cryptic

species (“Kleinarten”). No complete picture of the variability is available over the whole geographic range, however, and the species is here treated as a single, variable entity.

The bulbs (known as “sea onion”) of this species are medicinally used since ancient times for their diuretic and cardiac activity due to glycosides, and the plant was also traditionally believed to keep away evil spirits (Stearn 1978). Gemmill (1974) provides a summary of pharmacological knowledge. According to Speta (2001), the bulbs are also traditionally used as rodent poison. The same author in addition discusses the confusion with *Albuca bracteata* (“Pregnant Onion”, “False Sea Onion”). — [U. Eggli]

**D. media** Jacquin ex Willdenow (Spec. Pl. 2: 166, 1799). **Type:** [icon]: Jacquin, Icones 2: t. 1375, 1795. — **Distr:** RSA (Western Cape); near the sea or on slopes in Renosterveld vegetation.

$\equiv$  *Hyacinthus medius* (Jacquin ex Willdenow) Poiret (1813)  $\equiv$  *Idothea media* (Jacquin ex Willdenow) Kunth (1843).

Bulbs underground, ovoid, 3–9.5  $\times$  2.5–8 cm, with tight reddish tunics; **L** to 20, synanthous, to 8–40 cm, green, ascending to spreading, lamina succulent, terete, 1.5–4 mm  $\varnothing$ ; **Inf** racemose, to 60 cm, up to 35-flowered, erect; **Bra** to 2.5 mm, spurred, soon deciduous; **Fl** spreading, purplish; **Tep** reflexed, fused at the base, 10–16 mm; **Fil** linear-lanceolate, fused to the mouth of the perianth, to 6 mm; **Anth** to 2 mm; **Ov** to 3 mm, ovoid; **Sty** erect, 6–8 mm, 3-lobed; **Fr** oblong, 9–11 mm; **Se** 6–7 mm, flattened. — [E. Van Jaarsveld]

**D. multifolia** (G. J. Lewis) Jessop (J. South Afr. Bot. 43(4): 278, 1977). **Type:** RSA, Northern Cape (Lewis 60870 [SAM]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo vegetation. – Fig. 6.

$\equiv$  *Urginea multifolia* G. J. Lewis (1952)  $\equiv$  *Sypharissa multifolia* (G. J. Lewis) Obermeyer (1980)  $\equiv$  *Tenicroa multifolia* (G. J. Lewis) Obermeyer (1981).

Bulbs underground, solitary, to 4 cm long, globose to ellipsoid; **L** to 50, synanthous, 10–20 cm  $\times$  0.2 mm, green, terete, spirally



**Fig. 6** *Drimia multifolia*. (Copyright: U. Egli)

twisted; **Inf** racemose, erect, to 20 cm, up to 15-flowered; **Bra** triangular-lanceolate, to 4 mm, spurred at the base; **Ped** to 8 mm; **Fl** stellate; **Tep** elliptic, 12 × 5 mm, white with brownish median stripes, apex obtuse; **St** 5 mm; **Fil** filiform; **Ov** 4 mm, oblong-ellipsoid; **Sty** erect, 3 mm; **Fr** and **Se** unknown. — [E. Van Jaarsveld]

**D. mzimvubuensis** Van Jaarsveld (Aloe 42(4): 82–83, ills., 2006). **Type:** RSA, Eastern Cape (Van Jaarsveld & al. 58 [PRE]). — **Lit:** Martínez-Azorín & al. (2013: as *Sagittanthera*, with ills.). **Distr:** RSA (Eastern Cape: Mzimvubu River); Eastern Valley Bushveld vegetation, on shale cliffs.

≡ *Sagittanthera mzimvubuensis* (Van Jaarsveld) Martínez-Azorín & al. (2013).

Evergreen, bulbs just visible at ground-level, proliferating from the base to form loose clusters, ovoid, to 5 cm tall, tunics loosely arranged, club-shaped, 1.8–3 × 1.5–2.3 cm, succulent, maroon-brown, stipitate, apex obtuse, stalk-like base flattened, to 4 mm Ø; **R** white, fleshy, 2 mm Ø;

**L** linear, subterete, amplexicaul at the base, 4.7–5 cm × 3–5 mm, leathery, dark green, adaxial surface shallowly channelled, abaxial surface 12- to 14-grooved, minutely ciliate on the angles; **Inf** ascending, 34–38 cm, racemes 6–12 cm, with 20–30 pendent flowers; **Bra** caudate, 8 mm, white, linear-lanceolate, spur 10 mm, linear-lanceolate; **Ped** 15–18 mm, pendent; **Fl** 22–24 mm Ø, stellate; **Tep** white, 9 × 3 mm, lanceolate to strap-shaped, apices obtuse; **Fil** fused into a central cylindrical staminal column 2.5 mm high and 2 mm wide, apices free, triangular, 1 × 1 mm, together tapering into a cone-like structure consisting of acute appressed introrse anthers and in the centre exposing the white stigma for 0.5 mm; **Anth** 3 mm long, sagittate; **Ov** green, ovoid-tapering, 6-grooved, 3 × 1.5 mm; **Sty** 4.5 mm, white; **Sti** capitate; **Fr** 10 × 7.5 mm; **Se** 7 × 3 mm, oblong, flat. — [E. Van Jaarsveld]

**D. namibensis** (Obermeyer) J. C. Manning & Goldblatt (Strelitzia 9: 712, 2000). **Type:** Namibia (*Giess* 13781 [PRE, WIND]). — **Distr:** S Namibia; Succulent Karoo vegetation, midsummer-flowering.

≡ *Rhadamanthus namibensis* Obermeyer (1980) ≡ *Rhadamanthopsis namibensis* (Obermeyer) Speta (1998).

Bulb ovoid-globose, underground, to 5 cm Ø, tunics fleshy with transversely banded leaf bases, becoming white; **R** terete, succulent; **L** 2–4, hysteroanthous, linear-lanceolate, ascending, to 24 × 2.5 cm, glaucous, canaliculate; **Inf** to 70 cm, erect, many-flowered in the upper part; **Bra** spurred; **Ped** to 8 mm; **Fl** campanulate, 9 mm, pale mauve; **Tep** connate for ± 4 mm; **Fil** basally connate, 1.5 mm; **Ov** ovoid; **Fr** ovoid, to 7 mm; **Se** flat, black, oblong, to 5 mm. — [E. Van Jaarsveld]

**D. platyphylla** (B. Nordenstam) J. C. Manning & Goldblatt (Strelitzia 9: 712, 2000). **Type:** RSA, Western Cape (*Esterhuysen* 18135 [BOL]). — **Distr:** Namibia, RSA (Northern Cape, Western Cape, Free State); Fynbos vegetation, quartzitic sandstone rock crevices, midsummer-flowering. **I:** Nordenstam (1970: 171, as *Rhadamanthus*).

≡ *Rhadamanthus platyphyllus* B. Nordenstam (1970).

Bulb ovoid-globose, underground, to 5 × 4 cm, white, softly succulent; **L** 2, subopposite, flat, linear to ovate-elliptic, horizontally patent, to 4 × 2.5 cm, upper surface velutinous, apex obtuse; **Inf** to 30 cm, scape reddish-brown, erect, papillate-hirsute, raceme to 12 cm, to 50-flowered; **Bra** ovate-deltoid, acuminate, to 2 mm, spurred; **Ped** to 10 mm; **Fl** urceolate, drooping, to 6 mm; **Tep** brownish, to 6 × 2.5 mm, oblong, fused in the lower part; **Fil** basally connate, free parts hairy; **Anth** yellowish, to 1.8 mm; **Ov** ovoid, to 2 mm, glabrous; **Fr** subglobose to 7 mm; **Se** flat, oblong, to 4 mm. — [E. Van Jaarsveld]

**D. rotunda** (H. Perrier) J. C. Manning & Goldblatt (Edinburgh J. Bot. 60(3): 557, 2004). **Nom. inval.**, ICN Art. 39.1?. **Type:** Madagascar, Fianarantsoa (Perrier 16583 [P]). — **Lit:** Knirsch & al. (2015: as *Rhodocodon*, with ill.). **Distr:** W Madagascar (Fianarantsoa, Mahajanga, Toliara); sandy to rocky soils in deciduous forests. **I:** Perrier (1938: 121, Fig. 16: 7–8, as *Rhodocodon*).

≡ *Rhodocodon rotundus* H. Perrier ex Knirsch & al. (2015) ≡ *Rhadamanthus rotundus* (H. Perrier) Speta (1998) (*nom. inval.*, ICN Art. 39.1?); **incl.** *Rhodocodon rotundatus* hort. (s.a.) (*nom. inval.*, Art. 61.1); **incl.** *Rhodocodon rotundus* var. *campanulatus* H. Perrier (1931) (*nom. inval.*, ICN Art. 39.1); **incl.** *Rhodocodon campanulatus* Knirsch & al. (2015).

Bulb at ground-level or above-ground, broader than tall, greenish or covered with thin papery ochre tunics, often dividing and forming groups, succulent; **L** hysteranthous, numerous, semi-erect to flatly spreading, dark green, narrowly lanceolate, to 20 cm × 7 mm, slightly succulent with thickened midrib; **Inf** to 40 cm, scape to 20 cm; **Fl** laxly arranged; **Bra** narrowly lanceolate-linear, 5–8 mm, basally 3-veined, spur thin, 1.5–2 mm, variously shaped; **Ped** thin, 20–25 mm; **Per** globose, 7–8 mm Ø, greenish-white to greenish-brown; **Fil** subulate; **Anth** ovoid; **Fr** broadly ovoid, 7 × 6 mm; **Se** 1–2 per locule, ellipsoid to obovoid, 4 × 3 mm, black, inner face flattened.

Knirsch & al. (2015) argue that the name *Rhodocodon rotundus* was not validly published by Perrier in 1931 (and validate it in their paper), as it appears that the relevant journal issue was never published. If this interpretation is true, the name *Drimia rotunda* would be invalid. The same authors recently separated the invalidly published var. *campanulatus* as separate species, differing by longer, more richly flowered inflorescences. — [U. Eggli]

**D. secunda** (B. Nordenstam) J. C. Manning & Goldblatt (Strelitzia 9: 712, 2000). **Type:** Namibia (Giess 2350 [M, WHK]). — **Distr:** SW Namibia; Succulent Karoo vegetation, winter-rainfall region, spring-flowering. **I:** Nordenstam (1970: 169, as *Rhadamanthus*).

≡ *Rhadamanthus secundus* B. Nordenstam (1970).

Bulb lax and open, just visible at ground-level, tunics forming a rosette, clavate to fusiform, succulent, to 4 × 20 mm, apically contracted; **L** linear-filiform, 8 cm × 1.5 mm, apex obtuse; **Inf** to 5 cm, to 25-flowered, secund; **Bra** ovate, to 2 mm, spurred; **Ped** to 2 mm; **Fl** campanulate, to 5 mm; **Tep** connate in the lower ½, brownish; **Fil** basally connate, free parts filiform; **Anth** light yellow, to 1.6 mm; **Ov** subglobose, to 2.5 mm; **Fr** and **Se** unknown. — [E. Van Jaarsveld]

**D. sigmoidea** J. C. Manning & J. Deacon (South Afr. J. Bot. 30: 267–268, ill., 2014). **Type:** RSA, Western Cape (Deacon & al. 2820 [NBSG, MO]). — **Distr:** RSA (Western Cape); Robertson Karoo vegetation, winter rainfall, flowering late spring and summer.

≡ *Schizobasis sigmoidea* (J. C. Manning & J. Deacon) Martínez-Azorin & al. (2015); **incl.** *Schizobasis bruce-bayeri* U. & D. Müller-Doblies in schedis (s.a.) (*nom. inval.*, ICN Art. 29.1).

Bulb above or below ground, solitary, subglobose, 1–4 cm Ø, outer tunics greyish, inner pink to greenish; **L** not seen; **Inf** ascending, solitary, persistent, 0.5–20 cm, wiry, basally scabridulous, moderately branched; **Br** ascending at angles of 30–40°, straight; **Bra** spurred; **Ped**



deflexed from the base, 8–15 mm, sharply recurved apically in fruit; **Fl** subsecund, pendent; **Per** urceolate to campanulate, white to pale pink, 3–4 mm; **Tep** basally connate, lobes suberect to slightly spreading, elliptic to obovate, 2.5–3 × 1–1.5 mm, penicillate; **St** adnate to the tepals for 0.5–1 mm, and inserted at the top of the tube, connivent around the style; **Fil** filiform, sigmoid, apically inflexed, 2 mm; **Anth** connective ± 0.3 mm; **Ov** oblong with conspicuous shoulders about 1.5 mm long, greenish; **Sty** columnar, 1.5 mm, white; **Sti** obtuse, minutely 3-lobed; **Fr** ovoid, ± 3 × 2 mm, erect on pendent pedicels that are abruptly upcurved apically, reddish-brown, soon fragmenting and deciduous; **Se** 8 per locule, ellipsoid with peripheral wing, 1.5–2 × 1–1.5 mm, black, glossy.

Closely related to the widespread *D. intricata* from summer-rainfall regions. — [E. Van Jaarsveld]

**D. uniflora** J. C. Manning & Goldblatt (Strelitzia 9: 712, 2000). **Type:** RSA, Eastern Cape (*Zeyher* s.n. [TCD]). — **Lit:** Manning & al. (2014a: with ills.). **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape, KwaZulu-Natal, Free State, North-West, Gauteng, Limpopo), Swaziland, Lesotho, Zimbabwe; mainly Fynbos, Succulent Karoo and Albany Thicket vegetations, grassland and savanna vegetations.

≡ *Litanthus pusillus* Harvey (1884).

Bulbs dwarf, whitish, globose, clustering, above to below ground, to 1.3 cm Ø; **L** 1–3, hysteroanthous, filiform, to 7 cm; **Inf** reduced to 1- to 2-flowered racemes; **Bra** 2, to 1 mm, spurred; **Fl** pendulous, white to pink, tubular, to 5 mm; **Tep** fused in the lower ½; **St** fused to the perianth tube; **Anth** dorsifixed; **Ov** sessile, ellipsoid; **Fr** to 5 mm, transparent; **Se** angled, 0.5 mm.

Formerly treated as the only species of the segregate genus *Litanthus*. — [E. Van Jaarsveld]

## References

Aditya, S. (2013) An usual method for propagating *Drimia haworthioides* in the East Indian climate. *Alsterworthia* Int. 13(2): 27, ills.

Al-Tardeh, S. [ & al. 2008], Sawidis, T., Diannelidis, B.-E. & Delivopoulos, S. (2008) Water content and reserve allocation patterns within the bulb of the perennial geophyte Red Squill (*Liliaceae*) in relation to the Mediterranean climate. *Botany* 86: 291–299, ills. <https://doi.org/10.1139/B07-130>

Crouch, N. R. & Martínez-Azorín, M. (2015) *Drimia edwardsii* (*Asparagaceae*, *Scilloideae*), a new urgineoid species from the Mkhomazi River Valley of eastern South Africa. *Phytotaxa* 195(2): 135–144, map, ills. <https://doi.org/10.11646/phytotaxa.195.2.2>

Dyer, R. A. (1942) *Urginea delagoensis*. *Urginea lydenburgensis*. *Flow. Pl. South Afr.* 22: tt. 858–859 + 4 pp. text.

Eggle, U. & Nyffeler, R. (2009) Living under temporarily arid conditions – succulence as an adaptive strategy. *Bradleya* 27: 13–36, ills. <https://doi.org/10.5167/uzh-28825>

Gemmill, C. L. (1974) The pharmacology of squill. *Bull. New York Acad. Med.* 50(6): 747–750.

Goldblatt, P. & Manning, J. (2000) Cape plants. A conspectus of the Cape Flora of South Africa. Pretoria (ZA): National Botanical Institute of South Africa / St. Louis (US): Missouri Botanical Garden. = *Strelitzia* 9.

Jaarsveld, E. J. van & Wyk, A. E. (B.) van (2006) *Drimia loedolffiae*, a new succulent cliff-dwelling species from the Eastern Cape, South Africa. *Aloe* 43(2–3): 49–51, ills., map, key.

Jessop, J. P. (1975) Studies in the bulbous *Liliaceae* in South Africa. 5. Seed surface characters and generic groupings. *J. South Afr. Bot.* 41: 67–85.

Jessop, J. P. (1977) Studies in the bulbous *Liliaceae* in South Africa. 7. The taxonomy of *Drimia* and certain allied genera. *J. South Afr. Bot.* 43(4): 265–319, keys.

Knirsch, W. [ & al. 2015], Martínez-Azorín, M., Pfosser, M. & Wetschnig, W. (2015) The reinstatement and rediagnosis of the Madagascan genus *Rhodocodon* (*Asparagaceae*, *Scilloideae*), with validation and remarks on H. Perrier's taxa. *Phytotaxa* 195(2): 101–134, key. <https://doi.org/10.11646/phytotaxa.195.2.1>

Lebrun, J.-P. & Stork, A. L. (2014) Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (*Anthericaceae* – *Palmae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.

Maire, R. (1958) *Flore de l'Afrique du Nord*. Vol. 5. Paris (FR): Éditions Paul Lechevalier. <http://www.biodiversitylibrary.org/bibliography/76926>

Manning, J. C. [ & al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperae*. *Edinburgh J. Bot.* 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>

Manning, J. C. [ & al. 2014a], Deacon, J. & Goldblatt, P. (2014a) A review of the *Litanthus* group of *Drimia* Jacq. (*Hyacinthaceae*: *Urgineoideae*) with the description of a second species, *Drimia stenocarpa*, from



- Western Cape. South Afr. J. Bot. 90: 96–100, ills., map. <https://doi.org/10.1016/j.sajb.2013.10.006>
- Manning, J. C. [ & al. 2014b], Deacon, J. & Goldblatt, P. (2014b) A review of the *Schizobasis* group of *Drimia* Jacq. (*Hyacinthaceae: Urgineoideae*), and the new species *D. sigmoidea* from Western Cape, South Africa. South Afr. J. Bot. 94: 263–269, ills., map, key. <https://doi.org/10.1016/j.sajb.2014.07.011>
- Martínez-Azorín, M. [ & al. 2013], Crespo, M. B., Dold, A. P., Wetschnig, W., Pinter, M., Pfosser, M. F. & van Jaarsveld, E. (2013) *Sagittanthera* (*Hyacinthaceae, Urgineoideae*), a new buzz pollinated genus from the Eastern Cape Province of South Africa. Phytotaxa 98 (2): 43–54, ills., map, key. <https://doi.org/10.11646/phytotaxa.98.2.2>
- Maule, J. (2010) [Czech:] *Drimia* (*Schizobasis*) *intricata* (Baker) J. C. Manning & Goldblatt and changes in the former genus. Adenium 23: 18–20, ills.
- Nordenstam, B. (1970) Studies in South African *Liliaceae*. III. The genus *Rhadamanthus*. Bot. Not. 123: 155–182, key, ills.
- Perrier, H. (1938) 40e famille. Liliacées (*Liliaceae*). In: Humbert, H. (ed.): Flore de Madagascar. Tananarive (MG): Imprimerie Officielle. <http://biodiversitylibrary.org/page/12247520>
- Pfosser, M. F. (2007) Migration durch Dispersionsverbreitung und Vikarianz bei Pflanzen – eine Analyse evolutionärer Mechanismen anhand molekularer Daten am Beispiel der Pflanzenfamilie *Hyacinthaceae*. Denisia 20: 379–393, maps, ills.
- Pfosser, M. F. & Speta, F. (2001) Bufadienolide und DNA-Sequenzen: Über Zusammenhalt und Aufteilung der *Urgineoideae* (*Hyacinthaceae*). Stapfia 75: 177–250.
- Pfosser, M. F. & Speta, F. (2004) From *Scilla* to *Charybdis* – is our voyage safer now? Pl. Syst. Evol. 246(3–4): 245–263, maps. <https://doi.org/10.1007/s00606-004-0153-z>
- Pfosser, M. F. [ & al. 2006], Wetschnig, W. & Speta, F. (2006) *Drimia cryptopoda*, a new combination in *Hyacinthaceae* from Madagascar. Linzer Biol. Beitr. 38 (2): 1731–1739, ills.
- Sebsebe Demissew & Nordal, I. (2010) Aloes and lilies of Ethiopia and Eritrea. Ed. 2. Addis Ababa (ET): Shama Books.
- Snijman, D. A. [ & al. 1999], Manning, J. C. & Goldblatt, P. (1999) A new *Rhadamanthus* species (*Hyacinthaceae*) from the Northwestern Cape, South Africa. Novon 9(1): 111–113, ills. <http://www.biodiversitylibrary.org/page/640842/page/111>
- Speta, F. (1980) Karyosystematik, Kultur und Verwendung der Meerzwiebel (*Urginea* Steinh., *Liliaceae* s.l.). Linzer Biol. Beitr. 12(1): 193–238, ills., map.
- Speta, F. (1998) Systematische Analyse der Gattung *Scilla* L. (*Hyacinthaceae*). Phytol. (Horn) 38(1): 1–141, ills.
- Speta, F. (2001) Die Echte und die Falsche Meerzwiebel: *Charybdis* Speta und *Stellarioides* Medicus (*Hyacinthaceae*), mit Neubeschreibungen und Neukombinationen im Anhang. Stapfia 75: 139–176.
- Stearn, W. T. (1978) Mediterranean and Indian species of *Drimia* (*Liliaceae*): A nomenclatural survey with special reference to the medical squill, *D. maritima* (syn. *Urginea maritima*). Ann. Mus. Goulandris 4: 199–210, key, ills.
- Stedje, B. (1987) A revision of the genus *Drimia* (*Hyacinthaceae*) in East Africa. Nordic J. Bot. 7(6): 655–666, ills., maps, key. <https://doi.org/10.1111/j.1756-1051.1987.tb02034.x>
- Stedje, B. (1996) *Hyacinthaceae*. In: Polhill, R. M. (ed.): Flora of Tropical East Africa. Rotterdam (NL)/Brookfield (US): A. A. Balkema.
- Stedje, B. (2001) Notes on African plants. *Hyacinthaceae*. The generic delimitation within *Hyacinthaceae*, a comment on works by F. Speta. Bothalia 31(2): 192–195. <https://doi.org/10.4102/abc.v31i2.519>
- Stedje, B. (2002) Generic delimitation of *Hyacinthaceae*, with special emphasis on sub-Saharan genera. Syst. & Geogr. Pl. 71(2): 449–454.



## Lachenalia HYACINTHACEAE

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**Lachenalia** J. Jacquin *ex* Murray (Syst. Veg., ed. 14, 314, 1784). **Type:** *Lachenalia tricolor* J. Jacquin. — **Hyacinthoideae**—**Massonieae** — **Lit:** Duncan (2012: monograph). **Distr:** SW Namibia, RSA; Succulent Karoo, Renosterveld, Fynbos, mainly winter-rainfall regions. **Etym:** For Werner de [von] Lachenal (1736–1800), Swiss botanist in Basel.

**Incl.** *Coelanthus* Willdenow *ex* J. A. & J. H. Schultes (1830). **Type:** *Coelanthus complicatus* Willdenow *ex* J. A. & J. H. Schultes.

**Incl.** *Periboea* Kunth (1843). **Type:** *Hyacinthus corymbosus* Linné.

**Incl.** *Polyxena* Kunth (1843). **Type:** *Polyanthes pygmaea* Jacquin.

**Incl.** *Chloriza* Salisbury (1866). **Type:** *Lachenalia mediana* Jacquin [lectotype, designated by G. D. Duncan, Gen. Lachenalia, 97, 2012].

**Incl.** *Himas* Salisbury (1866). **Type:** *Lachenalia angustifolia* Jacquin [lectotype, designated by G. D. Duncan, Gen. Lachenalia, 96, 2012].

**Incl.** *Monoestes* Salisbury (1866). **Type:** *Lachenalia unifolia* Jacquin [lectotype, designated by G. D. Duncan, Gen. Lachenalia, 96, 2012].

**Incl.** *Orchiops* Salisbury (1866). **Type:** *Hyacinthus orchioides* Linné [lectotype, designated

by G. D. Duncan, Gen. Lachenalia, 97, 2012 (as *Lachenalia orchioides* (Linné) Aiton)].

**Incl.** *Platyestes* Salisbury (1866). **Type:** *Lachenalia purpureo-caerulea* Jacquin [lectotype, designated by G. D. Duncan, Gen. Lachenalia, 96, 2012].

**Incl.** *Brachyscypha* Baker (1871). **Type:** *Massonia undulata* Thunberg.

Perennial bulbous geophytes, solitary or clustering; L synanthous, variable, occasionally spotted or with cross-bands, erect or horizontally spreading; **Inf** racemose, ascending, with broad membranous floral **Bra**; **Fl** erect to pendulous; **Tep** 6, fused at the base, spreading or forming a tube, usually coloured, **ITep** occasionally longer than the **OTep**; **St** 6, free; **Fil** terete, included or exerted; **Anth** versatile, introrse; **Ov** ovoid; **Sty** terete; **Sti** capitate; **Fr** ovoid loculicidal capsules; **Se** globose, black.

*Lachenalia* ( $\pm 133$  species according to Duncan (2012)) is closely related to *Massonia*, *Namophila* and *Veltheimia* according to the molecular data of Manning & al. (2004), and is also shown as sister to *Massonia* and *Veltheimia* by Ali & al. (2012). The species of the former genus *Polyxena* differ from *Lachenalia* only by the amount of fusion of the tepals. While Wetschnig & Pfosser (2003) show *Polyxena* (incl. *Periboea*) as a clade separate from *Lachenalia* s.s., Manning & al. (2004) found that these species are imbedded in *Lachenalia*. This wide circumscription of the genus

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is also the concept adopted in the recent revision by Duncan (2012), who classifies *Lachenalia* into the two subgenera *Lachenalia* (126 species) and *Polyxena* (7 species).

Bulb architecture of *Lachenalia* was studied in detail by Toit & al. (2001) and was found to be a sympodial structure, where each season's growth starts with 2 (or rarely 3) cataphylls (the outer subterranean and desintegrating after senescence of the above-ground parts, the inner extending above-ground and tightly surrounding the leaf bases in most species), and this structure was already recognized as diagnostic by Jessop (1976).

Pollination in *Lachenalia* is diverse: Many species are pollinated by a variety of bees, while *L. aloides* and related taxa are visited by sunbirds. Pollination by rodents is suggested for some other taxa (Duncan 2012).

Only a few species can be regarded as being (weakly) succulent, and they all belong to subgen. *Lachenalia*. Many more taxa are, however, commonly encountered in cultivation, esp. *L. aloides* in its many colour variants.

**L. contaminata** Aiton (Hort. Kew. 1: 460–461, 1789). **Type:** RSA, Western Cape (*Anonymus* s.n. [BM]). — **Distr:** RSA (Western Cape: Lamberts Bay to De Hoop); various habitats, mostly Fynbos. **I:** Duncan (2012: 339–340).

≡ *Scillopsis contaminata* (Aiton) Lemaire (1856); **incl.** *Lachenalia angustifolia* Jacquin (1797) ≡ *Scillopsis angustifolia* (Jacquin) Lemaire (1856); **incl.** *Lachenalia hyacinthoides* Jacquin (1797) ≡ *Scillopsis hyacinthoides* (Jacquin) Lemaire (1856); **incl.** *Lachenalia albida* Trattinnick (1814); **incl.** *Lachenalia fragrans* Loddiges (1826) (*nom. illeg.*, Art. 53.1); **incl.** *Lachenalia hyacinthina* hort. (1906).

Geophytes 6–30 cm tall, offsetting from the base to form small clusters; bulb subglobose, 1–2 cm Ø, tunics multi-layered, outer tunics dark brown, spongy, inner tunics translucent, white; **L** 3–11, linear, 9–21 cm × 1–4 mm, rosulate, ascending-spreading, light to dark green, lower ½ canaliculate, becoming terete above, upper surface plane; **Inf** racemose, many-flowered, dense, scape erect, light green, mottled; **Bra** cup-shaped, green, fading to white above;

**Per** zygomorphic, narrowly campanulate, to 8 mm, spreading to suberect, spice-sented, tube cup-shaped, white, 2–3 mm long; **OTep** ovate, white; **ITep** narrowly obovate, spreading, white; **St** included to exerted; **Fil** white, 5–10 mm; **Anth** maroon, pollen yellow; **Ov** ellipsoid, 2–3 × 2 mm, light green; **Sty** included to exerted, white, 4–8 mm; **Fr** ellipsoid, 7–8 × 4–5 mm; **Se** globose, glossy black, ± 1 mm Ø.

**L. moniliformis** W. F. Barker (J. South Afr. Bot. 49(4): 438, 1983). **Type:** RSA, Western Cape (*Perry* 795 [NBG]). — **Distr:** RSA (Western Cape: Worcester Valley); Fynbos, narrowly endemic. **I:** Duncan (2012: 40, 316).

Geophytes 12–17 cm tall, offsetting from the base forming small groups; bulbs subglobose, to 1.5 cm Ø; tunics multi-layered; **L** 5–8, bright green, loosely clasping at the base, terete otherwise, 6–16 cm × 1–2 mm, lower ⅓ banded with dark maroon and magenta, upper ⅔ with prominent circular dark green raised fleshy bands; **Inf** racemose, few- to many-flowered, scape 5–9 cm; **Bra** ovate-lanceolate, white; **Ped** spreading to suberect, 5–6 mm, light bluish-white; **Per** oblong-campanulate, tube cup-shaped, 1 mm long, ice-blue; **OTep** ovate, 5–6 × 4 mm, light blue at the base, becoming lighter upwards; **ITep** obovate, 6–7 × 3 mm, white; **St** exerted; **Fil** white, 9–10 mm; **Ov** obovoid, 2 × 2 mm; **Sty** declinate, 9–11 mm; **Fr** obovate, 4–5 × 3–4 mm; **Se** globose, 1.2–1.3 mm.

**L. patula** Jacquin (Collectanea 4: 149–150, 1791). **Type:** [neo — icon]: Jacquin, Ic. Pl. Rar. 2: 12, t. 384, 1792/93. — **Distr:** RSA (Western Cape: Knersvlakte); Succulent Karoo. **I:** Duncan (2012: 370–371).

**Incl.** *Lachenalia succulenta* Masson ex Baker (1886).

Geophytes 6–15 cm tall, forming small groups; bulbs globose, 0.5–1.5 cm Ø, proliferating from the base forming small tufts, with dark tunics; **L** 2, opposite, linear-lanceolate, 4.5–15 × 0.2–1 cm, subterete, glabrous, fleshy, green, purple-tinged, apex obtuse, mucronate; **Inf** racemose, erect, 10–17 cm; sterile **Bra** deltoid; **Ped** 5–7 mm; fertile **Bra** cup-shaped; **Per** zygomorphic, widely

campanulate, 15 mm, ascending, white or pale pink; **Tep** fused at the base, forming a tube with spreading tips; **ITep** 8–9 × 7–8 mm, occasionally longer than the outer tepals; **Fil** included or exerted; **Fr** ovoid, 7–8 × 4 mm; **Se** globose, black, 0.5 mm.

**L. polypodantha** Schlechter *ex* W. F. Barker (J. South Afr. Bot. 45(2): 212–214, 1979). **Type:** RSA, Northern Cape (*F. Barker* 9049 [NBG]). — **Distr:** RSA (Northern Cape); Succulent Karoo.

**L. polypodantha** ssp. *eburnea* G. D. Duncan (Gen. Lachenalia, 376, 2012). **Type:** RSA, Northern Cape (*Duncan* 574 [NBG]). — **Distr:** RSA (Northern Cape); flowering in September. **I:** Duncan (2012: 373).

Differs from ssp. *polypodantha*: **L** glaucous, canaliculate; **ITep** ivory-white.

**L. polypodantha** ssp. *polypodantha* — **Distr:** RSA (Northern Cape); flowering in August. **I:** Duncan (2012: 373).

Geophytes 5.5–15 cm tall; bulbs globose, 0.5–2 cm Ø, solitary, tunics multi-layered, outer tunics spongy, light brown, inner tunics translucent-white; **L** solitary, lanceolate to broadly lanceolate, 1.4–4 × 0.5–2 cm, spreading, curved, dark green, flat, fleshy, upper face with short stellate trichomes and shallow depressed longitudinal grooves; **Inf** racemose, few- to many-flowered, conical, scape ascending, 1–4 cm; **Ped** perpendicular to the axis, 4–11 mm, white to light green or glaucous; **Per** zygomorphic, broadly campanulate, spreading, light bluish-white to light violet,

tube cup-shaped, 2–3 mm long; **OTep** ovate, 4–6 × 2.5–4 mm; **ITep** obovate, 4–7 × 2.5–3 mm, dark violet to greenish-violet, bright green or brown, tips recurved; **St** exerted, declinate; **Fil** uniformly ivory-white; **Ov** obovoid, 2–4 × 2.5–3 mm; **Sty** exerted, declinate, 10–12 mm; **Fr** obovoid, 4–5 × 3–4 mm; **Se** globose, 0.7–0.9 mm.

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## References

- Ali, S. S. [& al. 2012], Yu, Y., Pfosser, M. F. & Wetschnig, W. (2012) Inferences of biogeographical histories within subfamily *Hyacinthoideae* using S-DIVA and Bayesian binary MCMC analysis implemented in RASP (Reconstruct Ancestral State in Phylogenies). *Ann. Bot. (Oxford)*, n.s. 109(1): 95–107, maps, keys. <https://doi.org/10.1093/aob/mcr274>
- Duncan, G. (2012) The genus *Lachenalia*. Richmond (GB): Kew Publishing, Royal Botanic Gardens, Kew.
- Jessop, J. P. (1976) Studies in the bulbous *Liliaceae* in South Africa: 6. The taxonomy of *Massonia* and allied genera. *J. South Afr. Bot.* 42(4): 401–437, keys.
- Manning, J. C. [& al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperaeae*. *Edinburgh J. Bot.* 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>
- Toit, E. S. du [& al. 2001], Robbertse, P. J. & Niederwieser, J. G. (2001) An evaluation of bulb growth and structure of *Lachenalia* cv. Ronina bulbs. *South Afr. J. Bot.* 67(4): 667–670. [https://doi.org/10.1016/S0254-6299\(15\)31198-4](https://doi.org/10.1016/S0254-6299(15)31198-4)
- Wetschnig, W. & Pfosser, M. F. (2003) The *Scilla plumbea* puzzle — present status of the genus *Scilla* sensu lato in southern Africa and description of *Spetaea lachenaliiflora*, a new genus and species of *Massonieae* (*Hyacinthaceae*). *Taxon* 52(1): 75–91, ill., key. <https://doi.org/10.2307/3647303>







## Ledebouria HYACINTHACEAE

E. Van Jaarsveld

**Ledebouria** Roth (Nov. Pl. Sp., 194, 1821). **Type:** *Ledebouria hyacinthina* Roth. — **Hyacinthoideae** — **Massonieae** — **Lit:** Jessop (1970: 244–264, systematics S Africa); Müller-Doblies & Müller-Doblies (1997: 61–65, *Drimiopsis* S Africa); Venter (2008: synopsis RSA); Lebrun & Stork (2014: 88–94, synopsis tropical Africa). **Distr:** Tropical and S Africa, Madagascar, India. **Etym:** For Prof. Dr. Carl Friedrich von Ledebour (1785–1851), German botanist widely travelling in Russia.

**Incl.** *Eratobotrys* Fenzl ex Endlicher (1842). **Type:** *Eratobotrys lilacina* Fenzl ex Endlicher.

**Incl.** *Drimiopsis* Lindley & Paxton (1851). **Type:** *Drimiopsis maculata* Lindley.

**Incl.** *Sugillaria* Salisbury (1866). **Type:** *Lachenalia lanceifolia* Jacquin.

**Incl.** *Xeodolon* Salisbury (1866). **Type:** *Hyacinthus revolutus* Linné fil.

**Incl.** *Resnova* van der Merwe (1946). **Type:** *Scilla schlechteri* Baker.

Perennial bulbous plants; bulbs with  $\pm$  fleshy tunics, solitary or proliferating to form groups; **L** synanthous, variable, spreading, mostly spotted; **Inf** racemose, ascending, with small filiform floral **Bra**; **Tep** 6, all equal, fused at the base,

spreading to reflexed, papillate; **St** 6, free; **Fil** terete; **Anth** versatile, introrse; **Ov** ovoid or turbinate and 3- to 6-lobed, shortly stipitate, ovules 1–2 per locule; **Sty** terete; **Sti** capitate; **Fr** 3-angled obovoid loculicidal capsules; **Se** black or brown, obovoid.

In traditional classifications, *Ledebouria* was included in the synonymy of *Scilla*, but Jessop (1970) argued that it should be accepted at generic rank. This view was subsequently supported by molecular data (Stedje 1998; Pfosser & Speta 1999; Pfosser & al. 2003; Wetschnig & Pfosser 2003). *Drimiopsis* (perianth incurved and cucullate) was recognized as closely related to *Ledebouria* (perianth spreading) by Jessop (1975) but was shown as a separate clade in the species-poor analysis of Stedje (1998). In the phylogenies of Pfosser & Speta (1999) and Pfosser & al. (2003), it is, however (together with *Resnova*) embedded in *Ledebouria*. Lebach & al. (2006) also found *Drimiopsis* and *Resnova* embedded in *Ledebouria*, and this was corroborated by Ali & al. (2012). *Schizocarphus* (no succulents), sometimes also included in *Scilla* or *Ledebouria*, is a completely separate clade, however, in sister-group position to *Ledebouria* (Pfosser & al. 2003).

The genus counts  $\pm$ 45 species and is characterized by usually spotted leaves with threads when torn, inflorescences 2 or more per bulb and usually  $\pm$  flexuose, and usually purplish to greenish flowers and stipitate ovaries (Stedje 1998: 10). Only the following few species are  $\pm$  succulent:

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**L. concolor** (Baker) Jessop (J. South Afr. Bot. 36 (4): 254, 1970). **Type:** RSA, Eastern Cape (*Cooper* s.n. [K, PRE [photo]]). — **Distr:** RSA (Eastern Cape); arid savanna, summer-rainfall regions.

≡ *Scilla concolor* Baker (1870); **incl.** *Drimia cooperi* Baker (1868).

Above-ground bulbous succulents, cluster-forming; **R** succulent, 2 mm Ø; bulb conical, to 6 × 4.5 cm, purplish-green, proliferating from the base, tunics tight, withering grey, translucent; **L** 5–10, ovate-lanceolate to ovate, 8–11 × 4.5–6 cm, young ascending, old drooping, green, ± fleshy, unspotted, obscurely striate; **Inf** 30–45 cm, ascending; **Ped** 6–8 mm; **Bra** small, ovate; **Per** greenish, 8 mm.

**L. corrugata** D. M. Cumming (Cact. Succ. J. (US) 87(6): 238–239, ills., 2015). **Type:** RSA, Eastern Cape (*Cumming* 13844 [GRA]). — **Distr:** RSA (Eastern Cape: Alicedale); stony ground in opening in thicket vegetation.

Bulbs solitary, underground, ovoid, 2–2.5 × 1.5–2.5 cm, tunics tightly arranged, soft, white with few threads, withering to membranous and then light brown; **L** 2–4, spreading-ascending, lanceolate, 2.5–3.5 × 0.8–1.4 cm, threads absent, fleshy, immaculate, upper face dark green, distinctly corrugated and deeply pitted, lower face dark purple, margin entire, apex acute; **Inf** solitary, erect, 25- to 40-flowered, longer than the leaves, peduncle glabrous, terete, green suffused with purple, 5–6 cm, raceme oblong, 4–4.5 cm, bracteoles absent; **Ped** spreading, 6–7 mm, green or suffused with purple; **Per** 4 mm; **Tep** becoming recurved, linear-oblong, 4 × 1.5 mm, olive-green suffused with purple, apex acute; **St** erect, 3–4 mm; **Fil** purple; **Anth** 0.8 mm, yellow; **Ov** 2 × 1.8 mm, 6-lobed; **Sty** 4 mm, purple; **Se** drop-shaped, 2.8–3 × 1.1–1.6 mm, wrinkled, brown.

**L. cremnophila** S. Venter & Van Jaarsveld (Aloe 43(4): 78–79, ills., 2007). **Type:** RSA, Mpumalanga (*Venter* 13671 [PRE]). — **Distr:** RSA (Mpumalanga); cliffs in savanna (Barberton Serpentine Sourveld vegetation), midsummer-flowering.

Bulbs solitary, above-ground to halfway above-ground, cylindrical, 9–12 × 3–4 cm, dry tunics dark brown; **L** 6–8, spreading, lanceolate, 8–13 × 2–4 cm, fleshy, surface dull green with

purple blotches, venation sunken, apex acute, margin smooth but wavy; **Inf** 1 or rarely 2, flaccid, raceme oblong, 13–25 cm, laxly 50- to 120-flowered, with a pronounced coma of filiform bracts when young; **Ped** 8–12 mm, pink turning olive-green; **Tep** initially spreading then strongly recurved, 5–6 × 1.5 mm, olive-green; **Ov** depressed-ovoid; **Sty** 2.5–3 mm; **Fr** clavate, base tapering.

**L. ensifolia** (Ecklon) S. Venter & T. J. Edwards (Bothalia 33(1): 49, 2003). **Type** [lecto]: RSA, Eastern Cape (*Zeyher* 10 [K]). — **Distr:** RSA (E Western Cape, Eastern Cape, KwaZulu-Natal); stony slopes. **I:** Venter (2008: 110).

≡ *Drimia ensifolia* Ecklon (1830) ≡ *Scilla ensifolia* (Ecklon) Britten (1908); **incl.** *Drimia ludwigii* Miquel (1839) ≡ *Idothea ludwigii* (Miquel) Kunth (1843) ≡ *Scilla ludwigii* (Miquel) Baker (1870); **incl.** *Scilla prasina* Baker (1870); **incl.** *Scilla pusilla* Baker (1876); **incl.** *Scilla ecklonii* Baker (1892).

Above-ground bulbous succulents; **R** succulent, 2 mm Ø; bulb conical, to 1.5–1.8 × 3–3.5 cm, purplish-green, dividing to form small dense groups, tunics tight, withering grey and in horizontally truncate layers; **L** 2–3, narrowly ovate-lanceolate, 5–9 × 1.2–2.2 cm, ascending-spreading, ± fleshy, purplish-spotted, sometimes with transversely spotted bands, base canaliculate; **Inf** 1–3, 4–32 cm, 30- to 100-flowered; **Bra** 1 × 1 mm, deltoid; **Ped** patent, 3–4 mm; **Per** stellate, green to pink; **Tep** sharply reflexed, oblong, 3–3.5 × 1.5 mm, apex acute; **St** erect, 3 mm; **Ov** ellipsoid, 6-lobed, 1 × 2.5 mm; **Sty** trigonous, 1.5 mm, glabrous, purple; **Fr** 3-lobed, symmetrical, globose, base truncate; **Se** ellipsoid, wrinkled, brown.

**L. loedolffiae** Van Jaarsveld & S. Venter (Avonia 35(3): 139, ills. (pp. 133–138), 2017). **Type:** RSA, Eastern Cape (Van Jaarsveld 16595 [NBG]). — **Distr:** RSA (Eastern Cape); Albany Thicket vegetation in the summer-rainfall region, spring-flowering.

Bulbs above-ground, conical, tapering, 35 × 16 mm, with peeling dark purple papery tunics, proliferating from the base to form dense clusters; **R** succulent, 1–4.5 mm Ø; **L** 2–3, linear-lanceolate, 4–8.5 × 0.9–1.6 cm, ascending to spreading, mottled, with thread-like strings when broken, slightly fleshy; **Inf** 8–12.5 cm, spreading-

ascending; **Bra** small, ovate; **Ped** 2.5–5 mm; **Per** greenish; **Tep** spreading, soon becoming reflexed, 3 mm; **Fil** purple with green base, exerted; **Ov** globose, 6-lobed, stipitate; **Sty** 3 mm, translucent.

**L. megaphylla** (Hankey ex J. M. H. Shaw) Van Jaarsveld & Eggl (Bradleya 34: 143, 2016). **Type:** RSA (cultivated) (*Shaw* s.n. [WSY]). — **Distr:** RSA (Northern Prov., Mpumalanga); savanna, flowering mid-summer.

≡ *Resnova megaphylla* Hankey ex J. M. H. Shaw (2012).

Bulbs solitary, underground, rarely offsetting, cylindrical-ovoid, ±3 cm Ø, with few, large, fleshy scales; **L** 2 (rarely 1 or 3), ovate, fleshy, 6–7 × 4–5 cm, horizontally spreading, upper face glossy, minutely pustulate, light grey-green with darker blotches, lower face purple, smooth, margin entire, minutely ciliate towards the obtuse apex, base rounded subpetiolate; **Inf** 1, to 15 cm, dark purplish-green, 35- to 40-flowered, **Bra** cylindrical, persistent, 0.5–1 mm; **Ped** 1.5–2 mm; **Per** campanulate, pinkish-purple; **Tep** lanceolate, each with a green central band, tips recurved-spreading, 6–7 × 2.5 mm, apex emarginate and minutely mucronate; **St** in 2 series, outer **Fil** 3–3.5 mm, inserted on the tepals above the swollen nectary base, inner **Fil** 2.5–3 mm, inserted basally on the tepals; **Anth** yellow, 0.5 mm; **Ov** green, pear-shaped, 2.5 mm, shallowly grooved, 3-lobed in the apical ½; **Sti** minute, capitate; **Fr** 3-lobed, becoming slightly fleshy, with persistent perianth; **Se** 2 per locule, triangular to elongate, ovoid, 3–4 × 2–2.5 mm, black.

Quite frequent in cultivation.

**L. ovatifolia** (Baker) Jessop (J. South Afr. Bot. 36 (4): 262, 1970). **Type:** RSA, KwaZulu-Natal (*Cooper* s.n. [K]). — **Distr:** RSA (Eastern Cape, KwaZulu-Natal, Free State, Gauteng, Mpumalanga, Limpopo, North-West Prov.), Lesotho; Bushveld, autumn-flowering.

≡ *Scilla ovatifolia* Baker (1870); **incl.** *Scilla lancifolia* var. *ovatifolia* Baker (1870).

**L. ovatifolia** ssp. *ovatifolia* — **Distr:** RSA (Eastern Cape, KwaZulu-Natal, Free State, Gauteng, Mpumalanga, Limpopo, North-West Prov.), Lesotho; Bushveld, autumn-flowering.

**incl.** *Scilla cicatricosa* C. A. Smith (1930); **incl.** *Scilla climatocarpha* C. A. Smith (1930); **incl.** *Scilla guttata* C. A. Smith (1930); **incl.** *Scilla albo-marginata* Van der Merwe (1944); **incl.** *Scilla elevans* Van der Merwe (1944); **incl.** *Scilla collina* Hutchinson (1946).

Bulbs above- or underground, solitary or proliferating to form small clusters, globose, tapering, 2–3.5 × 2–3.5 cm, purplish-green with fleshy imbricate tunics in horizontal successive layers; **R** succulent, 1 mm Ø; **L** 3–5, ovate, 4–8.5 × 1.8–4.5 cm, spreading, ± appressed to the ground, attractively mottled with silvery sheen, fleshy, upper face smooth; **Inf** 4–19 cm, ascending; **Bra** small, inconspicuous, truncate; **Ped** 1 mm; **Per** 7 mm, greenish-white, campanulate; **St** 2 mm; **Ov** ovoid, stipitate, 1.5 mm; **Sty** 1.5 mm; **Sti** capitate.

**L. ovatifolia** ssp. *scabrada* N. Crouch & T. J. Edwards (Flow. Pl. Afr. 60: 14, t. 2223, 2007). **Type:** RSA, KwaZulu-Natal (*Edwards & Crouch* 3260 [NU]). — **Distr:** RSA (KwaZulu-Natal: Natal Midlands); savanna.

Differs from ssp. *ovatifolia*: Upper leaf face with distinctive papillae.

**L. socialis** (Baker) Jessop (J. South Afr. Bot. 36(4): 253, 1970). **Type:** RSA, KwaZulu-Natal (*Cooper* 3635 [K]). — **Distr:** RSA (Eastern Cape, KwaZulu-Natal); arid savanna, summer-rainfall regions. — Fig. 1.

≡ *Scilla socialis* Baker (1870); **incl.** *Scilla paucifolia* Baker (1870); **incl.** *Scilla laxiflora* Baker (1891); **incl.** *Scilla violacea* Hutchinson



**Fig. 1** *Ledebouria socialis*. (Copyright: E. Van Jaarsveld)

(1932)  $\equiv$  *Ledebouria violacea* (Hutchinson) W. L. Tjaden (1989).

Bulbs above-ground, conical, tapering, 1.5–3.5  $\times$  0.8–2 cm, green with peeling papery tunics, proliferating from the base to form dense clusters; **R** succulent, 1 mm  $\varnothing$ ; **L** 2–4, elliptic, 4–7  $\times$  1–1.3 cm, ascending to spreading, attractively mottled with silvery sheen, slightly fleshy; **Inf** 9–17 cm, spreading-ascending; **Ped** 6 mm, **Bra** small, ovate; **Per** greenish, campanulate, 3 mm; **Fil** purple, exserted; **Ov** globose, stipitate.

**L. venteri** Van Jaarsveld & A. E. van Wyk (Aloe 43(4): 75–76, ills., 2007). **Type:** RSA, Western Cape (*Van Jaarsveld* 17633 [NBG]). — **Distr:** RSA (Western Cape: Langeberg, Gouritz River); Southern Cape Valley Thicket vegetation, summer-flowering.

Bulbs globose, to 5  $\times$  4.5 cm, first solitary, soon forming (semi-) epigeous clusters of up to 14 individuals, covered with dense dry tunic remains, tunics thin, papery, brownish, translucent, with indistinct, transverse abscission layer; **R** fleshy, to 1.5 mm  $\varnothing$ ; **L** 6–12, succulent, spreading, linear-lanceolate to ovate-lanceolate, 5–10  $\times$  1.3–3.5 cm, green, glabrous, obscurely striate, abaxial surface suffused with a purple streak in the centre and towards the base, apex acute, margin white, minutely denticulate; **Inf** 7–10 cm; raceme 4–5 cm, with up to 14 flowers open simultaneously; **Fl** spreading and nodding; **Ped** 14–15 mm; **Tep** triangular-ovate, 5  $\times$  1.5 mm, purplish-green, soon becoming reflexed; **St** 3–3.5 mm; **Ov** 1  $\times$  2.5 mm.

## References

- Ali, S. S. [& al. 2012], Yu, Y., Pfosser, M. F. & Wetschnig, W. (2012) Inferences of biogeographical histories within subfamily *Hyacinthoideae* using S-DIVA and Bayesian binary MCMC analysis implemented in RASP (Reconstruct Ancestral State in Phylogenies). *Ann. Bot. (Oxford)*, n.s. 109(1): 95–107, maps, keys. <https://doi.org/10.1093/aob/mcr274>
- Jessop, J. P. (1970) Studies in the bulbous *Liliaceae*: 1. *Scilla*, *Schizocarphus* and *Ledebouria*. *J. South Afr. Bot.* 36(4): 233–266, keys.
- Jessop, J. P. (1975) Studies in the bulbous *Liliaceae* in South Africa. 5. Seed surface characters and generic groupings. *J. South Afr. Bot.* 41: 67–85.
- Lebatha, P. [& al. 2006], Buys, M. H. & Stedje, B. (2006) *Ledebouria*, *Resnova* and *Drimiopsis*: A tale of three genera. *Taxon* 55(3): 643–652. <https://www.jstor.org/stable/25065640>
- Lebrun, J.-P. & Stork, A. L. (2014) Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (*Anthericaceae* – *Palmae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Müller-Doblies, U. & Müller-Doblies, D. (1997) A partial revision of the tribe *Massonieae* (*Hyacinthaceae*). 1. Survey, including three novelties from Namibia: A new genus, a second species in the monotypic *Whiteheadia* and a new combination in *Massonia*. *Feddes Repert.* 108(1–2): 49–96, ills., keys. <https://doi.org/10.1002/fedr.19971080106>
- Pfosser, M. F. & Speta, F. (1999) Phylogenetics of *Hyacinthaceae* based on plastid DNA sequences. *Ann. Missouri Bot. Gard.* 86(4): 852–875. <https://doi.org/10.2307/2666172>
- Pfosser, M. F. [& al. 2003], Wetschnig, W., Ungar, S. & Prenner, G. (2003) Phylogenetic relationships among genera of *Massonieae* (*Hyacinthaceae*) inferred from plastid DNA and seed morphology. *J. Pl. Res.* 116: 115–132, ills. <https://doi.org/10.1007/s10265-003-0076-8>
- Stedje, B. (1998) Phylogenetic relationships and generic delimitation of sub-Saharan *Scilla* (*Hyacinthaceae*) and allied African genera as inferred from morphological and DNA sequence data. *Pl. Syst. Evol.* 211(1–2): 1–11. <https://doi.org/10.1007/BF00984908>
- Venter, S. (2008) Synopsis of the genus *Ledebouria* Roth (*Hyacinthaceae*) in South Africa. *Herbertia* [ser. 3], 62: 85–155, key, ills., maps.
- Wetschnig, W. & Pfosser, M. F. (2003) The *Scilla plumbea* puzzle — present status of the genus *Scilla* sensu lato in southern Africa and description of *Spetaea lachenaliiflora*, a new genus and species of *Massonieae* (*Hyacinthaceae*). *Taxon* 52(1): 75–91, ills., key. <https://doi.org/10.2307/3647303>



## Massonia HYACINTHACEAE

E. Van Jaarsveld and U. Eggli

**Massonia** Thunberg *ex* Houttuyn (Nat. Hist. 12: 424, t. 85: Fig. 1, 1780). **Type:** *Massonia depressa* Houttuyn. — **Hyacinthoideae**—**Massonieae** — **Lit:** Jessop (1976: systematics); Müller-Doblies & Müller-Doblies (1997: 66–77, systematics); Pfosser & al. (2003: classification); Martínez-Azorín & al. (2015: classification). **Distr:** S Namibia, RSA; mainly Succulent Karoo. **Etym:** For Francis Masson (1741–1805), British horticulturist collecting esp. in S Africa.

**Incl.** *Whiteheadia* Harvey (1868). **Type:** *Whiteheadia latifolia* Harvey.

**Incl.** *Neobakeria* Schlechter (1924). **Type:** *Massonia angustifolia* Linné *fil.* [lectotype, designated by Phillips, Gen., South Afr. Fl. Pl., ed. 2, 193, 1951].

**Incl.** *Desertia* Martínez-Azorín & al. (2015). **Type:** *Whiteheadia etesionamibensis* U. & D. Müller-Doblies.

Soft succulent perennial geophytes with globose bulbs to 4.5 cm Ø with fleshy tunics; **L** 2, opposite,

synanthous, large, appressed to the ground (or semi-ascending in cultivation), elliptic-oblong to lanceolate; **Inf** dense short or reduced-subcapitate racemes with short peduncle; basal **Bra** large, surrounding the inflorescence; **Fl** pedicellate; **Tep** fused into a tube with the oblong tips free; **St** 6, fused to the mouth of the perianth tube; **Ov** sessile, oblong to ovoid; **Sty** short; **Sti** capitate; **Fr** winged loculicidal lobed capsules; **Se** (sub-) globose, black, to 2 mm Ø.

The circumscription of *Massonia* was recently expanded by Manning & al. (2004) to include *Whiteheadia* (2 species), as these have been found to form a paraphyletic grade at the base of *Massonia* s.s. in their analysis, corroborating the earlier study of Pfosser & al. (2003). The differences on which the separation is based (low compressed inflorescences and filaments connate or not in *Massonia* s.s., cylindrical compact spikes and filaments connate in *Whiteheadia*) are not fundamental, and pollination by rodents has been documented for one species each of both groups.

A different approach is taken by Martínez-Azorín & al. (2015): These authors interpret the molecular phylogenies differently, and *M. etesionamibensis* is placed (together with a newly described additional species *D. luteovirens*) in the new genus *Desertia*, leaving the former *Whiteheadia* monotypic (only species *W. bifolia*). *Desertia* and *Whiteheadia* share long-racemose inflorescences with a coma of sterile bracts at the tip, which contrasts with the subcapitate

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inflorescences of *Massonia* s.s. In addition, these authors also accept the monotypic genus *Namophila*, which differs from *Massonia* in distinctly caudate tepals and fruit capsules enclosed by the fleshy perianth when ripe. Since no combination for the single species of the *Namophila* under *Massonia* is available, we accept *Namophila* for the time being.

Only a few of the  $\pm 10$  species are moderately succulent. They are only infrequently encountered in cultivation.

**M. bifolia** (Jacquin) J. C. Manning & Goldblatt (Edinburgh J. Bot. 60(3): 564, 2004). **Type:** [lecto — icono]: Jacquin, Icon. Pl. Rar. 2 (16): t. 449, 1795. — **Lit:** Manning & al. (2011: with ill.); Martínez-Azorín & al. (2015: as *Whiteheadia*, with ill.). **Distr:** S Namibia, RSA (Northern Cape); Succulent Karoo, in rock crevices. — Fig. 1.

≡ *Eucomis bifolia* Jacquin (1791) ≡ *Basilaea bifolia* (Jacquin) Poirlet (1810) ≡ *Whiteheadia bifolia* (Jacquin) Baker (1873); **incl.** *Melanthium massoniifolium* Andrews (1804); **incl.** *Whiteheadia latifolia* Harvey (1868).

Bulb small, to 2.5 cm Ø; tunics thin, fleshy; L 2, green, softly fleshy, to 13 × 9 cm, broadly



**Fig. 1** *Massonia bifolia*. (Copyright: U. Eggli)

ovate, horizontally spreading, fragile, longitudinally striate; **Inf** a dense terminal semi-pyramidal spike to 10 cm (lengthening to 35 cm at fruiting time) with a short peduncle; **Bra** large, ovate-acuminate, to 3.5 cm; **Per** to 15 mm, cup-shaped, green, lobes ovate, fused below; **St** 6, to 8 mm, basally fused to form a short tube; **Anth** to 4.5 mm; **Ov** triangular in outline, green, to 5 mm; **Sty** short, to 5 mm; **Sti** capitate; **Se** globose, black, shiny, to 2 mm Ø.

Wester & al. (2009) have documented pollination by nocturnal rodents, mainly the Namaqua Rock Mouse. The animals become dusted with pollen when they lick the viscous nectar from the slightly sourish-nutty-scented flowers. In later papers, the primarily insectivorous Cape Rock Elephant-Shrew is reported as additional pollinator (Wester 2010, 2015). — [E. Van Jaarsveld]

**M. depressa** Houttuyn (Nat. Hist. 12: 424, t. 85: Fig. 1, 1780). **Type:** [lecto — icono]: l.c., t. 85: Fig. 1. — **Distr:** RSA (Northern Cape, Western Cape, Eastern Cape, Free State); Succulent Karoo, winter-rainfall to all-year rainfall areas. — Fig. 2.

**Incl.** *Massonia latifolia* Linné fil. (1781); **incl.** *Massonia obovata* Jacquin (1804); **incl.** *Massonia sanguinea* Jacquin (1804); **incl.** *Massonia grandiflora* Lindley (1826); **incl.** *Massonia brachypus* Baker (1874); **incl.** *Massonia namaquensis* Baker (1897); **incl.** *Massonia triflora* Compton (1931).

Bulbs globose, to 4.5 cm Ø; tunics fleshy white; L 2, appressed to the ground, oblong to



**Fig. 2** *Massonia depressa*. (Copyright: E. Van Jaarsveld)

orbicular, to 26 × 15 cm (but frequently less), fleshy, green with purple spots; **Inf** dense, capitate, to 30-flowered; basal **Bra** large, surrounding the inflorescence; **Fl** shortly pedicellate, greenish.

Johnson & al. (2001) reported that the flowers of this species are visited by at least four species of rodents that act as pollinators, attracted by the copiously produced jelly-like nectar and the yeasty floral scent. — [E. Van Jaarsveld]

**M. etesionamibensis** (U. & D. Müller-Doblies) J. C. Manning & Goldblatt (Edinburgh J. Bot. 60(3): 564, 2004). **Type:** Namibia, Witputz (Müller-Doblies 88144n [WIND, B, BTU, G, K, LI, M, MO, NBG, PRE, S, Z]). — **Lit:** Martínez-Azorín & al. (2015: as *Desertia*, with ills.). **Distr:** S Namibia; winter-rainfall region.

≡ *Whiteheadia etesionamibensis* U. & D. Müller-Doblies (1997) ≡ *Desertia etesionamibensis* (U. & D. Müller-Doblies) Martínez-Azorín & al. (2015).

Bulb globose, 1.8–2.4 cm Ø; **L** 2, dissimilar, ovate, the first 6.5–15 × 4.5–10.5 cm, the second 5.5–13.5 × 3.7–8.5 cm, patent, succulent; **Inf** spicate, 4–6.5 cm tall, 5- to 80-flowered; **Bra** 10–17 × 4–8 mm, lanceolate; **Ped** 1–3 mm; **Fl** subcampanulate, honey-scented, white; **Per** 12–16 mm long, tube 2–3 mm; **OTep** lanceolate, 9.5–14 mm; **St** connate into a short filament tube; **Ov** ovoid, green, 2.5–5 mm; **Sty** white, 3.5–5.5 mm; **Sti** punctiform; **Fr** obovoid, 18–25 × 14–25 mm; **Se** globose, black, 2 mm, shiny, surface reticulate. — [E. Van Jaarsveld]

## References

- Jessop, J. P. (1976) Studies in the bulbous *Liliaceae* in South Africa: 6. The taxonomy of *Massonia* and allied genera. J. South Afr. Bot. 42(4): 401–437, keys.
- Johnson, S. D. [et al. 2001], Pauw, A. & Midgley, J. (2001) Rodent pollination in the African lily *Massonia depressa* (Hyacinthaceae). Amer. J. Bot. 88(10): 1768–1773, ills. <http://www.jstor.org/stable/3558351>
- Manning, J. C. [et al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperaeae*. Edinburgh J. Bot. 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>
- Manning, J. C. [et al. 2011], Goldblatt, P. & Saunders, R. (2011) *Massonia bifolia*. Curtis's Bot. Mag., ser. nov., 28(4): 324–332, ills., t. 721. <https://doi.org/10.1111/j.1467-8748.2011.01759.x>
- Martínez-Azorín, M. [et al. 2015], Pinter, M. & Wetschnig, W. (2015) *Desertia*, a new genus in *Massonieae* (Asparagaceae, Scilloideae), including the description of *Desertia luteovirens* and the taxonomic revisions of *Whiteheadia* and *Namophila*. Phytotaxa 221(3): 201–225, ills., maps, key. <https://doi.org/10.11646/phytotaxa.221.3.1>
- Müller-Doblies, U. & Müller-Doblies, D. (1997) A partial revision of the tribe *Massonieae* (Hyacinthaceae). 1. Survey, including three novelties from Namibia: A new genus, a second species in the monotypic *Whiteheadia* and a new combination in *Massonia*. Feddes Repert. 108(1–2): 49–96, ills., keys. <https://doi.org/10.1002/fedr.19971080106>
- Pfossor, M. F. [et al. 2003], Wetschnig, W., Ungar, S. & Prenner, G. (2003) Phylogenetic relationships among genera of *Massonieae* (Hyacinthaceae) inferred from plastid DNA and seed morphology. J. Pl. Res. 116: 115–132, ills. <https://doi.org/10.1007/s10265-003-0076-8>
- Wester, P. (2010) Sticky snack for sengis: The Cape Rock Elephant-Shrew, *Elephantulus edwardii* (Macroscelidea), as a pollinator of the Pagoda Lily, *Whiteheadia bifolia* (Hyacinthaceae). Naturwissenschaften 97(12): 1107–1112, ills. <https://doi.org/10.1007/s00114-010-0723-6>
- Wester, P. (2015) The forgotten pollinators: First field evidence for nectar-feeding by primarily insectivorous elephant-shrews. Veld Fl. (1975+) 101(2): 84–85, ills.
- Wester, P. [et al. 2009], Stanway, R. & Pauw, A. (2009) Mice pollinate the Pagoda Lily, *Whiteheadia bifolia* (Hyacinthaceae) — first field observations with photographic documentation of rodent pollination in South Africa. South Afr. J. Bot. 75(4:Spec.Ed.): 713–719. <https://doi.org/10.1016/j.sajb.2009.07.005>





## Merwillia HYACINTHACEAE

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**Merwillia** Speta (Phyton (Horn) 38(1): 107, 1998). **Type:** *Scilla dracomontana* Hilliard & Burt. — **Hyacinthoideae**—**Massonieae** — **Distr:** Zimbabwe, Malawi, Moçambique, RSA, Swaziland, Lesotho; summer-rainfall regions, grassland biome. **Etym:** Combined from Merwe and the generic name *Scilla*; for the previous placement of the species, and for Frederick Ziervogel van der Merwe (1894–1968), South African medical inspector of schools, and specialist for *Aloe* and *Scilla*.

Perennial winter-deciduous bulbous plants; bulbs ovoid, solitary or in clusters, above-ground, covered with imbricate brown leaf bases and pale greyish-yellow tunics; **R** rather thick; **L** few, broad, ovate, glabrous; **Inf** ascending, to 80 cm, few- to many-flowered; scape 6 mm  $\varnothing$  at the base, terete; **Bra** small; **Ped** pointing upwards; **Tep** free, stellately spreading, to 7 mm, bluish; **Fil** adnate to the base of the tepals, spreading, acutely triangular, basally fused, white; **Anth** small, versatile; **Ov** subglobose, white, 3-locular, with 4–10 ovules per locule; **Sty** 1 mm; **Sti** simple, glandular; **Fr** globose acuminate capsules; **Se** oblong, flattened, wine-red when fresh, brownish when dry.

A genus of 2 species (3 species in Lebrun & Stork (2014: 94)) that were traditionally included

in *Scilla* (and informally referred to as the *Scilla natalensis* group). Independent generic status was confirmed by Wetschnig & Pfosser (2003) and Manning & al. (2004). The genus is completely separate from *Scilla* s.s. and forms the most basal clade within tribe *Massonieae* (Wetschnig & Pfosser 2003).

The fleshy bulbs are frequently grown in cultivation and are quite frost-resistant.

**M. dracomontana** (Hilliard & B. L. Burt) Speta (Phyton (Horn) 38(1): 109, 1998). **Type:** RSA, KwaZulu-Natal (Hilliard & Burt 6960 [E, NU]). — **Distr:** RSA (KwaZulu-Natal); among cliffs in rock crevices, 1600–2600 m.

≡ *Scilla dracomontana* Hilliard & B. L. Burt (1982).

Bulbs globose, 3 × 3 cm, dividing to form dense groups, above-ground or underground, bulb scales membranous, brownish and becoming truncate at the apex; **L** ± 5, synanthous, patent and spreading, 3–8 × 1–3.5 cm, ovate, acute, densely pubescent; **Inf** 6–11 cm, pubescent, densely flowered; **Bra** linear-lanceolate, 3–9 × 0.5–1 mm, membranous, green to violet; **Ped** 8–18 mm, sparsely pubescent; **Tep** 5 × 2 mm, lanceolate, spreading, deep blue or rarely white; **Fil** 2 mm, white, expanded at the base; **Anth** 1 mm; **Ov** 2 × 2 mm, globose, 3-lobed, white; **Sty** 1.5 mm; **Sti** truncate; **Fr** globose, 7 × 7 mm; **Se** not seen.

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**M. plumbea** (Lindley) Speta (Phyton (Horn) 38: 109, 1998). **Type:** [icono]: Edward's Bot. Reg. 16: t. 1355, 1830. — **Distr:** RSA (Eastern Cape, KwaZulu-Natal, Free State, Mpumalanga), Lesotho, Swaziland; among rocks in grassland, spring-flowering. **I:** Pole-Evans (1930: as *Scilla natalensis*).

≡ *Scilla plumbea* Lindley (1830); **incl.** *Scilla natalensis* Planchon (1855) ≡ *Merwillia natalensis* (Planchon) Speta (1998); **incl.** *Scilla kraussii* Baker (1873) ≡ *Merwillia kraussii* (Baker) Speta (1998).

Bulbs ovoid, above-ground, to 8 cm tall and 6.5 cm Ø at the base, covered with brown membranous leaf bases; **L** ± 9, 14–76 × 4.2–11 cm, ovate, acuminate, acute with a distinct midvein and numerous lateral veins, glabrous; **Inf** ascending, to 80 cm, ± 20- to 50-flowered; **Tep** 7 × 3.5 mm, elliptic, obtuse, bluish, with a minute tuft of glandular hairs at the tip; **Ov** 3 mm Ø, globose, glabrous; **Sty** 2 mm; **Sti** simple, glandular; **Fr** 10 × 9 mm; **Se** 0.6 × 2.8 mm.

In the traditional wide circumscription, this species also included elements that were recently named *Spetaea lachenaliiflora* (see there). Zukulu & al. (2012: 21) report traditional usage

as soap, as well as local usage in Pondoland as a strengthening charm in dance competitions.

## References

- Lebrun, J.-P. & Stork, A. L. (2014) Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (*Anthericaceae* – *Palmae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Manning, J. C. [& al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperaeae*. *Edinburgh J. Bot.* 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>
- Pole-Evans, I. B. (1930) *Scilla natalensis*. *Flow. Pl. South Afr.* 10: t. 365 + 2 pp. text.
- Wetschnig, W. & Pfosser, M. F. (2003) The *Scilla plumbea* puzzle — present status of the genus *Scilla* sensu lato in southern Africa and description of *Spetaea lachenaliiflora*, a new genus and species of *Massonieae* (*Hyacinthaceae*). *Taxon* 52(1): 75–91, ills., key. <https://doi.org/10.2307/3647303>
- Zukulu, S. [& al. 2012], Dold, T., Abbott, T. & Raimondo, D. (2012) Medicinal and charm plants of Pondoland. Pretoria (ZA): South African National Biodiversity Institute SANBI.





## Namophila HYACINTHACEAE

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**Namophila** U. & D. Müller-Doblies (Feddes Repert. 108(1–2): 77–79, ills., 1997). **Type:** *Namophila urotepala* U. & D. Müller-Doblies. — **Hyacinthoideae** — **Massonieae** — **Lit:** Martínez-Azorín & al. (2015: classification). **Distr:** S Namibia. **Etym:** Gr. ‘nama’, spring, stream; and Gr. ‘philos’, friend; for the occurrence in a valley with a seasonal stream.

Bulbous geophytes to 5 cm tall, bulbs usually solitary, globose, 1.5–2.3 cm Ø; **L** 2, ovate, 11–16 × 8–11.7 cm, (sub-) succulent, prostrately spreading; **Inf** 1, corymbose-capitate, between the leaves, 2- to 3-flowered (to 19-flowered in cultivation), raceme 1–4 cm; **Bra** linear, inconspicuous, lowest 17–36 × (1.3–) 2.5–3.5 mm; **Ped** 7–18 mm; **Fl** stellate, green, to 33 mm Ø; **Tep** 19–23 mm, basally united and forming a 4–6 mm long tube, lobes (12–) 15–17 × 3.5–4.5 mm, narrowly triangular, with a distinctly caudate tip 1–4.7 mm long; **St** basally fused to the tepal tube; free part of **Fil** 6–8 mm, white; **Anth** 2–2.5 mm, green with yellow pollen; **Ov** obclavate, green, 3.5–5 × 3–3.7 mm; **Sty** 8–10 mm, green; **Sti** punctiform; **Fr** enveloped by the fleshy perianth, 10 mm; **Se** globose, 2 × 1.2–1.8 mm, black, glossy.

The monotypic genus *Namophila* is closely related to *Massonia* according to the molecular

study by Manning & al. (2004). See *Massonia* for further comments on the classification of the group.

*N. urotepala* U. & D. Müller-Doblies (Feddes Repert. 108(1–2): 77–79, ills., 1997). **Type:** Namibia, Witputz (Müller-Doblies 88064g [WIND, B, BOL, BR, BTU, E, G, K, LI, M, MO, NBG, PRE, S, Z]). — **Lit:** Martínez-Azorín & al. (2015: with ills.). **Distr:** S Namibia (Witputz: S Namibian Escarpment); winter-rainfall area, ±700 m, spring-flowering.

Description as for the genus.

### References

- Manning, J. C. [& al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperaeae*. *Edinburgh J. Bot.* 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>
- Martínez-Azorín, M. [& al. 2015], Pinter, M. & Wetschnig, W. (2015) *Desertia*, a new genus in *Massonieae* (*Asparagaceae*, *Scilloideae*), including the description of *Desertia luteovirens* and the taxonomic revisions of *Whiteheadia* and *Namophila*. *Phytotaxa* 221(3): 201–225, ills., maps, key. <https://doi.org/10.11646/phytotaxa.221.3.1>

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## Ornithogalum HYACINTHACEAE

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**Ornithogalum** Linné (Spec. Pl. [ed. 1], 306, 1753). **Type:** *Ornithogalum umbellatum* Linné [lectotype, designated by Hitchcock, Prop. Brit. Bot., 145, 1929]. — **Ornithogaloideae**—**Ornithogaleae** — **Lit:** Obermeyer (1978: monograph S Africa); Müller-Doblies & Müller-Doblies (1996: partial revision); Manning & al. (2007: revision sect. *Aspasia*); Manning & al. (2009: phylogeny & classification); Martínez-Azorín & al. (2011a: phylogeny & classification). **Distr:** Mediterranean, W Asia, Near East, Africa. **Etym:** Lat. ‘ornithogale’ = Gr. ‘ornithogalon’, “Bird’s Milk”, a plant (from Gr. ‘ornis, ornithos’, bird, and Gr. ‘gala’, milk); for the egg-shale-coloured flowers of some European taxa; or going back to a Roman allusion of something beautiful or rare “as bird’s milk”.

**Incl.** *Celsia* Heister ex Fabricius (1763) (*nom. illeg.*, Art. 53.1). **Type:** *Ornithogalum umbellatum* Linné [lectotype, designated by Stearn, Ann. Mus. Goulandris 6: 140, 1983].

**Incl.** *Honorius* Gray (1821). **Type:** *Ornithogalum nutans* Linné.

**Incl.** *Myogalum* Link (1829) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum nutans* Linné.

**Incl.** *Albucca* Reichenbach (1830) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum nutans* Linné.

**Incl.** *Eliokarmos* Rafinesque (1837). **Type:** *Ornithogalum thyrsoides* Jacquin.

**Incl.** *Ethesia* Rafinesque (1837). **Type:** *Ornithogalum prasinum* Ker Gawler.

**Incl.** *Loncomelos* Rafinesque (1837). **Type:** *Ornithogalum pyrenaicum* Linné [lectotype, designated by Stearn, Ann. Mus. Goulandris 6: 140, 1983].

**Incl.** *Melomphis* Rafinesque (1837). **Type:** *Ornithogalum arabicum* Linné.

**Incl.** *Nicipe* Rafinesque (1837). **Type:** *Ornithogalum niveum* Aiton.

**Incl.** *Syncodium* Rafinesque (1837) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum nutans* Linné.

**Incl.** *Caruelia* Parlato (1854) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum arabicum* Linné.

**Incl.** *Aspasia* Salisbury (1866) (*nom. illeg.*, Art. 53.1). **Type:** *Ornithogalum conicum* Jacquin [lectotype, designated by Obermeyer, Bothalia 12: 333, 1978].

**Incl.** *Beryllis* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum pyrenaicum* Linné [lectotype, designated by Stearn, Ann. Mus. Goulandris 6: 140, 1983].

**Incl.** *Brizophile* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum nutans* Linné.

**Incl.** *Cathissa* Salisbury (1866). **Type:** *Ornithogalum concinnum* Salisbury [lectotype, designated by J. C. Manning & Goldblatt, Taxon 58: 103, 2009].

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- Incl.** *Eustachys* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum latifolium* Linné [type according to J. C. Manning & Goldblatt, Taxon 58: 103, 2009].
- Incl.** *Myanthe* Salisbury (1866) (*nom. illeg.*, Art. 52.1). **Type:** *Ornithogalum arabicum* Linné.
- Incl.** *Phaeocles* Salisbury (1866). **Type:** *Ornithogalum maculatum* Jacquin.
- Incl.** *Galtonia* Decaisne (1880). **Type:** *Hyacinthus candicans* Baker [lectotype, designated by Phillips, Gen. S. Afr. Fl. Pl., ed. 2: 190, 1951].
- Incl.** *Neopatersonia* Schönland (1912). **Type:** *Neopatersonia uitenhagensis* Schönland.
- Incl.** *Elsiea* F. M. Leighton (1944). **Type:** not designated.
- Incl.** *Avonsera* Speta (1998). **Type:** *Ornithogalum convallarioides* H. Perrier.
- Incl.** *Zahariadia* Speta (1998) (*nom. inval.*, Art. 36.1, 37.1). **Type:** not typified.

Perennial bulbous plants; bulbs variable, above-ground or underground, globose to pear- or drop-shaped, rarely asymmetrical, tunics usually fleshy; **L** 1 to many, in a rosette or rarely distichous, very variable, withering in the dry season, rarely evergreen, terete to flattened, glabrous or variously hairy to ciliate; **Inf** racemose, subspicate to subcorymbose, erect, with a bract-less smooth scape; **Bra** small to large, membranous to foliaceous; **Fl** actinomorphic, diurnal or nocturnal, spreading, ascending or nutant; **Per** stellate, uniform in colour (most commonly white, but also yellow, orange or green) with at most a narrow dark midrib area, or basal-most part black (rarely with a dark spot near the tip, e.g. *O. maculatum*); **Tep** 6, free (rarely fused at the base), in 2 whorls of 3, thin- or thick-textured; **St** 6, the 3 outer with narrower filaments; **Fil** sometimes with appendages; **Anth** versatile; **Ov** 3-locular; **Sty** erect or deflexed, cylindrical; **Sti** 3-lobed; **Fr** 3-locular loculicidal capsules, subglobose to ellipsoid, tip acute to retuse; **Se** very variable in size and shape, angular to subglobose, black, shiny, papillate to echinulate.

A genus of  $\pm 160$  species with a main centre of diversity in S Africa, and secondary centres in the Mediterranean and the Near East. A few species,

such as *O. thyrsiflora*, are cultivated commercially for the flower trade. Only a few species can be regarded as truly succulent, but as in many other bulbous plants, many more species show weakly expressed succulence either in the form of above-ground bulbs, or somewhat fleshy leaves.

**Classification and History:** The classification of the genus, and that of subfam. *Ornithogaloideae*, is in continued dispute and was controversially discussed in recent years. Speta (1998) recognized 14 genera for the subfamily, while Manning & al. (2004) lumped all of them into a massively enlarged single genus *Ornithogalum*. This radical approach likewise appeared unsatisfactory, and based on additional evidence and increased sampling for molecular analyses, Manning & al. (2009) concluded that the 4 genera *Ornithogalum*, *Albuca*, *Pseudogaltonia* and *Dipcadi* (the latter two closely related) should be recognized. Martínez-Azorín & al. (2011a) recovered the same 3 major clades, but propose to split *Ornithogalum* into no less than 19 different genera. They claim that each can be diagnostically circumscribed by a combination of morphological characters and biogeography.

In comparison with traditional classifications (e.g. Obermeyer (1978)), the circumscription of *Ornithogalum* has changed considerably on the basis of the molecular studies just mentioned, and subgen. *Osmyne* and the majority of the species of subgen. *Urophyllon* have been moved to *Albuca*. *Ornithogalum* is the only genus of tribe *Ornithogaleae* (Manning & al. 2009).

**Infrageneric classification:** Manning & al. (2009) divide *Ornithogalum* into the following 4 subgenera:

- [1] Subgen. *Ornithogalum*: **Bra** lanceolate to linear-acuminate, membranous or papery; **Tep** fleshy or thin-textured, white or pale green; **Fil** sometimes toothed; **Se** large (2–8 mm), semi-lunate to discoid. — Divided into 7 sections by Manning & al. (2009)
- [2] Subgen. *Aspasia* (Salisbury) Obermeyer 1978 ( $\equiv$  *Aspasia* Salisbury 1866): **L** mainly hysteroanthous; **Bra** cymbiform; **Tep** thin-textured, white, yellow or orange; **Fil** with outgrowths in the lower  $\frac{1}{2}$ ; **Fr** fusiform to

ellipsoid; **Se** variable in shape, small (0.5–2 mm), not flattened, papillate to echinate. — Mainly from winter-rainfall regions. Manning & al. (2009) propose a division into 2 sections, and Manning & al. (2007) provide a revision of sect. *Aspasia*.

- [3] Subgen. *Avonsera* (Speta) J. C. Manning & Goldblatt 2009 (≡ *Avonsera* Speta 1998): Lowermost **Bra** 2-flowered; **Tep** thin-textured, white, connate below; **Se** ovoid. — Only *O. convallarioides* (not succulent, Madagascar).
- [4] Subgen. *Galtonia* (Decaisne) J. C. Manning & Goldblatt 2009 (≡ *Galtonia* Decaisne 1880): **Bra** membranous or papery; **Tep** fleshy, white or pale green, free or fused into a short tube; **Se** large (5–8 mm), semi-lunate to discoid. — Here belong the 7 non-succulent species of the formerly separate genus *Galtonia*.

**Ecology:** Some S African species (but no succulents studied) of *Ornithogalum* have been found to be pollinated by hopliine beetles (monkey beetles) (Goldblatt & Manning 2011).

**O. britteniae** F. M. Leighton (Bothalia 12: 352, Fig. 26 (p. 353), 1978). **Type:** RSA, Eastern Cape (*Britten* s.n. in *BOL* 23902 [BOL, PRE [photo]]). — **Lit:** Dold (2005); Hammer (2008).

≡ *Nicipe britteniae* (F. M. Leighton ex Obermeyer) Martínez-Azorín & al. (2011).

[1] Bulbs ovoid, 1.5–2.5 cm Ø, tunics fibrous to papery; **L** 5–7, distichous, ensiform, conduplicate, 5 × 1 cm, hard, glaucous, apex curving outwards, obtuse, base clasping, tubular, margin sclerotic, densely and shortly fimbriate; **Inf** slender, scape laxly curved, raceme to 25 cm; **Bra** minute, auriculate, aristate, membranous; **Ped** filiform, 5 mm; **Tep** narrowly ovate, 6–8 mm, cream to cinnamon; **Fil** ovate-acuminate, 4 mm; **Ov** oblong-globose, trigonous, 3 mm; **Sty** terete, 3 mm, shortly 3-lobed; **Sti** papillate.

Propagation by division of bulbs is possible (Hammer 2008).

**O. comptonii** F. M. Leighton (J. South Afr. Bot. 10: 119, 1944). **Type:** RSA, Western Cape (*Leighton* 269 [BOL, NBG, PRE]). — **Distr:**

RSA (Western Cape, Eastern Cape); widespread in the Great Karoo, in Succulent Karoo and Thicket vegetation.

≡ *Nicipe comptonii* (F. M. Leighton) Martínez-Azorín & al. (2011); **incl.** *Stellarioides spiralifolia* Van Jaarsveld (2016).

[1] Bulbs shallow-seated to above-ground, solitary or dividing to form groups of up to 3 bulbs, globose to depressed, 2–5.5 × 3.5–4 cm Ø, outer tunics loose, papery, grey-white, inner tunics yellowish-green; **R** 1–2 mm Ø, whitish; **L** up to 12, in a rosette, erect, succulent, leathery and firm, linear and spirally twisted, 4–17 cm, 2.5 mm Ø (at the base ±3.5 mm), dorsiventrally flattened, glaucous-green, adaxial surface channelled, lower surface flattened, faintly striate, 5- to 7-ribbed, margin entire, apex obtuse to subacute with a cartilaginous whitish margin, leaf base withering to a fibrous neck; **Inf** erect, 45–52 cm, scape 40 cm, 2 mm broad at the base, biconvex, terete upwards; raceme 11 cm, to 25-flowered; **Bra** scarious, deltoid, acuminate, 4–4.5 × 1.5 mm; **Ped** 8–10 mm, ascending; **Fl** rotate, 14 mm Ø, whitish; **Tep** with a green median stripe; **OTep** 8 × 2 mm; **ITep** 8 × 2.7 mm; **St** 5 mm; **Anth** 2 × 0.8 mm; **Ov** ovoid, 2.5 mm, grooved, green, stipitate; **Sty** 1.8 mm; **Fr** ovoid, 6 × 4 mm; **Se** 1.5 × 1 mm, crescent-shaped.

**O. geniculatum** Obermeyer (Bothalia 12(3): 344, fig. 18, 1978). **Type:** RSA, Northern Cape (*Marloth* 13249 [PRE]). — **Distr:** Namibia (S Namib Desert), RSA (Northern Cape); Succulent Karoo, spring-flowering.

≡ *Eliokarmos geniculatus* (Obermeyer) Martínez-Azorín & al. (2011).

[2] Dwarf solitary geophytes; bulbs globose-ovoid, to 1 cm Ø and high, tunics white, fleshy, outer tunics dry; **L** synanthous, variable, oblong, succulent, lower leaves 4–5 × 2 cm, oblong, upper leaves 3 × 0.3 cm, tubular at the base and clasping the stem; **Inf** to 15 cm, racemose, up to 5-flowered; scape wiry, geniculate at the base; **Bra** linear-acuminate; **Ped** 1 cm; **Tep** white, 10 × 3 mm, linear-elliptic; **St** 5 mm, outer **Fil** filiform, inner ovate; **Ov** ovoid; **Sty** erect; **Sti** capitate; **Fr** 10 × 10 mm Ø, transparent, oblong-ovoid; **Se** flat, 1 mm Ø.



**O. juncifolium** Jacquin (Pl. Hort. Schoenbr. 1: 46, t. 90, 1797). **Type:** [icono]: l.c., t. 90. — **Distr:** RSA (North-West Prov., Gauteng, Mpumalanga, Free State, Western Cape, KwaZulu-Natal, Eastern Cape), Lesotho; widespread on rocky well-drained terrain.

≡ *Nicipe juncifolia* (Jacquin) Martínez-Azorín & al. (2011).

**O. juncifolium** var. **emmsii** Van Jaarsveld & A. E. van Wyk (Bothalia 35(1): 83, ill., 2005). **Type:** RSA, Eastern Cape (*Van Jaarsveld & Emms* 16808 [NBG]). — **Distr:** RSA (Eastern Cape: Koonap River); cliffs in Albany Thicket vegetation, flowering in December.

[1] Differs from var. *juncifolium*: Forming numerous bulbils at the base of the bulb; **Tep** 10–12 mm.

**O. juncifolium** var. **juncifolium** — **Distr:** RSA (North-West Prov., Gauteng, Mpumalanga, Free State, Western Cape, KwaZulu-Natal, Eastern Cape), Lesotho; widespread on rocky well-drained terrain.

**Incl.** *Ornithogalum setifolium* Kunth (1843); **incl.** *Ornithogalum griseum* Baker (1873); **incl.** *Ornithogalum subulatum* Baker (1874); **incl.** *Ornithogalum leptophyllum* Baker (1897); **incl.** *Ornithogalum oliganthum* Baker (1897); **incl.** *Ornithogalum stenostachyum* Baker (1901); **incl.** *Ornithogalum tenuipes* C. H. Wright (1901); **incl.** *Ornithogalum capillifolium* Fourcade (1934) ≡ *Nicipe capillifolia* (Fourcade) Martínez-Azorín & al. (2011); **incl.** *Ornithogalum limosum* Fourcade (1934); **incl.** *Ornithogalum petraeum* Fourcade (1934) ≡ *Nicipe petraea* (Fourcade) Martínez-Azorín & al. (2011); **incl.** *Ornithogalum brevifolium* F. M. Leighton (1943); **incl.** *Ornithogalum epigeum* F. M. Leighton (1943); **incl.** *Ornithogalum langebergense* F. M. Leighton (1945).

[1] Bulbs above-ground and cluster-forming, globose, to 4 cm Ø and tall, tunics grey-brown, leathery and exposing green living tissue; **L** synanthous, 10–20 cm × 2–3 mm, linear, filiform, green, base sheathing and tubular forming a membranous neck on top of the bulb; **Inf** to 40 cm, racemose, to 15-flowered, scape terete,

erect; **Bra** deltoid-cuspidate, auriculate; **Ped** ± 2 mm, lengthening to 7 mm in fruit; **Per** stellate, white; **Tep** linear-lanceolate, 7–10 × 2.5 mm; **Fil** 5 mm, outer linear, inner shorter and ovate-acuminate; **Ov** ovate, 3 mm, shortly stipitate; **Sty** erect, 2.5 mm; **Fr** 5 mm, ovoid.

**O. lithopsoides** Van Jaarsveld (Aloe 46(1): 20–21, ill., 2009). **Type:** RSA, Western Cape (*Van Jaarsveld* 15240 [NBG]). — **Distr:** RSA (Western Cape: near Oudtshoorn); conglomerate gravel hills in Succulent Karoo, spring-flowering.

≡ *Nicipe lithopsoides* (Van Jaarsveld) Martínez-Azorín & al. (2014).

[1] Bulbs dwarf, above-ground, solitary or dividing to form small clusters, globose, 1.5–2 cm Ø, tunics grey-white; **L** 12–15, hysteroanthous, 1.2–5 cm × 1–2 mm, linear, ascending-spreading, dark green, surfaces sparingly hairy but becoming glabrous, adaxial surface shallowly canaliculate, margins minutely ciliolate, apex acute, mucronate; **Inf** 10–18 cm, 8- to 25-flowered; **Bra** deltoid-cuspidate, auriculate; **Ped** 3–4 mm; **Per** stellate, white, to 11 mm Ø; **Tep** linear-lanceolate; **OTep** 7–8 × 1.5–2 mm; **ITep** 5–6 × 1.4 mm, white with green median stripe; **St** 3–4 mm, flattened; **Ov** ovoid, 2 × 1.5 mm; **Sty** 3 mm; **Sti** capitate; **Fr** ovoid, 3 × 2 mm; **Se** 1.3–1.5 × 0.5 mm.

Incorrectly regarded as synonym of *O. juncifolium* by Manning & Goldblatt (2012: 806).

**O. maculatum** Jacquin (Collectaneorum Suppl., 2: 368, t. 18: Fig. 3, 1789). **Type:** [lecto — icono]: l.c., t. 18: Fig. 3. — **Lit:** Duncan (2013). **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo, in shallow quartzitic sandstone rock pockets. – Fig. 1.

**Incl.** *Ornithogalum maculatum* Thunberg (1818) (*nom. illeg.*, Art. 53.1); **incl.** *Ornithogalum notatum* Schultes fil. (1829) (*nom. illeg.*, Art. 52.1); **incl.** *Ornithogalum thunbergianum* Baker (1873) ≡ *Eliokarmos thunbergianus* (Baker) Martínez-Azorín & al. (2015); **incl.** *Ornithogalum speciosum* Baker (1891) ≡ *Ornithogalum maculatum* var. *speciosum* (Baker) F. M. Leighton (1944) (*nom. inval.*, Art. 43.1); **incl.** *Ornithogalum thunbergianum* var.



**Fig. 1** *Ornithogalum maculatum*. (Copyright: E. Van Jaarsveld)

*concolor* Baker (1897); **incl.** *Ornithogalum splendens* L. Bolus (1931)  $\equiv$  *Ornithogalum maculatum* var. *splendens* (L. Bolus) F. M. Leighton (1944); **incl.** *Ornithogalum insigne* F. M. Leighton (1943); **incl.** *Ornithogalum magnificum* Von Poellnitz (1946); **incl.** *Ornithogalum roussouwii* U. & D. Müller-Doblies (1996); **incl.** *Eliokarmos neomaculatus* Martínez-Azorín & al. (2011) (*nom. illeg.*, Art. 52.1).

[2] Bulbs underground, solitary, subglobose, 1.2–3.5 cm  $\varnothing$ , white, outer tunics becoming dark brown when dry; **L** 2–5, synanthous, 11–15  $\times$  1–1.6 cm, suberect, lanceolate, glaucous, canaliculate, ascending; **Inf** erect, 30–42 cm, 1- to 5-flowered, scape terete, bright green; **Bra** naviculate, 9–27  $\times$  5–9 mm, papery, tips attenuate; **Ped** 2–18 mm; **Fl** stellate, orange to yellow, broadly cup-shaped; **OTep** broadly lanceolate with a black spot towards the tip, 14–32  $\times$  8–14 mm; **ITep** oblanceolate or spatulate, 17–35  $\times$  10–19 mm; **Fil** 4–7 mm, light yellow to orange; **Ov** narrowly-ovoid, 4–9  $\times$  4–5 mm; **Sty** capitate, 2  $\times$  1–2 mm; **Fr** ovoid, 8–12  $\times$  6–10 mm; **Se** irregularly compressed, 1.1–1.3  $\times$  1–1.2 mm.

Some yellow-flowering forms are superficially similar to yellow forms of *O. dubium*, which has fleshy filaments, however (Duncan 2013: 41).

**O. naviculum** W. F. Barker ex Obermeyer (Bothalia 12(3): 348, Fig. 23, 1978). **Type:** RSA, Western Cape (Hall 2869 [NBG]). — **Distr:** RSA (N Western Cape); Succulent Karoo, flowering in mid-summer.

$\equiv$  *Eliokarmos naviculum* (W. F. Barker ex Obermeyer) Martínez-Azorín & al. (2011).

[2] Dwarf solitary geophytes; bulbs globose; **L** hysteroanthous, obovoid to oblong-obovoid, 20  $\times$  8 mm, cymbiform, succulent, canaliculate above, basally amplexicaul; **Inf** to 10 cm, racemose, erect, up to 12-flowered; **Bra** deltoid-acuminate, 3 mm; **Ped** 15 mm, ascending; **Tep** spreading, becoming reflexed, white, 7  $\times$  2 mm, narrowly ovate; **St** 5 mm, **Fil** filiform; **Ov** narrowly obovoid, yellow; **Sty** erect; **Sti** capitate; **Fr** and **Se** not seen.

**O. pendens** Van Jaarsveld & A. E. van Wyk (Aloe 46(2): 30–31, ills., 2009). **Type:** RSA, Northern Cape (Van Jaarsveld & al. 21108 [NBG]). — **Distr:** RSA (Northern Cape: between Steinkopf and Spektakel); quartzitic sandstone cliffs in Succulent Karoo, spring-flowering.

$\equiv$  *Eliokarmos pendens* (Van Jaarsveld) Martínez-Azorín & al. (2015).

[2] Geophytes, forming dense clusters to 10 cm  $\varnothing$ ; bulbs globose-ovoid, to 5–10  $\times$  5–8 mm, tunics white; **L** 2, synanthous, 5–10  $\times$  1–1.6 cm, pendent, linear, fleshy and somewhat succulent, channelled, somewhat translucent, surface glaucous, smooth, striate, lower surface with slight keel, margin entire; **Inf** 1 per plant, 5–7 cm, raceme subcorymbose, 2.5–3 cm, 3- to 6-flowered; scape terete, 1 mm  $\varnothing$  at the base, erect, same colour as the leaves; **Bra** ascending, lanceolate to linear-lanceolate, cymbiform, same colour as the leaves, clasping the pedicels, channelled, 10–14  $\times$  2–4 mm, becoming smaller further up; **Ped** to 12–20 mm; **Per** stellate, white, 15–18 mm  $\varnothing$ ; **Tep** white, ovate-elliptic, 7–12  $\times$  3–4 mm; **St** 4–7 mm; **Fil** white, linear, inner flattened, 1 mm broad at the base; **Anth** 1.4 mm; **Ov** oblong, abruptly tapering at the apex, 3.5  $\times$  2 mm, green, 3-ridged, sessile; **Sty** erect, 1.2 mm, yellowish; **Sti** capitate.

An easily cultivated winter-grower. — The recently described *Eliokarmos craibii* (no combination under *Ornithogalum* available yet) with distinctly succulent leaves is compared with *E. pendens* in the protologue.

**O. perdurans** A. P. Dold & S. A. Hammer (Bothalia 33(1): 112–113, ills., 2003). **Type:**

RSA, Eastern Cape (*Dold & Hammer* 4441 [GRA]). — **Distr:** RSA (Eastern Cape); Nama Karoo.

≡ *Nicipe perdurans* (A. P. Dold & S. A. Hammer) Martínez-Azorín & al. (2011).

[1] Bulb above-ground, 2–3 cm Ø, outer tunics thin, wrinkled; **L** 4–23, evergreen, semiterete, linear, 4–6 cm × 1–1.4 mm, ascending, wiry, somewhat twisting, adaxial surface with a narrow channel, blackish-green, surface rugose with parallel, undulating, transverse grooves and short, stiff hairs, tip subacute; **Inf** racemose, 20- to 40-flowered, scape 19–25 cm, erect; **Bra** deltoid, 4.4 × 2.8 mm, auriculate; lower **Ped** 7 mm; **Per** stellate; **Tep** pale fawn-coloured, spreading to reflexed; **OTep** ovate, 7 × 3.2 mm; **ITep** elliptic, 6.4 × 2.8 mm; **St** patent; **Ov** ovoid, 3 × 2 mm; **Sty** 2.5 mm, terete; **Sti** 3-lobed, 1 mm Ø, with glandular hairs; **Fr** ovoid-acute, 4.5–5 × 3–4 mm; **Se** angular, 1.4 × 0.5 mm, rugose, black.

**O. richtersveldensis** Van Jaarsveld (*Aloe* 52 (1): 24–27, ill., 2016). **Type:** RSA, Northern Cape (*Van Jaarsveld & Deacon* 24600 [NBG]). — **Distr:** RSA (Northern Cape: Richtersveld); Succulent Karoo, flowering October–November.

[2] Bulbs mainly above-ground, summer-deciduous, solitary or sparingly proliferous forming small clusters, globose-ovoid, 1.2–2.5 × 1.4–3 cm, tunics fleshy, greenish, becoming yellowish-green with the outer layer becoming brownish; **L** 3–5, synanthous, 12–17 × 1.6–3 cm, in lax basal rosettes, horizontally spreading to ascending, sometimes becoming pendent, linear-ovate, fleshy and slightly channelled, glaucous-green, glabrous, faintly striate, margin entire, lower surface with slight keel, apex acute, mucronate, juvenile leaves linear-lanceolate, subterete, succulent; **Inf** 11.5–15 cm, raceme subcorymbose, 1.5–2.5 cm, 8- to 25-flowered; **Bra** ascending, linear-lanceolate, cymbiform, whitish-green, clasping pedicel and channelled, 23–30 × 2–4 mm, smaller upwards; lower **Ped** 15–20 mm, becoming shorter upwards; **Fl** stellate, white, 28–33 mm Ø; **Tep** ovate to ovate-elliptic, 15–16 × 5–7 mm; **St** 5–7 mm; **Fil** linear, inner ones flattened and up to 1.5 mm broad at the base; **Anth** 1.5 mm; **Ov** oblong, abruptly tapering at the tip, 5.5 × 2.5 mm, green, 3-rigged; **Sty** green,

erect, 3.5 mm, yellowish; **Sti** punctiform; **Fr** 7 × 4 mm; **Se** 1 × 0.6 mm, flattened.

**O. rupestre** Linné *fil.* (Suppl. Pl., 199, 1782).

**Type:** RSA, Western Cape (*Thunberg* 8320 [UPS]). — **Distr:** RSA (Northern Cape, Western Cape); Succulent Karoo in shallow quartzitic sandstone rock pockets. **I:** Obermeyer (1978: 341 and plate opposite p. 340, as *O. multifolium*).

**Incl.** *Ornithogalum multifolium* Baker (1873); **incl.** *Ornithogalum aurantiacum* Baker (1878); **incl.** *Ornithogalum ranunculoides* L. Bolus (1933); **incl.** *Ornithogalum perpulchrum* Schlechter ex Von Poellnitz (1944).

[2] Bulbs underground, solitary or forming clusters, ovoid, to 4 cm Ø, tunics grey-brown, leathery and exposing green living tissue; **L** to ±10, synanthous, 2–10 cm × 2–3 mm, linear-terete, glaucous, often spreading; **Inf** erect, 4–15 cm, 1- to 15-flowered; **Bra** cymbiform, acuminate, 4–25 mm; lower **Ped** to 20 mm; **Per** stellate, yellow to orange; **Tep** ovate-lanceolate to obovate, 6–15 × 4 mm; **St** ± 3–7 mm, linear-ovate, outer **Fil** narrower; **Ov** broadly ovoid, 3–6 mm; **Sty** erect, 1–2 mm; **Fr** to 10 mm, ovoid.

**O. sardienii** Van Jaarsveld (*Bradleya* 12: 32–34, ill., 1994). **Type:** RSA, Western Cape (*Van Jaarsveld & al.* 10854 [NBG]). — **Distr:** RSA (Western Cape: Little Karoo); Succulent Karoo.

≡ *Nicipe sardienii* (Van Jaarsveld) Martínez-Azorín & al. (2011).

[1] Dwarf, bulb above-ground, globose, 0.8–2 × 0.5–1.8 cm Ø, solitary or forming small clumps, tunics grey-white, succulent, slightly translucent; **R** fibrous, terete; **L** evergreen, numerous (20–50) in a dense basal rosette, ascending to erectly spreading, linear-lanceolate, green with up to 6 rows of white translucent porrect cilia, 1.5–2.5 cm × basally 1 mm, keeled, triangular in cross-section, adaxially flat, margin ciliate, abaxially convex in the lower part, apex with a yellowish-green mucro; **Inf** 1–5, 15–24 cm, racemose, up to 30-flowered, erect; **Fl** pointing upwards, ± 12 mm Ø; lower **Bra** 3.5 mm, upper ones smaller; lowest **Ped** 20 mm; **Per** stellate; **Tep** 5–6 mm, white, obtuse; **OTep** 2 mm broad; **ITep**

1.5 mm broad; outer **St** 3 mm, inner 4 mm; **Fil** filiform; **Ov** 2 mm, obovoid-ellipsoid to globose, 6-grooved with light green tubercles along the middle part; **Sty** erect, 2 mm, 6-grooved; **Sti** obscurely 3-lobed, yellow; **Fr** ovoid, 3.5 mm; **Se** pear-shaped, 0.5 mm, many-angled.

**O. tortuosum** Baker (in Thiselton-Dyer, Fl. Cap. 6: 510, 1897). **Type:** RSA, Western Cape (*Pappe* s.n. [K, PRE [photo], SAM]). — **Distr:** RSA (Western Cape); Fynbos vegetation.

≡ *Nicipe tortuosa* (Baker) Martínez-Azorín & al. (2011); **incl.** *Anthericum filifolium* Thunberg (1794) ≡ *Nicipe filifolia* (Thunberg) Martínez-Azorín & al. (2011); **incl.** *Ornithogalum comptum* Baker (1873); **incl.** *Ornithogalum thunbergianulum* U. & D. Müller-Doblies (1996).

[1] Dwarf, bulbs ovoid to almost globose, 0.8–1.3 cm Ø, solitary or proliferating forming groups; **R** fibrous; **L** 6–8, filiform, spirally twisted or straight, glabrous, 4–5 cm; **Inf** 12.5–20 cm, scape slender, 10–15 cm, raceme 2.5–5 cm; **Ped** ascending, 5–7 mm; **Bra** minute, ovate, cuspidate; **Fl** stellate; **Tep** white; **St** as long as the perianth; **Fil** flattened; **Sty** as long as the ovary.

## References

- Dold, T. (2005) The rediscovery of *Ornithogalum britteniae*. Cact. Succ. J. (US) 77(3): 148–151, ills., maps. [https://doi.org/10.2985/0007-9367\(2005\)77\[148:TROOB\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2005)77[148:TROOB]2.0.CO;2)
- Duncan, G. (2013) *Ornithogalum maculatum*. Curtis's Bot. Mag., ser. nov., 30(1): 36–48, ills., t. 754. <https://doi.org/10.1111/curt.12015>
- Goldblatt, P. & Manning, J. C. (2011) Hopliine beetles (*Scarabaeidae: Rutelinae: Hopliini*), specialized pollinators of the southern African flora. Curtis's Bot. Mag., ser. nov., 28(4): 238–259, ills. <https://doi.org/10.1111/j.1467-8748.2011.01752.x>
- Hammer, S. (2008) Oaks and acorns. *Ornithogalum britteniae* revisited. Cact. Succ. J. (US) 80(1): 18, ills. [https://doi.org/10.2985/0007-9367\(2008\)80\[18:OAA\]2.0.CO;2](https://doi.org/10.2985/0007-9367(2008)80[18:OAA]2.0.CO;2)
- Manning, J. C. & Goldblatt, P. (2012) Plants of the Greater Cape Floristic Region. 1: The core Cape Flora. Pretoria (ZA): SANBI.
- Manning, J. C. [ & al. 2004], Goldblatt, P. & Fay, M. F. (2004) A revised generic synopsis of *Hyacinthaceae* in sub-Saharan Africa, based on molecular evidence, including new combinations and the new tribe *Pseudoprosperae*. Edinburgh J. Bot. 60(3): 533–568, keys. <https://doi.org/10.1017/S0960428603000404>
- Manning, J. C. [ & al. 2007], Martínez-Azorín, M. & Crespo, M. B. (2007) A revision of *Ornithogalum* subgenus *Aspasia* section *Aspasia*, the Chincherichees (*Hyacinthaceae*). Bothalia 37(2): 133–164, ills., key, maps. <https://doi.org/10.4102/abc.v37i2.310>
- Manning, J. C. [ & al. 2009], Forest, F., Devey, D. S., Fay, M. F. & Goldblatt, P. (2009) A molecular phylogeny and a revised classification of *Ornithogaloideae* (*Hyacinthaceae*) based on an analysis of four plastid DNA regions. Taxon 58(1): 77–107, ills., key. <http://www.jstor.org/stable/27756826>
- Martínez-Azorín, M. [ & al. 2011a], Crespo, M. B., Juan, A. & Fay, M. F. (2011) Molecular phylogenetics of subfamily *Ornithogaloideae* (*Hyacinthaceae*) based on nuclear and plastid DNA regions, including a new taxonomic arrangement. Ann. Bot. (Oxford), n.s. 107: 1–37, ills. key. <https://doi.org/10.1093/aob/mcq207>
- Müller-Doblies, U. & Müller-Doblies, D. (1996) Revisionula incompleta *Ornithogalorum* austro-africanorum (*Hyacinthaceae*). Feddes Repert. 107 (5–6): 361–548, ills., key. <https://doi.org/10.1002/fedr.19961070511>
- Obermeyer, A. A. (1978) *Ornithogalum*: A revision of the southern African species. Bothalia 12(3): 323–376, ills., key. <https://doi.org/10.4102/abc.v12i3.1793>
- Speta, F. (1998) *Hyacinthaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 261–285, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_35](https://doi.org/10.1007/978-3-662-03533-7_35)







## Spetaea HYACINTHACEAE

E. Van Jaarsveld

**Spetaea** Wetschnig & Pfosser (Taxon 52(1): 75, 2003). **Type:** *Spetaea lachenaliiflora* Wetschnig & Pfosser. – **Hyacinthoideae** – **Massonieae** – **Distr:** RSA (Western Cape). **Etym:** For Dr. Franz Speta (1941–2015), Austrian botanist and specialist of petaloid monocotyledons.

Perennial summer-deciduous bulbous plants; bulbs underground, ovoid, 3.5 cm Ø, bulb scales firm, dark brown; **R** fibrous; **L** up to 6, succulent, canaliculate, linear to lanceolate, acuminate, 15–25 × 1–3 cm, glabrous, surface shining, without spots; **Inf** solitary, erect, 20–50 cm, raceme 4–5 cm Ø, densely flowered; **Bra** 2–3 mm, recurved; **Ped** horizontally spreading, 9–19 mm, glabrous; **Fl** campanulate; **Tep** 9–11 × 1.8–2.5 mm, basally fused to form a narrow cup, blue to violet, 1-veined; **Fil** fused at the base, spreading, blue or violet, 9–12 mm; **Anth** 2.5 mm, violet to purple, dorsifixed, pollen yellow; **Ov** 3 × 2 mm Ø; **Fr** obovoid, obtusely 3-lobed, 10 × 8 mm; **Se** 2.6 × 1.7 mm, slightly wrinkled, black. — **Cytology:** 2n = 20 (protologue).

The single species of this genus was for long regarded as part of a widely circumscribed *Scilla plumbea* auct. (not *S. plumbea* Lindley, see *Merwillia plumbea*), but the studies of Wetschnig and Pfosser (2003) showed that the plants from

the Du Toits Kloof area are an independent taxon distinct from any other member of the tribe. In their molecular analysis, *Spetaea* forms a subclade with *Daubenya*, *Androsiphon*, *Amphisiphon* and *Massonia*. *Spetaea* is distinct within the tribe due to its almost uniquely wrinkled seeds.

**S. lachenaliiflora** Wetschnig and Pfosser (Taxon 52(1): 75, ills. (p. 76), 2003). **Type:** RSA, Western Cape (*Drège* 1997 [B, W]). – **Distr:** RSA (Western Cape: Du Toits Kloof); rocky parts in Hawequas Sandstone Fynbos vegetation, winter-rainfall region; flowering during mid-summer. **I:** Lewis (1947, as *Scilla plumbea*).

Description as for the genus.

### References

- Lewis, G. J. (1947) *Scilla plumbea*. Flow. Pl. Afr. 26: t. 1006 + 2 pp. text.
- Wetschnig, W. & Pfosser, M. F. (2003) The *Scilla plumbea* puzzle — present status of the genus *Scilla* sensu lato in southern Africa and description of *Spetaea lachenaliiflora*, a new genus and species of *Massonieae* (*Hyacinthaceae*). Taxon 52(1): 75–91, ills., key. <https://doi.org/10.2307/3647303>

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**Part XIV**

**The Family Laxmanniaceae**





# Laxmanniaceae

C. C. Walker

**Including** *Lomandraceae* Lotsy.

**Including** *Eustrephaceae* Chupov.

Monoecious or dioecious erect, mainly tufted herbs or shrubs, a few arborescent perennials to 10 m (*Cordyline*); roots fibrous or thickened and fleshy; **L** spiral or distichous,  $\pm$  sheathing, lamina dorsiventral, cylindrical or linear to linear-lanceolate, margins entire; **Inf** erect, simple or compound spikes, racemes, bracteate umbels or cymes; **Fl** small to medium-sized; **Tep** 3 + 3, free or united, petaloid, scarious or fleshy; **St** 3 + 3 or 0 + 3; **Anth** dehiscent mainly by slits; **Ov** superior, syncarpous, 3-locular with several ovules per locule; **Sty** 1- to 3-lobed; **Fr** a berry, loculicidal capsule or nutlet; **Se** few to numerous, testa thin, pale yellow to dark brown.

**Order:** Asparagales

**Important Literature:** Chase & al. (1996: classification); Conran (1998: synopsis) (both as *Lomandraceae*).

**Distribution:** Tropical and temperate Australasia, SE Asia, Mascarenes, New Caledonia, New Guinea, New Zealand, S and N America, Pacific Islands.

A family of 15 genera and 180 species, of which *Cordyline* is the most important horticulturally and the only one exhibiting succulence, albeit very borderline.

**Classification and History:** Chase & al. (1996) expanded the circumscription of the *Lomandraceae* to include a range of 15 genera from the families *Agavaceae* (only *Cordyline*), *Anthericaceae* and *Philesiaceae*. This recircumscription was based on rbcL sequence data and a characteristic nucellus type. This position was adopted by Conran (1998). However, for nomenclatural reasons the family name *Laxmanniaceae*, published in 1902, has priority over the later (1911) *Lomandraceae* (Reveal 2012). *Laxmanniaceae* were included by APG (2009) in their radically expanded *Asparagaceae*, and can be referred to as *Asparagaceae* subfamily *Lomandroideae* (Chase & al. 2009).

Here we maintain the *Laxmanniaceae* separate from the *Asparagaceae* along the same lines of evidence as discussed for *Agavaceae*, etc., and in sister-group position to *Asparagaceae* s.s., *Eriospermaceae* and *Ruscaceae* (Nyffeler & Eggl 2010). *Laxmanniaceae* (as *Asparagaceae* s.l. subfam. *Lomandroideae*) are supported by Steele & al. (2012) as a distinct clade and basal sister to *Asparagaceae* s.s. (as subfam. *Asparagoideae*) and *Ruscaceae* (as *Asparagaceae* subfam. *Nolinoideae*). *Laxmanniaceae* are accepted as family by Seberg & al. (2012) and Judd & al. (2016), forming a clade sister to the *Asparagaceae* s.s. plus *Ruscaceae*.

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In terms of infrafamilial classification, Chase & al. (1996) identified two informal groups within the *Laxmanniaceae* that might represent subfamilies: the *Lomandra*-group and the arthropodioid group. *Cordyline* (previously in the *Agavaceae* or *Asteliaceae*) and *Chamaescilla* (no succulents) form a sister pair in the arthropodioid group. The phylogeny presented by Seberg & al. (2012) shows *Cordyline* in a clade that is sister to the *Arthropodium* clade; these together are basal to a clade including *Lomandra*.

**Succulence:** In several genera the roots are fleshy, tuberous or rhizomatous. The stem of *Cordyline* is woody rather than succulent, so inclusion of the genus here is therefore on the basis of very borderline succulence.

## References

- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- Chase, M. W. [& al. 1996], Rudall, P. J. & Conran, J. G. (1996) New circumscriptions and a new family of asparagoid lilies: Genera formerly included in *Anthericaceae*. *Kew Bull.* 51(4): 667–680, ill., diags. <https://doi.org/10.2307/4119721>
- Chase, M. W. [& al. 2009], Reveal, J. L. & Fay, M. F. (2009) A subfamilial classification for the expanded Asparagalean families *Amaryllidaceae*, *Asparagaceae* and *Xanthorrhoeaceae*. *Bot. J. Linn. Soc.* 161(2): 132–136. <https://doi.org/10.1111/j.1095-8339.2009.00999.x>
- Conran, J. G. (1998) *Lomandraceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*, 3: 354–365. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_42](https://doi.org/10.1007/978-3-662-03533-7_42)
- Judd, W. S. [& al. 2016], Campbell, C. S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J. (2016) *Plant systematics: A phylogenetic approach*. Ed. 4. Sunderland (US): Sinauer Associates.
- Nyffeler, R. & Egli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>
- Reveal, J. L. (2012) An outline of a classification scheme for extant flowering plants. *Phytoneuron* 2012(37): 1–221. <https://www.phytoneuron.net/PhytoN-MagnoIiidae.pdf>
- Seberg, O. [& al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ill. <https://doi.org/10.3732/ajb.1100468>
- Steele, P. R. [& al. 2012], Hertweck, K. L., Mayfield, D., Mckain, M. R., Leebens-Mack, H. & Pires, J. C. (2012) Quality and quantity of data recovered from massively parallel sequencing: Examples in Asparagales and *Poaceae*. *Amer. J. Bot.* 99(2): 330–348. <https://doi.org/10.3732/ajb.1100491>



## Cordyline LAXMANNIACEAE

C. C. Walker

**Cordyline** Commerson *ex* R. Brown (Prodr., 280, 1810). **Type:** *Cordyline canniifolia* R. Brown. [conserved type (ICBN 2006: 260; cited as *Asparagus terminalis* Linné by ING)]. — **Lit:** Pedley (1986: 81–86 — Fl. Australia). **Distr:** SE Asia, Australia, New Zealand, the Pacific, S America and the Mascarenès. **Etym:** Gr. ‘kordyle’, club, pestle; for the club-like roots of some taxa.

**Incl.** *Taetsia* Medikus (1786) (*nomen rejiciendum*, Art. 56.1). **Type:** *Taetsia ferrea* Medikus [*nom. illeg.*, = *Dracaena ferrea* Linné, *nom. illeg.*, = *Convallaria fruticosa* Linné (ICBN 2006: 260)].

**Incl.** *Charlwoodia* Sweet (1827). **Type:** *Charlwoodia congesta* Sweet.

**Incl.** *Calodracon* Planchon (1850). **Type:** not typified.

**Incl.** *Cohnia* Kunth (1850). **Type:** not typified.

Woody shrubs or trees to 20 m with thick creeping rhizomes and fleshy **R**; stems moderately branched; **L** in terminal **Ros**, linear-lanceolate to broadly ovate, sessile or pseudopetiolate, sheathing, conduplicate; **Inf** terminal racemose or spike panicles; **Fl** hermaphrodite; **Ped**

non-articulated with 3 **Bra** at the base; **Tep** 3 + 3, free or basally fused forming a short tube, white to dark purple-grey; **St** inserted on the tepal bases; **Anth** medifixed, introrse; **Ov** superior, 3-locular, small, ovoid, ovules 2 to numerous per locule; **Sty** shortly filiform; **Sti** capitate or 3-lobed; **Fr** ovoid berries, drying with age; **Se** few, rounded, black, smooth. — **Cytology:**  $2n = 38$  Satô (1942).

*Cordyline* was recently classified in the small segregate family *Lomandraceae* or the *Asteliaceae*. Later it was placed in the arthropodioid group (Chase & al. 1996) or the “*Cordyline* group” of *Lomandroideae* in the expanded *Asparagaceae* (APG 2009). Here, the genus is included in the *Laxmanniaceae* in a clade whose sister includes *Arthropodium* (Seberg & al. 2012; Steele & al. 2012).

A separate genus *Cohnia* Kunth is sometimes recognised for the free-tepalled species from New Caledonia and the Mascarenès. Succulence is very borderline and the leaves are merely tough and fibrous. The genus has  $\pm 20$  species. Some species have massive pachycaul stems, and some non-succulent species are well-known as foliage houseplants. *C. australis*, with its massive pachycaul stems, is widely cultivated outside of Australasia and is the only taxon treated here.

**C. australis** (G. Forster) Hooker *fil.* (Gard. Chron. 1860: 792, 1860). — **Lit:** Simpson (2000). **Distr:** New Zealand (N and S Island); widespread except the far S, swamps, river banks, lake margins,

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**Fig. 1** *Cordyline australis*. (Copyright: R. Lucas)

rocky slopes, forests, 0–1000 m. **I:** Everett (1981–1982: 3: 866). – Fig. 1.

≡ *Dracaena australis* G. Forster (1786).

Woody trees to 10–15 (–20) m, stem sparingly branched below, well branched above, eventually massive to 1.5 m Ø at the base, bark rough, fissured; **L** clustered at the branch tips in rosettes, lanceolate-linear, 30–100 × 3–6 cm, arching, light green, veins indistinct; **Inf** paniculate, to 1.5 × 0.6 m, well branched with 4 orders of branching, open, **Br** ± at right angles, axes hidden by the flowers; **Fl** numerous, sweetly fragrant, subsessile, 5–6 mm Ø; **Tep** equal, free almost to the base, slightly keeled, reflexed, creamy-white; **St** 6; **Anth** yellow; **Ov** 3-locular; **Sti** 3-lobed; **Fr** globose berries, creamy-white or speckled cream and very pale blue, 4 mm Ø; **Se** 3–6 per fruit, shiny, black.

Simpson (2000) published a highly readable, authoritative and well-illustrated account of New Zealand’s iconic cabbage trees, dealing with all aspects of the plant, its habitat, native uses,

cultivation and appearance in the world of art and design. The Maori have a wide range of uses for the tree, including as a source of food, soap, but especially fibres for making baskets and bags (Simpson 2000). Vernacular names: “New Zealand Cabbage Tree”, “cabbage tree”, “ti kouka”.

The species is in decline in New Zealand, principally due to loss of habitat with increased urbanisation, agriculture, alien invasion and lack of regeneration, but it is currently not endangered (Simpson 2000).

Best grown in frost-free warm-temperate gardens where it can develop its massive pachycaul stems and produce the impressive, highly scented flower spikes. Many variegated cultivars are available.

## References

- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- Chase, M. W. [et al. 1996], Rudall, P. J. & Conran, J. G. (1996) New circumscriptions and a new family of asparagoid lilies: genera formerly included in *Anthericaceae*. *Kew Bull.* 51(4): 667–680, ills., diags. <https://doi.org/10.2307/4119721>
- Everett, T. H. (1981–1982) New York Botanical Garden illustrated encyclopedia of horticulture. New York (US): Garland Publishing.
- Pedley, L. (1986) *Cordyline. Doryanthes*. In: George, A. S. (ed.): *Flora of Australia*, 46: 81–88. Canberra (AU): Australian Government Publishing Service.
- Satō, D. (1942) Karyotype alteration and phylogeny in *Liliaceae* and allied families. *Jap. J. Bot.* 12: 57–161.
- Seberg, O. [et al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ills. <https://doi.org/10.3732/ajb.1100468>
- Simpson, P. (2000) *Dancing leaves. The story of New Zealand’s Cabbage Tree, ti kouka*. Christchurch (NZ): Canterbury University Press
- Steele, P. R. [et al. 2012], Hertweck, K. L., Mayfield, D., McKain, M. R., Leebens-Mack, H. & Pires, J. C. (2012) Quality and quantity of data recovered from massively parallel sequencing: Examples in Asparagales and *Poaceae*. *Amer. J. Bot.* 99(2): 330–348. <https://doi.org/10.3732/ajb.1100491>

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**Part XV**

**The Family Orchidaceae**







# Orchidaceae

U. Eggli

**Including** *Apostasiaceae* Lindley.  
**Including** *Cypripediaceae* Lindley.  
**Including** *Limodoraceae* Horaninow.  
**Including** *Liparidaceae* Vines.  
**Including** *Neottiaceae* Horaninow.  
**Including** *Neuwiediaceae* Reveal & Hoogland.  
**Including** *Ophrydaceae* Vines.  
**Including** *Pycnanthaceae* Ravenna.  
**Including** *Vanillaceae* Lindley.

Perennial terrestrial or predominantly epiphytic herbs, rarely shrubs or lianas or aquatics (*Habenaria repens*), rarely saprophytic and without chlorophyll or completely subterranean; **R** often tuberous in terrestrial taxa, with multi-layered velamen in epiphytic taxa; stems virtually absent, or forming corms or rhizomes, or conspicuous and often distinctly swollen to form pseudo-bulbs, often rooting at the nodes; **L** entire, alternate and spirally arranged (sometimes distichous, rarely opposite or whorled), often fleshy, sometimes scale-like or completely absent (“root orchids” with green roots for photosynthesis); **Inf** lateral racemes or panicles, or flowers solitary; **Fl** mostly bisexual (rarely unisexual and plants dioecious), 3-merous, usually zygomorphic, often resupinate; **Per** of 3 + 3 usually petaloid tepals,

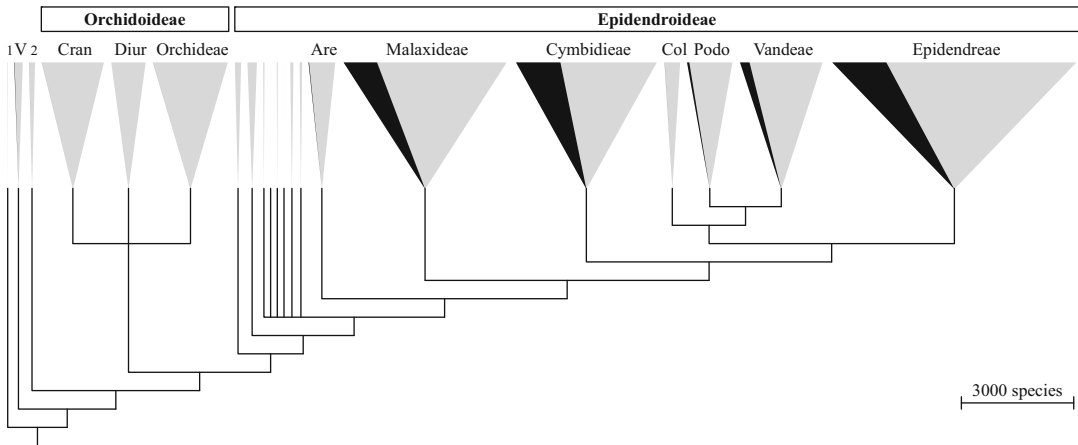
one of the inner tepals (labellum) usually much larger and/or differently coloured; **St** 1 (–3), mostly united with the style to form a gynostegium; pollen normally united into complex pollinia (rarely pollen dustlike, *Apostasioideae*); **Ov** of 3 united **Ca**, inferior, normally 1-locular (3-locular in *Apostasioideae*); **Fr** capsules opening with 3 (or 6) longitudinal slits but remaining closed at either end; **Se** very numerous, dust-like with undeveloped minute embryo.

**Order:** Asparagales

**Important Literature:** Pridgeon (1992: illustrated encyclopedia); Bechtel & al. (1992: synopsis cultivated taxa); Dressler (1993: traditional classification); Cameron & al. (1999: molecular phylogeny); Pridgeon & al. (1999: synopsis *Apostasioideae*, *Cypripedioideae*); Pridgeon & al. (2001: synopsis *Orchidoideae* part 1); Chase & al. (2003: molecular phylogeny); Pridgeon & al. (2003: synopsis *Orchidoideae* part 2, *Vanilloideae*); Pridgeon & al. (2005: synopsis *Epidendroideae* part 1); Cameron (2006: molecular phylogeny); Pridgeon & al. (2009: synopsis *Epidendroideae* part 2); Górnjak & al. (2010: molecular phylogeny); Gustafsson & al. (2010: evolution & diversification); Pridgeon & al. (2014: synopsis *Epidendroideae* part 3); Stern (2014: anatomy); Chase & al. (2015: updated classification).

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**Fig. 1** Summary phylogeny of *Orchidaceae* (26,400 species total, data from Chase & al. 2015 and Govaerts 2014+). The monospecific clades *Codonorchideae* (*Orchidoideae*) and *Thaieae* (*Epidendroideae*) are omitted. 1 =

*Apostasioideae*, 2 = *Cypripedioideae*, V = *Vanilloideae*; Are = *Arethuseae*, Col = *Collabieae*, Cran = *Cranichideae*, Diur = *Diurideae*, Podo = *Podochileae*. (Copyright: U. Eggli)

**Distribution:** Worldwide but concentrated in the tropics and subtropics.

With 736 genera (Chase & al. 2015) and (depending on the source consulted) 17,500 to 35,000 species (Pires & al. 2006), the orchids are the largest plant family. Orchids show a number of special developments. Like in the *Apocynaceae* — *Asclepiadoideae*, the pollen is united into complex pollinia in most orchids. Unlike the pollinia of the asclepiads with their clasping mechanism of the translator, orchid pollinia have a sticky plate (viscidium) at the basal end of the caudicle and are glued on the body of the pollinator. The minute orchid seeds in nature normally germinate only in the presence of certain mycorrhizal fungi (but can be germinated on appropriate laboratory media in cultivation). Mycorrhiza are probably universally present throughout the family also in adult plants.

**Classification:** The family has been unambiguously found to be monophyletic, and to represent the basal sister to the remaining families of the Asparagales by all recent studies (Bogler & al. 2006; Givnish & al. 2006; Graham & al. 2006; Pires & al. 2006; Gustafsson & al. 2010; Seberg & al. 2012).

The infrafamilial classification of this vast family is a challenge in view of the species number,

but also because of the traditional reliance on characters of floral morphology. Floral morphology has been found to be evolutionarily much more labile than accepted in the past (Carlswald & al. 2003; Kocyan & al. 2008), and floral convergencies due to shared pollination syndromes are frequent.

The correct placement of many genera has been elusive for long (Dressler 1993), but DNA-based studies in the past 20 years have added considerably to our knowledge. They have provided a firm classificatory backbone, but have also shown that many large genera need to be restudied carefully with regard of their morphology-based circumscription and infrageneric classification (e.g. *Dendrobium*, Adams (2011)).

The epiphytic habit so common in the family has evolved several times in parallel (Chase & al. 2003) and the more basal clades are all terrestrial.

A classification into five subfamilies was first proposed by Cameron & al. (1999), who found that *Vanilla* and related genera should be recognized as separate subfamily *Vanilloideae*, and that *Spiranθοideae*, *Neottioideae* and *Vandoideae* are imbedded in other clades. This backbone classification (Fig. 1) was corroborated by several subsequent studies (Chase & al. 2003; Cameron 2006; Górnjak & al. 2010).

The *Apostasioideae* (**L** spiral, plicate; **Fl** sometimes resupinate, indistinctly irregular; **St** 2–3, pollen never in pollinia; sometimes treated as family of their own, *Apostasiaceae*) represent the basal clade, and they are sister to the rest of the family.

The *Cypripedioideae* (**L** spiral or distichous, sometimes plicate; **Fl** resupinate, labellum slipper-shaped; **St** 2 (of the inner whorl) + 1 staminode (of the outer whorl); pollen rarely in true pollinia) is another small group that is sometimes regarded as a separate family *Cypripediaceae*.

The classification of the largest subfamily, *Epidendroideae*, is still in a state of some flux: Chase & al. (2003) recognize the 3 tribes *Epidendreae* (confined to the New World), *Vandaeae* and *Cymbidieae*, while Cameron (2006) accepts a larger number of molecularly well-supported tribes. Górnjak & al. (2010) recognize 31 clades (tribes and subtribes) for the subfamily. The most recent classification is that of Chase & al. (2015), which recognizes 16 tribes and a total of 37 clades for *Epidendroideae*.

**Succulence:** Numerous orchids occur in semi-arid climates or as epiphytes in semi-arid niches, and can be considered to be truly succulent. Leaf succulence predominates, esp. amongst epiphytic taxa, but stem and root succulence also occurs. While the roots esp. of epiphytic orchids in general are somewhat thickened, they appear genuinely fleshy in many species (e.g. Kaushik 1983; Figueroa & al. 2008). Water-storage idioblasts are common in the cortex of the roots esp. of epiphytic taxa (Pridgeon in Stern (2014: 35)).

In stem-succulent species, the stem is either uniformly thickened over part or all its length (e.g. many species of *Dendrobium*), or succulence is confined to the basal internode or few internodes, and such thickened stem parts are termed a pseudobulb. The stem tissue of such orchids is usually parenchymatous and mucilaginous, with scattered large water-storage cells (Kaushik 1983). In many epiphytic *Epidendroideae*, a 1- to 5-layered hypodermis is present, with scleric, parenchymatous or collenchymatous cells and a “probable function in water storage” (Pridgeon in Stern (2014: 27)). The ground tissue is continuous or commonly interrupted by a sclerotic sheath

(referred to as sclerenchyma sheath, pericyclic ring, sclerenchymatous ring, or sclerenchyma band in the literature), and when present, this sheath delimits the outer cortex from the pith. It is often continuous with the outermost vascular bundles, while the cortex is only rarely also provided with vascular bundles. The more peripheral cells of the cortex are usually smaller and contain chloroplasts, while the inner cells have fewer or no chloroplasts. Within the ground tissue, conspicuous larger water-storage idioblasts with or without spiral thickenings are common (Pridgeon in Stern (2014: 27)). According to Stern & Carlswald (2006), these storage cells are usually devoid of a proplast.

Leaf-succulence is without doubt the prevailing type of succulence in the family, but the anatomy of water storage is variable. According to Metzler (1924), four different types of water storage anatomies can be distinguished, ranging from epidermal water storage to hypodermal or central water storage tissues, and to isolated water-storage idioblasts scattered in the photosynthetic parenchyma. A true hypodermis is present in many epiphytic *Epidendroideae*, commonly consisting of 1–4 (rarely up to 10) cell layers on the adaxial side, and 1–2 layers on the abaxial side. Its cells are often elongate and the hypodermis then resembles a palisade mesophyll that accounts for up to 80% of the leaf volume and “almost certainly functions in water storage” (Pridgeon in Stern (2014: 21)). The water-storage idioblasts show various wall sculpturings (annular or helical), and are usually devoid of proplastids, except for *Maxillariinae* (Stern & Carlswald 2006: 265). The wall thickenings are cellulosic according to Pridgeon (1982), while Olatunji & Nengim (1980) report varying degrees of lignification. These mesophyll idioblasts likely serve for mechanical support to prevent tissue collapse during drought conditions. Olatunji & Nengim (1980) use the term “tracheoidal elements” for these cells, but they are not of tracheoidal origin and are better referred to as spirally thickened water-storage idioblasts. The mesophyll chlorenchyma can be differentiated into palisade and spongy mesophyll, or it is uniform spongy mesophyll, but conditions are variable even within

genera (Pridgeon in Stern (2014: 22)). Pridgeon (1981) reports the presence of specialized trichomes on the leaves of species of subtribe Pleurothallidinae. The trichomes are likely comparable in function to the much better known water-absorbing multicellular trichomes in *Tillandsia*. They consist of an apical thin-walled cell and a stalk formed by 1 or 2 cells with thick lateral walls, and their bases are adjacent to the water-storing hypodermal layer.

Numerous studies have investigated the occurrence of CAM photosynthesis in the orchid family. While CAM is neither a prerequisite for succulence nor dependent on the existence of succulence in orchids, there is some correlation between the degree of succulence (measured as leaf thickness) and the degree of CAM expression. CAM is most prevalent in epiphytes from low elevations and markedly seasonal climates with a dry season (Earnshaw & al. 1987; Silvera & al. 2010). Winter & Smith (1996) estimate the number of CAM orchid species as c. 7100, which is close to the 7800 species estimate of Silvera & al. (2010). Conventional C3 photosynthesis has been identified as ancestral condition for the family, and CAM photosynthesis has evolved several times in parallel (Reyes-García and Andrade 2009).

The number of succulent orchid species is unknown, and is difficult to establish in view of the complete grade from slightly thickened and coriaceous leaves to distinctly succulent leaves. A first guess of c. 2200 species (Eggli 2007) is certainly far too low, and a recent superficial analysis (pers. obs.) results in a figure of at least 4500 succulent taxa.

Despite the undisputed claim to succulence, the orchids are not covered in detail in the present handbook series. Orchids rival with cacti and bromeliads as the horticulturally most important group of plants, and there is a vast selection of specialist literature, and numerous hobby groups are devoted to cultivating and admiring orchid diversity.

## References

- Adams, P. B. (2011) Systematics of *Dendrobium* (*Orchidaceae*), with special reference to Australian taxa. Bot. J. Linn. Soc. 166(2): 105–126, ill., keys. <https://doi.org/10.1111/j.1095-8339.2011.01141.x>
- Bechtel, H. [ & al. 1992], Cribb, P. & Launert, E. (1992) The manual of cultivated orchid species. Ed. 3. Cambridge (US): MIT Press.
- Bogler, D. J. [ & al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on *ndhF*, *rbcL*, and its sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): Monocots. Comparative biology and evolution excluding Poales. Aliso 22: 313–328.
- Cameron, K. M. (2006) A comparison and combination of plastid *atpB* and *rbcL* gene sequences for inferring phylogenetic relationships within *Orchidaceae*. In: Columbus, J. T. & al. (eds.): Monocots. Comparative biology and evolution excluding Poales. Aliso 22: 447–464.
- Cameron, K. M. [ & al. 1999], Chase, M. W., Whitten, M. W., Kores, P. J., Jarrell, D. C., Albert, V. A., Yukawa, T., Hills, J. G. & Goldman, D. H. (1999) A phylogenetic analysis of the *Orchidaceae*: Evidence from *rbcL* nucleotide sequences. Amer. J. Bot. 86(2): 208–224. <http://www.jstor.org/stable/2656938>
- Carlswald, B. S. [ & al. 2003], Whitten, W. M. & Williams, N. H. (2003) Molecular phylogenetics of neotropical leafless *Angraecinae* (*Orchidaceae*): Reevaluation of generic concepts. Int. J. Pl. Sci. 164(1): 43–51. <https://doi.org/10.3732/ajb.93.5.770>
- Chase, M. W. [ & al. 2003], Cameron, K. M., Barrett, R. L. & Freudenstein, J. V. (2003) DNA data and *Orchidaceae* systematics: A new phylogenetic classification. In: Dixon, K. W. & al. (eds.): Orchid conservation; pp. 69–89. Kota Kinabalu (MY): Natural History Publications (Borneo).
- Chase, M. W. [ & al. 2015], Cameron, K. M., Freudenstein, J. V., Pridgeon, A. M., Salazar, G., Berg, C. van den & Schuiteman, A. (2015) An updated classification of *Orchidaceae*. Bot. J. Linn. Soc. 177: 151–174. <https://doi.org/10.1111/boj.12234>
- Dressler, R. L. (1993) Phylogeny and classification of the orchid family. Cambridge (GB) etc.: Cambridge University Press.
- Earnshaw, M. J. [ & al. 1987], Winter, K., Ziegler, H., Stichler, W., Cruttwell, N. E. G., Kerenga, K., Cribb, P. J., Wood, J., Croft, J. R., Carver, K. A. & Gunn, T. C. (1987) Altitudinal changes in the incidence of Crassulacean Acid Metabolism in vascular epiphytes and related life forms in Papua New Guinea. Oecologia 73: 566–572. <https://doi.org/10.1007/BF00379417>
- Eggli, U. (2007) Biodiversität — Vielfalt der Sukkulenten. Sukkulentenwelt 12: 2–35, ill., map.
- Figueroa, C. [ & al. 2008], Salazar, G. A., Araceli Zavaleta, H. & Englemann, E. M. (2008) Root character evolution and systematics in *Cranichidinae*, *Prescottiiinae* and *Spiranthinae* (*Orchidaceae*, *Cranichideae*). Ann. Bot. (Oxford), n.s. 101: 509–520, ill. <https://doi.org/10.1093/aob/mcm328>
- Givnish, T. J. [ & al. 2006], Pires, J. C., Graham, S. W., McPherson, M. A., Prince, L. M., Patterson, T. B., Rai,

- H. S., Roalson, E. H., Evans, T. M., Hahn, W. J., Millam, K. C., Meerow, A. W., Molvray, M., Kores, P. J., O'Brien, H. E., Hall, J. C., Kress, W. J. & Sytsma, K. J. (2006) Phylogenetic relationship of Monocots based on the highly informative plastid gene *ndhF*: Evidence for widespread concerted convergence. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 28–51.
- Górniak, M. [ & al. 2010], Paun, O. & Chase, M. W. (2010) Phylogenetic relationships within *Orchidaceae* based on a low-copy nuclear coding gene, *Xdh*: Congruence with organellar and nuclear ribosomal DNA results. *Molec. Phylogen. Evol.* 56(2): 784–795. <https://doi.org/10.1016/j.ympev.2010.03.003>
- Govaerts, R. H. A. (comp.) (2014+) World checklist of selected plant families [continuously updated]. Richmond (GB): Trustees of the Royal Botanic Gardens, Kew. DOI / Stable URL: <http://apps.kew.org/wcsp>
- Graham, S. W. [ & al. 2006], Zgurski, J. M., McPherson, M. A., Chermiawsky, D. M., Saarela, J. M., Horne, E. F. C., Smith, S. Y., Wong, W. A., O'Brien, H. E., Biron, V. L., Pires, J. C., Olmstead, R. G., Chase, M. W. & Rai, H. S. (2006) Robust inference of Monocot deep phylogeny using an expanded multigene plastid data set. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 3–21.
- Gustafsson, A. L. S. [ & al. 2010], Verola, C. F. & Antonelli, A. (2010) Reassessing the temporal evolution of orchids with new fossils and a Bayesian relaxed clock, with implication for the diversification of the rare South American genus *Hoffmannseggella* (*Orchidaceae: Epidendroideae*). *BMC Evol. Biol.* 10 (177): [1–13]. <https://doi.org/10.1186/1471-2148-10-177>
- Kaushik, P. (1983) *Ecological and anatomical marvels of the Himalayan Orchids*. New Delhi (IN): Today & Tomorrow's Printers & Publishers.
- Kocyan, A. [ & al. 2008], Fogel, E. F. de, Conti, E. & Gravendeel, B. (2008) Molecular phylogeny of *Aerides* (*Orchidaceae*) based on one nuclear and two plastid markers: A step forward in understanding the evolution of the *Aeridinae*. *Molec. Phylogen. Evol.* 48: 422–443. <https://doi.org/10.1016/j.ympev.2008.02.017>
- Metzler, W. (1924) Beiträge zur vergleichenden Anatomie blattsukkulenter Pflanzen. *Bot. Arch.* 6(1–3): 50–83, ills.
- Olatunji, O. A. & Nengim, R. O. (1980) Occurrence and distribution of tracheoidal elements in the *Orchidaceae*. *Bot. J. Linn. Soc.* 80(4): 357–370, ills. <https://doi.org/10.1111/j.1095-8339.1980.tb01669.x>
- Pires, J. C. [ & al. 2006], Maureira, I. J., Givnish, T. J., Sytsma, K. J., Seberg, O., Petersen, G., Davis, J. I., Stevenson, D. W., Rudall, P. J., Fay, M. F. & Chase, M. W. (2006) Phylogeny, genome size, and chromosome evolution of *Asparagales*. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso* 22: 287–304.
- Pridgeon, A. M. (1981) Absorbing trichomes in the *Pleurothallidinae* (*Orchidaceae*). *Amer. J. Bot.* 68(1): 64–71, ills. <http://www.jstor.org/stable/2442992>
- Pridgeon, A. M. (1982) Diagnostic anatomical characters in the *Pleurothallidinae* (*Orchidaceae*). *Amer. J. Bot.* 69(6): 921–938, ills. <http://www.jstor.org/stable/2442889>
- Pridgeon, A. M. (ed.) (1992) *The illustrated encyclopedia of Orchids*. Sydney (AU): Kevin Weldon/Portland (US): Timber Press.
- Pridgeon, A. M. [ & al. 1999], Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (eds.) (1999) *Genera Orchidacearum*. Volume 1. General introduction, Apostasioideae, Cyrtipedioideae. Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [ & al. 2001], Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (eds.) (2001) *Genera Orchidacearum*. Volume 2. Orchidoideae (part one). Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [ & al. 2003], Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (eds.) (2003) *Genera Orchidacearum*. Volume 3. Orchidoideae (part two), Vanilloideae. Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [ & al. 2005], Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (eds.) (2005) *Genera Orchidacearum*. Volume 4. Epidendroideae (part one). Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [ & al. 2009], Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (eds.) (2009) *Genera Orchidacearum*. Volume 5. Epidendroideae (part two). Oxford (GB): Oxford University Press.
- Pridgeon, A. M. [ & al. 2014], Cribb, P. J., Chase, M. W. & Rasmussen, F. N. (eds.) (2014) *Genera Orchidacearum*. Volume 6. Epidendroideae (part three). Oxford (GB): Oxford University Press.
- Reyes-García, C. & Andrade, J. L. (2009) Crassulacean Acid Metabolism under global climate change. *New Phytol.* 181(4): 754–757. <https://doi.org/10.1111/j.1469-8137.2009.02762.x>
- Seberg, O. [ & al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the *Asparagales* based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ills. <https://doi.org/10.3732/ajb.1100468>
- Silvera, K. [ & al. 2010], Neubig, K. M., Whitten, W. M., Williams, N. H., Winter, K. & Cushman, J. C. (2010) Evolution along the Crassulacean Acid Metabolism continuum. *Funct. Pl. Biol.* 37(11): 995–1010. <https://doi.org/10.1071/FP10084>
- Stern, W. L. (2014) *Orchidaceae*. In: Gregory, M. & Cutler, D. F. (eds.): *Anatomy of the Monocotyledons*. Volume X. Oxford (GB): Oxford University Press.



- Stern, W. L. & Carlswald, B. S. (2006) Comparative vegetative anatomy and systematics of the *Oncidiinae* (*Maxillarieae*, *Orchidaceae*). *Bot. J. Linn. Soc.* 152: 91–107, ill. <https://doi.org/10.1111/j.1095-8339.2006.00548.x>
- Winter, K. & Smith, J. A. C. (1996) An introduction to Crassulacean Acid Metabolism: Biochemical principles and ecological diversity. In: Winter, K. & Smith, J. A. C. (eds.): *Crassulacean Acid Metabolism: Biochemistry, ecophysiology and evolution*; pp. 1–10. Berlin (DE): Springer-Verlag. [https://doi.org/10.1007/978-3-642-79060-7\\_1](https://doi.org/10.1007/978-3-642-79060-7_1)

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**Part XVI**

**The Family Poaceae**





## Poaceae

E. Van Jaarsveld and U. Eggli

Perennial and usually rhizomatous herbs, or annual herbs, or perennial woody (to rarely tree-like) shrubs (bamboos), usually with strongly silicified cell-walls (esp. the epidermis); stems mostly terete, with prominent thickened nodes and usually hollow internodes; **L** alternate, distichous (rarely spiralling, but never 3-ranked), with a prominent usually open sheathing base and an elongate lamina with a pair of basal auricles and a distinct midrib, usually with an adaxial ligule (membranous or a fringe of hairs) at the junction of sheath and lamina, sheathing base tightly enveloping the stem, usually open or rarely fused into a tube; **Inf** 1- to 8-flowered spikelets aggregated into spike- to panicle-like, cymose or racemose inflorescences; spikelets consisting of basal overlapping **Bra** (glumes, usually 2) and 1 to many flowers (florets); **Fl** small and reduced, usually bisexual and wind-pollinated, subtended by a **Bra** (lemma, sometimes extended into an awn) and an accessory bract-like prophyll (palea); **Per** reduced to usually 2 rudiments (lodicles); **St** 3 or 6, rarely 1 or >100, often with long filiform **Fil** and basifixed basally deeply

sagittate **Anth** opening with longitudinal slits; **Ov** superior, consisting of 3 **Ca**, 1-locular with a single ovule and with 2 (-3) often long and feathery **Sti**; **Fr** a caryopsis (grain) consisting of a single **Se** usually fused with the fruit wall, usually enclosed in the dry persistent lemma and palea, indehiscent.

**Order:** Poales

**Important Literature:** Grass Phylogeny Working Group (2011: phylogeny); Kellogg (2015: synopsis).

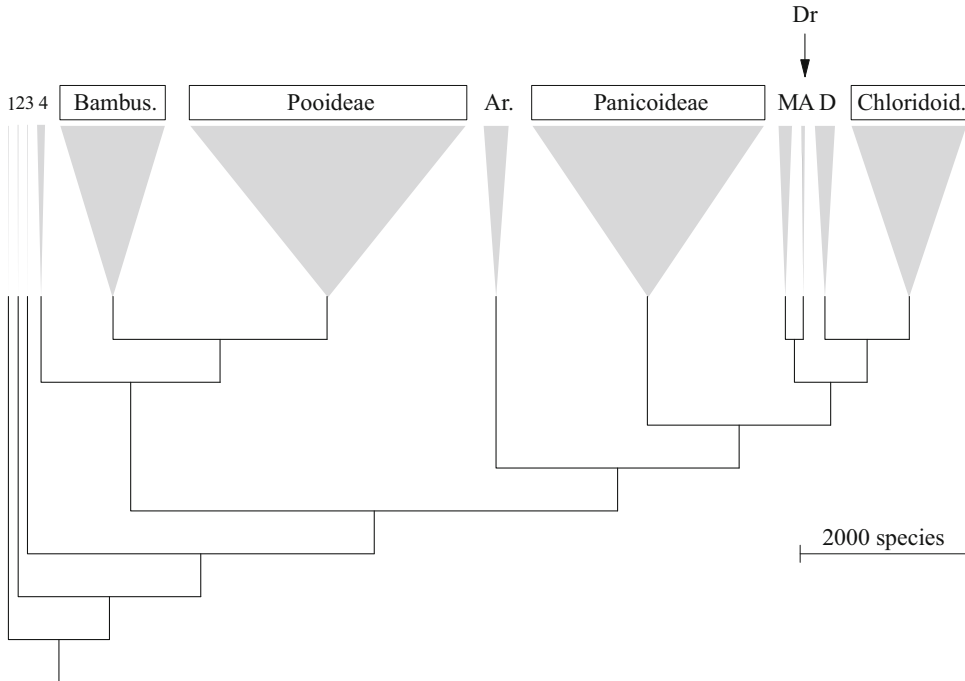
**Distribution:** Worldwide.

Grasses (alternatively known by the family name *Gramineae*) embrace some 700 genera and 11'127 species, and they are sister to a group of restioid families, either as sister to the *Ecdeiocoleaceae* (Graham & al. 2006), or as sister to the *Joinvilleaceae* (Givnish & al. 2006). The Grass family is among the economically and ecologically most important plants worldwide, and many species such as wheat, oats, rice, corn are important food plants – wheat, rice, and maize provide >50% of all calories consumed by humans (Mabberley 2008), and many species are important elements of animal (esp. cattle) fodder. Numerous other species are of ethnobotanical importance, from building material (bamboos) to sugar (*Saccharum officinarum*, “sugar cane”) and spices (*Cymbopogon citratus*, “lemon grass”).

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**Fig. 1** Summary phylogeny of Poaceae (11'127 species total, based on Grass Phylogeny Group (2012). 1 = Anomochloideae, 2 = Pharoideae, 3 = Puelioideae, 4 =

Ehrhartoideae, A = Arundinoideae, Ar. = Aristidoideae, D = Danthoioideae, Dr = Dregeochloa, M = Micraioideae. (Copyright: U. Eggli)

Many vegetation communities are dominated by grasses, esp. in regions with periodic drought, and grasslands such as prairie and pampas or steppes cover almost 25% of the planet's land surface.

**Succulence:** Leaf succulence has evolved only in the small genus *Dregeochloa*, placed in sub-family *Arundinoideae* by Kellogg (2015) (Fig. 1). *D. pumila* co-occurs with many other succulents in South Africa (Jaarsveld 2009). Goebel (1889: 46) reports a small degree of succulence (confined to the upper hypodermis) for the leaves of *Spinifex squarrosus*, but the species appears to be merely xerophytic.

## References

Givnish, T. J. [ & al. 2006], Pires, J. C., Graham, S. W., McPherson, M. A., Prince, L. M., Patterson, T. B., Rai,

H. S., Roalson, E. H., Evans, T. M., Hahn, W. J., Millam, K. C., Meerow, A. W., Molvray, M., Kores, P. J., O'Brien, H. E., Hall, J. C., Kress, W. J. & Sytsma, K. J. (2006) Phylogenetic relationship of Monocots based on the highly informative plastid gene *ndhF*: Evidence for widespread concerted convergence. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso 22*: 28–51. <https://doi.org/10.5642/aliso.20062201.04>

Goebel, K. (1889) *Pflanzenbiologische Schilderungen*. Erster Teil. Marburg (DE): N. G. Elwert'sche Verlagsbuchhandlung. <https://doi.org/10.5962/bhl.title.1665>

Graham, S. W. [ & al. 2006], Zgurski, J. M., McPherson, M. A., Cherniawsky, D. M., Saarela, J. M., Horne, E. F. C., Smith, S. Y., Wong, W. A., O'Brien, H. E., Biron, V. L., Pires, J. C., Olmstead, R. G., Chase, M. W. & Rai, H. S. (2006) Robust inference of Monocot deep phylogeny using an expanded multigene plastid data set. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. *Aliso 22*: 3–21. <https://doi.org/10.5642/aliso.20062201.02>

Grass Phylogeny Working Group (2011) New grass phylogeny resolves deep evolutionary relationships and



- discovers C4 origins. *New Phytol.* 193: 304–312. <https://doi.org/10.1111/j.1469-8137.2011.03972.x>
- Jaarsveld, E. J. van (2009) Kleinduimpie grass. *Dregeochloa pumila*, the only succulent grass in the world. *Veld Fl.* (1975+) 95(1): 19–21, ill.
- Kellogg, E. A. (2015) *Poaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants. Vol. XIII. Flowering plants. Monocots. Cham (CH) etc: Springer International Publishing Switzerland. <https://doi.org/10.1007/978-3-319-15332-2>
- Mabberley, D. J. (2008) *Mabberley's Plant-Book. A portable dictionary of plants, their classification and uses.* Ed. 3. Cambridge (GB): Cambridge University Press.





## Dregeochloa POACEAE

E. Van Jaarsveld

**Dregeochloa** Conert (Senckenberg. Biol. 47(4): 335, 1966). **Type:** *Danthonia pumila* Nees. — **Arundinoideae** — **Lit:** Gibbs Russel & al. (1991); Jaarsveld (2009). **Distr:** Namibia, NW RSA. **Etym:** For Jean François Drège (1794–1881), German plant collector in S Africa 1826–1833; and Gr. ‘chloe, chloa’, young green sprouts, grass.

Tufted stoloniferous or caespitose perennials with short spreading rhizomes, rooting at the nodes; **L** lamina linear to ovate or ovate-lanceolate, succulent or not, involute, ligule minutely ciliate; **Inf** racemose or paniculate with 4–12 spikelets; spikelets solitary, with 4–6 fertile florets, ± laterally compressed, lanceolate, acute, disarticulated above the glumes, rachis and **Ped** hairy; glumes 2, 5- to 7-veined, lanceolate, without awn; incomplete florets distal, awned, lemmas ovate, 7- to 9-veined, apex with 2 acute bristle-tipped lobes, membranous, with transverse rows of minutely hairy tufts; awns solitary, geniculate; palea present, narrowly elliptic, prominently 2-veined, apex rounded to emarginate, ciliate distally, hyaline; lodicules 2, fleshy; **Ov** sparingly hairy; **Fr** small, pericarp free.

A small genus of just 2 species, mainly native to the desert and semi-desert regions of the

Northern Cape and Western Cape, and adjacent Namibia. Only 1 is succulent. In an anatomical study, Ellis (1977) found weakly expressed all-cell succulence.

**D. pumila** (Nees) Conert (Senckenberg. Biol. 47(4): 335–343, ill., 1966). **Type:** RSA, Northern Cape (*Drège* 2562 [B, K]). — **Distr:** S Namibia, NW RSA (Northern Cape); Western Gariiep Lowland Desert vegetation, on sandy rocky wind-blown hills of the narrow coastal belt, flowers spring to early summer.

≡ *Danthonia pumila* Nees (1899).

Plants with short rhizomes, tufted and forming small mats, to 7 cm tall, base of individual growths with broad scales; **L** lamina succulent, 10–25 × 1.6–3.5 mm, minutely pubescent, apex obtuse, spiny-apiculate; **Inf** racemose or paniculate; spikelets 6- to 10-flowered; glumes 9–13 mm, 5- to 7-veined; lemma 3–3.5 mm; central awn 4–7 mm.

The species was discovered by Drège in 1830 in the Richtersveld. Difficult to cultivate away from its native habitat, and best grown in a greenhouse under controlled conditions.

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## References

- Ellis, R. P. (1977) Leaf anatomy of the South African *Danthonieae* (*Poaceae*). I. The genus *Dregeochloa*. *Bothalia* 12(2): 209–213, ill., map. <https://doi.org/10.4102/abc.v12i2.1398>
- Gibbs Russel, G. E. [& al. 1991], Watson, L., Koekemoer, M., Smook, L., Barker, N. P., Anderson, H. M., Dallwith, M. J. & Leistner, O. A. (ed.) (1991) Grasses of southern Africa. *Mem. Bot. Surv. South Afr.* 58: 437 pp., keys.
- Jaarsveld, E. J. van (2009) Kleinduimpie grass. *Dregeochloa pumila*, the only succulent grass in the world. *Veld Fl.* (1975+) 95(1): 19–21, ill.

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**Part XVII**

**The Family Rusceae**







## Ruscaceae

U. Eggli

**Including** *Aspidistraceae* Hasskarl.  
**Including** *Convallariaceae* Horaninow.  
**Including** *Dracaenaceae* Salisbury.  
**Including** *Nolinaceae* Nakai.  
**Including** *Ophiopogonaceae* Meissner.  
**Including** *Peliosanthaceae* Salisbury.  
**Including** *Polygonataceae* Salisbury.  
**Including** *Sansevieriaceae* Nakai.  
**Including** *Tupistraceae* Schnizlein.

Trees or shrubs and then often pachycaulous, deciduous herbaceous perennials, or rhizomatous herbs; **L** alternate, spiral or rarely distichous, sometimes reduced to scales and replaced by phylloclades (*Ruscaceae* s.s.), basally somewhat to distinctly amplexicaul, often in rosettes, strap-shaped to ensiform, more rarely terete, or angular-wiry, usually fibrous-tough and xeromorphic, sometimes slightly to distinctly succulent, margins entire or rarely with prickles, tips blunt, tapering and hardened, or fibrous, almost never sharp and pungent; **Inf** usually terminal but sometimes lateral, or appearing lateral due to later growth of branches, small to huge, usually richly branched and often paniculate, or elongate with condensed lateral branches or fascicles of flowers, or condensed and capitate; **Fl** often smallish and

inconspicuous, usually numerous to very numerous, actinomorphic, hermaphrodite or unisexual, white, whitish, greenish or yellowish, very rarely orange-reddish; **Te** 3 + 3 (or sometimes 4), free or more commonly fused and **Pe** tubular to urceolate; **St** 6, often long exserted; **Ov** superior, 1- or 3-locular with 1 ovule per locule; **Fr** few-seeded globose red to orange berries, or dry indehiscent capsules (functionally nutlets); **Se** globose to elongate, without true testa, pale-coloured.

**Order:** Asparagales

**Important Literature:** Trelease (1911: synopsis *Nolineae*); Bogler (1998a: synopsis *Nolinaceae*); Perry & Rudall (1998: synopsis *Dracaenaceae* s.s.); Rudall & al. (2000: phylogeny); Kim & al. (2010: molecular phylogeny); Lu & Morden (2014: molecular phylogeny dracaenoid genera).

**Distribution:** Tropical and subtropical Africa, Arabia, Asia and Australasia, arid N America.

A family of 25 genera and 375 species, including several horticulturally important taxa (incl. species of *Dracaena* and *Sansevieria*), whose circumscription has changed considerably in the past.

**Classification and History:** Traditionally, *Ruscaceae* embraced only 3 genera and some 10 species with reduced leaves and photosynthetic phylloclades from the Mediterranean and Asia Minor, but all recent molecular phylogenies agree that *Ruscaceae* s.s. and the traditional

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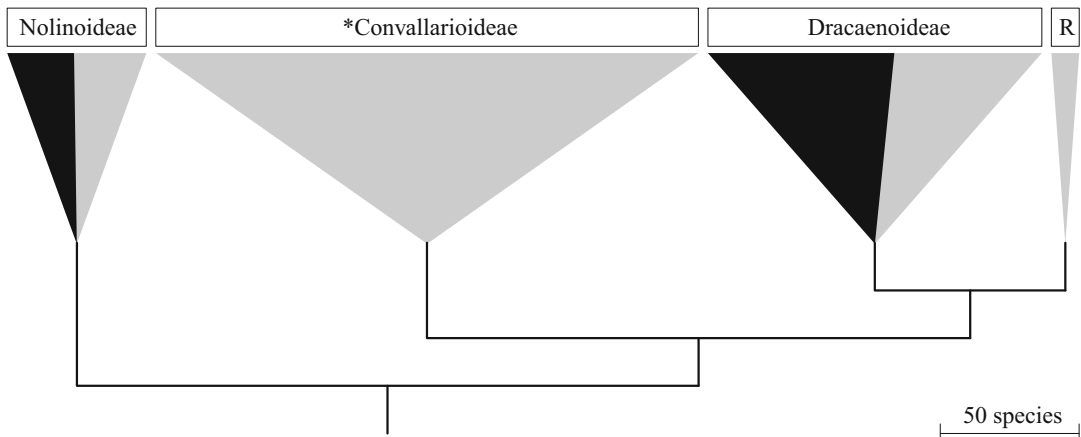
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families *Dracaenaceae*, *Eriospermaceae* and *Nolinaceae*, together with the non-succulent *Convallariaceae* and related herbaceous perennials, form a monophyletic clade that could be recognized as a widely circumscribed *Ruscaceae* s.l. as part of the core Asparagales (Rudall & al. 2000, Bogler & al. 2006, Givnish & al. 2006, Graham & al. 2006, Kim & al. 2010). Together with the *Asparagaceae* s.s., the clade diagnostically shows articulated pedicels (Graham & al. 2006) and (with the exception of *Eriospermaceae*) juicy or dry berrylike fruits (Givnish & al. 2006). Janssen & Bremer (2004) and APG (2009) opted for inclusion of the *Ruscaceae* in their very widely circumscribed *Asparagaceae* s.l. (as subfam. *Nolinoideae*) (Chase & al. 2009). Nyffeler & Eggli (2010) argued against such a wide circumscription of *Asparagaceae*, and also felt that the *Eriospermaceae*, identified as basal sister to the remaining *Ruscaceae* s.l., and characterized by their tuberous corms, herbaceous growth, capsular fruits and woolly seeds, should be recognized as separate taxon. Seberg & al. (2012) found the same general topology for the core Asparagales but stress that the clade of *Ruscaceae* s.l. is one of the most weakly supported parts of their phylogeny, and also Steele & al. (2012) have limited support for the relationships within *Asparagaceae* s.l., where *Ruscaceae* s.l. are found as sister of *Asparagaceae* s.s. The inconclusiveness of the data thus not automatically supports a wide

circumscription of *Ruscaceae* or *Asparagaceae*. Here we follow Judd & al. (2016) and Nyffeler & Eggli (2010) and recognize *Ruscaceae* s.l. as separate from *Eriospermaceae*. *Ruscaceae* s.l. in this circumscription represent a clade with many drought-adapted species with fibrous and therefore “tough” leaves, conspicuous to smallish to insignificant white or pale-coloured flowers, and juicy berries or indehiscent capsules.

Within the expanded *Ruscaceae*, subfam. *Nolinoideae* (representing the former *Nolinaceae*) occupies a basal position in sister-group position to a grade of “*Convallariaceae*” tribes, with subfam. *Ruscoideae* (= *Ruscaceae* s.s.) and subfam. *Dracaenoideae* (= former *Dracaenaceae*) as sisters in terminal position (Fig. 1). The subfamilies with succulents are characterized as follows:

- ***Dracaenoideae*** (3 genera,  $\pm$  150 species): Trees, shrubs, or rhizome geophytes; **L** in rosettes, rarely bifarious, usually fibrous, xeromorphic, not to distinctly succulent, flat or semi-terete to terete, tip at most hardend but not strongly pungent; **Inf** terminal but sometimes appearing lateral, appearing spicate to paniculate, sometimes capitate; **Fl** many to very numerous, bisexual, actinomorphic, small to conspicuous, pale-coloured (often white); **Ov** superior, 3-locular; **Fr** globose berries; **Se** without true testa and therefore remaining fleshy, but covered by a flimsy scarios envelope derived



**Fig. 1** Summary phylogeny of *Ruscaceae* based on Kim & al. (2010) (375 spp.; data from Bogler & al. (1998) and Bos (1998), and own counts). R = *Ruscoideae*. (Copyright: U. Eggli)

from the innermost part of the endocarp (Budweg 2015). — This subfamily was formerly recognized as separate family *Dracaenaceae*. The close relationship between *Dracaena* and *Sansevieria* (both in the more distant past classified as *Agavaceae*) was known for long, and Bos (1984) and Bos (1998) suggested that they should be treated as congeneric. According to Jankalski (2004) the two genera differ in pollen morphology, and should not be united. Preliminary observations by Budweg (2015) suggest that there might also be differences in germination and seedling root systems between the genera. The chloroplast DNA data of Lu & Morden (2014) shows that the dracaenoid genera form a monophyletic clade, and that monophyletic *Sansevieria* is nested within *Dracaena*, rendering the latter paraphyletic. For a phylogenetically correct classification, *Sansevieria* ought to be included in *Dracaena*, but this appears impractical, and unpublished results (L. E. Newton, pers. comm.) appear to support recognition of *Sansevieria*.

In the first issue of this handbook, *Cordyline* was also included in the *Dracaenaceae*, but this genus is now part of *Laxmanniaceae*.

- **Nolinoideae** (4 genera, c. 50 species): Woody pachycaul trees or shrubs, or rosette plants, or

caudiciform, or rhizome geophytes; **L** in rosettes, fibrous, xeromorphic, at most very slightly succulent with fibrous (never pungent) tip; **Inf** terminal, often very large, paniculate; **Fl** usually very numerous, unisexual (and plants dioecious or polygamo-dioecious), actinomorphic, small, pale-coloured; **Ov** superior, 1- or 3-locular; **Fr** dry indehiscent capsules. — This subfamily was formerly recognized as separate family *Nolinaceae*. Earlier, these genera were placed in the *Agavaceae*. Rowley (1990) considered *Beaucarnea* and *Calibanus* to be synonymous with *Nolina*. However, molecular data strongly indicates that *Calibanus* should be included in *Beaucarnea*, which is closely related but distinct from *Nolina*.

**Succulence:** While tough, somewhat thickish and xeromorphic leaves are not rare in the family, undisputed leaf succulence is restricted to *Sansevieria*. Scant parenchymatic water storage tissue in leaves is otherwise known from a handful of species such as *Dasyilirion wheeleri* or *Nolina microcarpa* (Walter 1931: 99, 153).

The massive pachycaulous stems of *Beaucarnea* and *Dracaena* consist of voluminous parenchymatic tissue with numerous scattered vascular bundles, and the basal swelling in *Beaucarnea* is the result

#### Key to genera with succulents

1a	<b>L</b> usually distinctly succulent, flat to terete, margins never armed; stems short, often horizontal, subterranean and rhizomatous, or absent:	<i>Sansevieria</i>
1b	<b>L</b> not truly succulent, flat to narrow and wiry, sometimes with marginal prickles; stems evident and often with richly branched crown, or massively pachycaulous, or as a globose caudex, or apparently absent or subterranean:	2
2a	Stems evident, of $\pm$ even diameter over their length, branching after flowering and often forming huge crowns; <b>Fl</b> bisexual:	<i>Dracaena</i>
2b	Stems absent or largely subterranean, as caudex, or pachycaulous and basally swollen; <b>Fl</b> unisexual:	3
3a	<b>L</b> margins with sharp curved prickles:	<i>Dasyilirion</i>
3b	<b>L</b> margins without sharp prickles:	4
4a	Stem large depressed to globose caudex without apparent branches; <b>L</b> $\pm$ wiry; <b>Fr</b> globular:	<i>Dasyilirion</i> ( <i>Calibanus</i> )
4b	Stem absent or subterranean, or small to large and pachycaulous (globose only when young), with few to numerous branches in old plants:	5
5a	Stem prominent, pachycaulous and basally swollen in adult plants (globose only when young); <b>Ov</b> 1-celled; <b>Fr</b> 3-winged capsules:	<i>Beaucarnea</i>
5b	Stem absent, when present woody at maturity, never swollen basally and never globose when young; <b>Ov</b> 3-celled; <b>Fr</b> with 1 seed per locule but often only 1 locule developing:	<i>Nolina</i>

of secondary thickening growth due to a “monocot cambium” (Stevenson 1980, Carlquist 2012). The stems and rhizomes of *Dasylyrion* and *Nolina* are merely woody with at most minimal water-storage capacity.

## References

- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- Bogler, D. J. (1998a) *Nolinaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 392–397, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_46](https://doi.org/10.1007/978-3-662-03533-7_46)
- Bogler, D. J. [ & al. 2006], Pires, C. & Francisco-Ortega, J. (2006) Phylogeny of *Agavaceae* based on ndhF, rbcL, and its sequences: Implications of molecular data for classification. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. Aliso 22: 313–328.
- Bos, J. J. (1984) *Dracaena* in West Africa. Agric. Univ. Wageningen Pap. 84-1: 126 pp., ills., maps, key.
- Bos, J. J. (1998) *Dracaenaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 238–241, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_30](https://doi.org/10.1007/978-3-662-03533-7_30)
- Budweg, H.-G. (2015) Vom Beginn des Lebens der Sansevierien: Beobachtungen an meinen Pflanzen. *Sansevieria Online* 3(2): 24–34, ills.
- Carlquist, S. (2012) Monocot xylem revisited: New information, new paradigms. *Bot. Rev. (Lancaster)* 78: 87–153, ills. <https://doi.org/10.1007/s12229-012-9096-1>
- Chase, M. W. [ & al. 2009], Reveal, J. L. & Fay, M. F. (2009) A subfamilial classification for the expanded Asparagalean families *Amaryllidaceae*, *Asparagaceae* and *Xanthorrhoeaceae*. *Bot. J. Linn. Soc.* 161(2): 132–136. <https://doi.org/10.1111/j.1095-8339.2009.00999.x>
- Givnish, T. J. [ & al. 2006], Pires, J. C., Graham, S. W., McPherson, M. A., Prince, L. M., Patterson, T. B., Rai, H. S., Roalson, E. H., Evans, T. M., Hahn, W. J., Millam, K. C., Meerow, A. W., Molvray, M., Kores, P. J., O'Brien, H. E., Hall, J. C., Kress, W. J. & Sytsma, K. J. (2006) Phylogenetic relationship of Monocots based on the highly informative plastid gene ndhF: Evidence for widespread concerted convergence. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. Aliso 22: 28–51.
- Graham, S. W. [ & al. 2006], Zgurski, J. M., McPherson, M. A., Chemiawsky, D. M., Saarela, J. M., Horne, E. F. C., Smith, S. Y., Wong, W. A., O'Brien, H. E., Biron, V. L., Pires, J. C., Olmstead, R. G., Chase, M. W. & Rai, H. S. (2006) Robust inference of Monocot deep phylogeny using an expanded multigene plastid data set. In: Columbus, J. T. & al. (eds.): *Monocots. Comparative biology and evolution excluding Poales*. Aliso 22: 3–21.
- Jankalski, S. (2004) *Sansevieria* versus *Dracaena*. *Sansevieria* 8: 17–18, ill.
- Janssen, T. & Bremer, K. (2004) The age of major monocot groups inferred from 800+ rbcL sequences. *Bot. J. Linn. Soc.* 146(4): 385–398. <https://doi.org/10.1111/j.1095-8339.2004.00345.x>
- Judd, W. S. [ & al. 2016], Campbell, C. S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J. (2007) *Plant systematics: A phylogenetic approach*. Ed. 4. Sunderland (US): Sinauer Associates.
- Kim, J.-H. [ & al. 2010], Kim, D.-K., Forest, F., Fay, M. F. & Chase, M. W. (2010) Molecular phylogenetics of *Ruscaceae sensu lato* and related families (Asparagales) based on plastid and nuclear DNA sequences. *Ann. Bot. (Oxford)*, n.s. 106: 775–790. <https://doi.org/10.1093/aob/mcq167>
- Lu, P.-L. & Morden, C. W. (2014) Phylogenetic relationships among Dracaenoid genera (*Asparagaceae: Nolinoideae*) inferred from chloroplast DNA loci. *Syst. Bot.* 39(1): 90–104. <https://doi.org/10.1600/036364414X678035>
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>
- Perry, P. L. & Rudall, P. J. (1998) *Eriospermaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 241–244, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_31](https://doi.org/10.1007/978-3-662-03533-7_31)
- Rowley, G. D. (1990) *Nolina* en culture. *Cact.-Avent.* 5: 2–4.
- Rudall, P. J. [ & al. 2000], Conran, J. G. & Chase, M. W. (2000) Systematics of *Ruscaceae / Convallariaceae*: A combined morphological and molecular investigation. *Bot. J. Linn. Soc.* 135(1–2): 73–92. <https://doi.org/10.1111/j.1095-8339.2000.tb02346.x>
- Seberg, O. [ & al. 2012], Petersen, G., Davis, J. I., Pires, J. C., Stevenson, D. W., Chase, M. W., Fay, M. F., Devey, D. S., Jørgensen, T., Sytsma, K. J. & Pillon, Y. (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *Amer. J. Bot.* 99(5): 875–889, ills. <https://doi.org/10.3732/ajb.1100468>
- Steele, P. R. [ & al. 2012], Hertweck, K. L., Mayfield, D., Mckain, M. R., Leebens-Mack, H. & Pires, J. C. (2012) Quality and quantity of data recovered from massively parallel sequencing: Examples in Asparagales and *Poaceae*. *Amer. J. Bot.* 99(2): 330–348. <https://doi.org/10.3732/ajb.1100491>
- Stevenson, D. W. (1980) Radial growth in *Beaucarnea recurvata*. *Amer. J. Bot.* 67(4): 476–489. <https://www.jstor.org/stable/2442287>
- Trelease, W. (1911) The desert group *Nolineae*. *Proc. Amer. Philos. Soc.* 50(200): 404–443, tt. 1–17. <https://www.jstor.org/stable/983932>
- Walter, H. (1931) Die Hydratur der Pflanze und ihre physiologisch-ökologische Bedeutung. (Untersuchungen über den osmotischen Wert). Jena (DE): Verlag von Gustav Fischer.





## Beaucarnea RUSCACEAE

C. C. Walker

**Beaucarnea** Lemaire (Ill. Hort. 8(Misc.): 59, 1861). **Type:** *Beaucarnea recurvata* Lemaire. — **Nolinoideae** — **Lit:** Trelease (1911: synopsis); Hernández-Sandoval (1993: conservation); Lott & García-Mendoza (1994: Fl. Mesoamericana); Walker (2001: introduction); Hernández-Sandoval & al. (2012: management and conservation); Rivera-Lugo & Solano (2012: Fl. Tehuacán-Cuicatlán); Rojas-Piña & al. (2014: phylogeny, checklist, key); Martínez & al. (2014: leaf anatomy); Walker (2015: update). **Distr:** Mexico, C America (Guatemala, Belize, Honduras, Nicaragua?). **Etym:** For Monsieur Beaucarne (fl. 1861), Belgian succulent plant grower and notary from Eename near Audenarde, who first collected flowers of *Beaucarnea recurvata*.

**Incl. *Pincenectitia*** hort. ex Lemaire (1861). **Type:** not typified.

**Incl. *Calibanus*** Rose (1906). **Type:** *Dasylyrion caespitosum* Scheidweiler.

Hermaphrodite, dioecious or polygamo-dioecious shrubs to trees <0.6–10 (–18) m; stem subglobose to elongate, basally greatly swollen, tapering towards the tip, unbranched or

moderately branched above, bark smooth, squamous or irregularly scarred by the remains of the leaf base; **L** in **Ros**, persistent, erect to recurved, broadly linear or grass-like (*B. hookeri*), stiff, acuminate, grooved, bases broadened, glabrous, margin smooth or slightly rough; **Inf** paniculate, well branched; **Ped** articulated; **Fl** unisexual, rarely a few bisexual, numerous, very small, white to slightly tinged purple or red, slightly fragrant, **male Fl** short-lived; **Tep** 6, midveins evident; **Ov** 1-celled with 2–3 ovules; **Sti** 3-lobed; **Fr** prominently 3-winged capsules or unwinged, indehiscent, round, ellipsoid or obovoid, wings papery, with a single **Se**; **Se** 3-lobed, globose, yellow to brown, testa rugose.

A genus of 13 species (all treated here), sometimes previously included in *Nolina*. Two species, *B. glassiana* and *B. hookeri*, were previously included in *Calibanus*. Recently a cladogram of Rojas-Piña & al. (2014) based on molecular evidence showed these species to be nested within *Beaucarnea*, hence *Calibanus* cannot be supported as a distinct genus and was reduced to synonymy under *Beaucarnea*. However, these species together with *B. compacta*, do form a distinct clade. The fruit characters previously considered to be diagnostic, namely fleshy globose unwinged fruit in *Calibanus* versus the 3-winged capsule of *Beaucarnea* are no longer considered to be distinguishing features.

11 species are endemic to Mexico, 1 species has a wider distribution in Mexico and C America, 1 species is endemic to Guatemala, and a natural

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population, as yet unidentified, is recorded for Nicaragua (Lott & García-Mendoza 1994). The genus is poorly understood and in need of revision. All species are pachycaul, some with nearly globular caudices when immature, but only basally swollen when mature. *B. compacta*, *B. glassiana* and *B. hookeri* form a distinct group with a subglobose stem at maturity with greatly reduced branching.

Throughout their range, most populations of *Beaucarnea* are in a critical state because of continuing destruction of their habitat (e.g. agriculture, goat herding) and removal for commercial purposes (Cardel & al. 1997). *B. recurvata* is the most commonly cultivated species, making an attractive pot plant when small. All tree-like species have the common name of “ponytail palm”, especially in the US-American horticultural trade. In Mexico the vernacular name “Pata de Elefante” is possibly applicable to all species (Hernández-Sandoval & al. 2012).

Trelease (1911) classified the genus into the two unranked taxa *Eubeaucarnea* and *Papillatae*. Thiede (2012) accepted these two groupings at sectional level, and provided a valid new combination for the latter. However, the cladogram of Rojas-Piña & al. (2014) does not support such a division of the genus and hence it is not followed here. An alternative subdivision might be more appropriate, with a so-called “southern clade” forming a well-defined group consisting of *B. goldmanii*, *B. guatemalensis* and *B. plibilis*, separated from the rest, which might more accurately reflect the evolutionary relationships within the genus.

Martínez & al. (2014) studied the xeromorphic leaf anatomy of *Beaucarnea*, but this study excluded the two former species of *Calibanus*. They divided the genus into two groups, one (partly corresponding to the *Papillatae*) having a grooved leaf outline in transverse section (*B. compacta*, *B. gracilis*, *B. purpusii* and *B. stricta*), whereas other species have an undulate leaf outline. Other characters, such as epicuticular waxes, stomatal distribution and density and marginal teeth length were also found to have taxonomic value.

The following name is of unresolved application but is referred to this genus:

*Beaucarnea congesta* L. Hernández (s.a.) (*nom. inval.*, Art. 29.1).

**B. compacta** L. Hernández & Zamudio (Brittonia 55(3): 226–228, ills., 2003). **Type:** Mexico, Guanajuato (Zamudio & al. 10465 [IEB, CHAPA, ENCB, MEXU, QMEX]). — **Distr:** Mexico (Guanajuato: Sierra Madre Oriental); only on igneous outcrops in xerophytic scrub.

Dioecious shrub with subglobose stem, 40–60 × 80–100 cm Ø, bark fissured with polyhedral pattern, reddish-grey to reddish-brown; **Ros** leafy, sessile, obconical; **Br** reduced; **L** linear, erect, long acuminate, to 50–75 × 1–1.2 cm, glaucous-green, papillate, margin denticulate; **Inf** paniculate, ovoid to ellipsoid, 1.5–2 m × 1–1.2 cm Ø at the base; primary **Br** 29–32 cm, shorter **Br** 11–15 cm; **male Fl** creamy yellow tinged with purple, fragrant; **Ped** 0.5–1.5 mm, articulated below the flower; **Tep** oblong, concave, 1.5–1.7 mm; **female Fl** creamy yellow; **Ped** 1.5–3 mm, articulated at or above the middle; **Tep** ovate to lanceolate, 1.5–2 mm; **Fr** pyriform-ovoid, 8–9 × 4–5 mm, yellow at maturity; **Se** ovoid, 4 × 3 mm, testa rugose, red-brown.

In the cladogram of Rojas-Piña & al. (2014) *B. compacta* forms a “*Calibanus* clade” with *B. glassiana* and *B. hookeri*, characterised by having subglobose caudices and greatly reduced branching. Morphologically it is also similar to *B. gracilis*, but its distinguishing features are the absence of a main stem, its sessile foliar rosettes, short inflorescence branches, smaller flowers and fruits and the median articulated pedicel. The species is probably not in cultivation.

**B. glassiana** (L. Hernández & Zamudio) V. Rojas-Piña (Taxon 63(6): 1207, 2014). **Type:** Mexico, Guanajuato (Pérez-Calix & al. 3719 [IEB, CHAPA, ENCB, MEXU, QMEX]). — **Lit:** Rojas-Piña & al. (2014). **Distr:** Mexico (NE Guanajuato); limestone outcrops in the Sierra Madre Oriental, ecotone between tropical deciduous forest and piedmont scrub, 900–1000 m.

≡ *Calibanus glassianus* L. Hernández & Zamudio (2003).

Caudex conical, 60–80 × 40–60 cm, bark fissured into a polyhedral pattern below and rugose above, dark grey; **Br** > 4 at maturity, sessile or reduced, grouped at the stem apex; **L** erect, recurved and reflexed from above the base, linear, long, acuminate, 1.1–1.2 m × 0.7–0.9 cm in the middle, glaucous-green, scarcely papillate, margins denticulate, teeth translucent, leaf base deltate; **Inf** paniculate, ovoid, 1.5–1.7 m; primary **Br** 28–30 cm, shorter **Br** 16–18 cm; **Bra** subtending the branches linear, 23–29 cm; **Fl** normally unisexual; **male Fl Tep** oblong, elliptic to orbicular, concave, 1.8–2.75 × 1.5–2 mm, **OTep** slightly smaller than the **ITep**; **St** 6, exserted, 2–3 mm, **Anth** dorsifixed, **Ov** reduced; **female Fl Tep** elliptic, orbicular to oblate, concave, 1.2–2 mm; **Ov** 3-carpellate, 2 ovules per carpel, unilocular, ellipsoid, 6-angled at the base; **Sty** ± 0.7 mm, **Sti** lobes tuberculate; **Fr** depressed globose, 4.5–5 × 4–4.5 mm, yellow with purple spots when mature, costae reddish; **Se** melon-shaped, 2.5–4.5 mm Ø, testa rugose, red-brown.

In the cladogram of Rojas-Piña & al. (2014) *B. glassiana* forms a “*Calibanus* clade” with *B. compacta* and *B. hookeri*, characterised by having subglobose caudices and greatly reduced branching. *B. glassiana* is closest to *B. hookeri* from which it differs in its general habit with fewer apical branches, significantly longer glaucous-green leaves, long exserted, well-branched inflorescences, and smaller depressed globose fruits with reddish costae. Discovered in 1996 around Xichú by Charlie Glass, intrepid botanical explorer of Mexico and former editor of the *Cactus & Succulent Journal* (US). His collection later flowered in cultivation enabling confirmation of its generic placement.

**B. goldmanii** Rose (Contr. US Nation. Herb. 12: 261, t. 20, 1909). **Type:** Mexico, Chiapas (*Goldman* 887 [US]). — **Lit:** Lott & García-Mendoza (1994); Rojas-Piña & al. (2014). **Distr:** SW Mexico (Chiapas), Guatemala; rocky slopes in deciduous forests, 800–1400 m.

Stem to 10 m, slender, branched above, bark thin, rough; **L** linear, to 100 × 1.5 cm, strongly recurved, shiny, smooth, long acuminate towards the apices, margins minutely serrulate with

appressed denticles; **Inf** compound-paniculate, nearly sessile, primary divisions 15–20 cm, **Br** few, to 10 cm; **female Inf Bra** linear-filiform, 19–21 × 1 cm; bracteoles 1–3 mm; **Ped** articulated; **Tep** ± 2 mm; **Fr** ellipsoid, glaucous, broadly 3-winged, very large, 18–20 × 12–15 mm; **Se** 5–5.5 × 5–5.5 mm, rugose, blackish, opaque.

Resembles *B. guatemalensis*, but the leaves are large and the fruits are narrower and glaucous. It is especially poorly known and probably not in cultivation.

**B. gracilis** Lemaire (Ill. Hort. 8(Misc.): 61, 1861). **Type** [neo]: Mexico, Puebla (*Hernández S.* 2354 [MEXU, TEX, UAT]). — **Lit:** Cardel & al. (1997: ecology); Rivera-Lugo & Solano (2012); Rojas-Piña & al. (2014). **Distr:** Mexico (Puebla, Oaxaca: Endemic to the Tehuacán-Cuicatlán valley); thorn scrub, 1300–2000 m. **I:** Cact. Succ. J. (US) 48: 64, 1976; Rowley (1987: 89, as *Nolina*); Walker (2001: 217, fig. 4). — Fig. 1.

≡ *Dasylyrion gracile* (Lemaire) J. F. Macbride (1918) (*nom. illeg.*, Art. 53.1) ≡ *Nolina gracilis* (Lemaire) Ciferri & Giacomini (1950); **incl.** *Nolina histrix* hort. (s.a.) (*nom. inval.*, Art. 29.1); **incl.** *Pincenectitia gracilis* hort. ex Lemaire (1861) (*nom. inval.*, Art. 34.1c?); **incl.** *Beaucarnea oedipus* Rose (1906).

Dioecious tree, stem basally enormously swollen, circular in cross-section, variously and irregularly branched, to 12 m overall; **L** linear, erect, 30–60 × 0.4–0.7 cm, very glaucous, margins minutely but sharply serrulate-scabrous; **Inf** short-stalked, ovoid- or oblong-paniculate, 0.6–1 m, primary divisions to 30 cm, **Br** rather weak, to 14 cm; **Ped** 3.2–3.5 mm; **Tep** 1.2 × 1 mm; **Fr** round-ellipsoid, openly notched at tip and base, 10 × 7–9 mm; **Se** smooth, 3.6 × 2.8 mm.

Morphologically similar to *B. compacta*, but differing in the elongated (instead of subglobose) stem, longer inflorescence branches, and larger flowers and fruits. It has a limited distribution in the Tehuacán-Cuicatlán Valley, Puebla/Oaxaca (Hernández-Sandoval & Zamudio 2003; Rivera-Lugo & Solano 2012). García-Franco & al. (1995) record a relatively high population density in the

**Fig. 1** *Beaucarnea gracilis*. (Copyright: J. Etter & M. Kristen)



valley of Zapotitlán de las Salinas (Puebla) with a sex ratio close to 1:1. A rare occurrence of parasitism by *Psittacanthus calyculatus* (*Loranthaceae*) is also reported.

Cardel & al. (1997) recorded that plants with stem diameter < 0.7 m were absent from their study site (n = 404) and observed that low recruitment, removal of seedlings for commerce, grazing by goats and land clearance for corn cultivation, highway construction and urbanization, threaten the establishment and survival of seedlings.

The leaves are used to make hats and arrangements for religious offerings (Rivera-Lugo & Solano 2012).

**B. guatemalensis** Rose (Contr. US Nation. Herb. 10: 88, Fig. 1, 1906). **Type:** Guatemala (Kellermann 4320 [US, F, LL, MEXU, MICH, TEX, UC]). — **Lit:** Lott & García-Mendoza (1994); Rojas-Piña & al. (2014). **Distr:** Guatemala; rocky slopes, ecotone between deciduous forest to oak-pine forests, 700–1600 m.

≡ *Nolina guatemalensis* (Rose) Ciferri & Giacomini (1950).

Trees 6–12 m with thickened bulbous base, abruptly contracted into a slender stem often with slender multiple **Br**; **L** linear, to 100 × 2.5–3 cm, minutely scabrous, with papillose ridges, margins minutely papillate; **Inf** short-stalked, broadly ovoid-paniculate, primary divisions 30 cm, **Br** rather spreading, to 15 cm, branchlets to 6 cm; **Bra** 15 cm, lanceolate-linear; bracteoles 10–12 mm; **male Fl Tep** 3 mm; **female**

**Fl Ped** 8 mm, articulated above the middle; **Fr** ellipsoid-obovate, 15–18 × 13–15 mm, openly notched at the tip for 4–5 mm; **Se** irregularly 3-lobed, 5 mm diam.

Related to *B. pliabilis*, but the fruit has broader wings and the leaves are broader with a scabrous as opposed to smooth surface.

**B. hiriartiae** L. Hernández (Acta Bot. Mex. 18: 25–29, ills., 1992). **Type:** Mexico, Guerrero (*Hernández-Sandoval & Martínez* 1629 [MEXU, TEX, UAT]). — **Lit:** Rojas-Piña & al. (2014). **Distr:** Mexico (Guerrero: Río Balsas drainage); deciduous tropical forest, in canyons on very steep slopes of shale or limestone, 250–700 m; reported to have two flowering and fruiting periods.

Trees to 8 m; stem basally swollen, oval in cross-section, often with slender multiple **Br**; **L** recurved, linear, to 70–90 × 1–1.5 cm, pale green, concave, papillate, margin minutely serrulate; **Inf** short-stalked, ovoid-elliptically paniculate, primary divisions 20–25 cm, **Br** rather spreading, 3–10 cm; **Ped** 5.5–6.5 mm; **Tep** ovate, 2.5 × 2 mm; **Fr** obovate-oblong, 8–11 × 7–10 mm; **Se** ellipsoid-obovate, 3.5 × 3.1 mm.

Considered to be closely related to *B. stricta* from neighbouring Oaxaca in the protologue, but appearing to differ only quantitatively in the length of organs such as leaves and pedicels. It differs though in that the stem base in cross-section is oval and the leaves are recurved. Hernández-



Sandoval (2001) compared *B. hiriartiae* with *B. recurvata* and *B. sanctomariana*. He recorded a unique stem architecture for this species, in that meristems of a single branch develop apical dominance, leaving the remaining branches with reduced growth rates. Consequently, the habit of *B. hiriartiae* resembles a tree with its branches growing only to one side. This feature alone enables this species to be distinguished easily in the field from *B. recurvata* and *B. sanctomariana*. *B. hiriartiae* has papillate leaves, in contrast to the smooth ones of the other two species (Hernández-Sandoval 2001). Vernacular names: “Izote Delgado”, “Ixtotl”. This species is probably not in cultivation.

**B. hookeri** (Lemaire) Baker (J. Bot. 10: 327, 1872). **Type:** K (ex cult. Kew 1873). — **Lit:** Hernández-Sandoval & Zamudio (2003); Rojas-Piña & al. (2014). **Distr:** Mexico (Hidalgo, San Luis Potosí); apparently well-camouflaged on hilltops. **I:** Glass & Foster (1970: 269); Rowley (1987: 32, 90); Brand (2007); Spee (2007). — Fig. 2.

≡ *Dasyilirion hookeri* Lemaire (1859) ≡ *Calibanus hookeri* (Lemaire) Trelease (1911) ≡ *Nolina hookeri* (Lemaire) G. D. Rowley (1990); **incl.** *Dasyilirion hartwegianum* Hooker (1859) (*nom. illeg.*, Art. 53.1); **incl.** *Dasyilirion caespitosum* Scheidweiler (1861) ≡ *Calibanus caespitosus* (Scheidweiler) Rose (1906); **incl.** *Dasyilirion flexile* K. Koch (1867).

Caudex globose, slightly flattened, to 50 cm Ø, bark thick, corky and fissured, later woody, with numerous crowns of leaves from very short monocarpic **Br** not elevated over the surface of the caudex; **L** thin, grass-like, wiry, narrowly linear, somewhat concave and keeled, to 30 cm × 2–3 mm, margins serrulate-scabrous, tip entire; **Inf** simple panicles, normally unisexual or rarely with some hermaphrodite flowers, to 25 cm, shorter than the leaves, shortly pedunculate, lax with thin spreading **Br** 6–8 cm; **Bra** scarious, ovate or lanceolate, much shorter than the subtended branches; **Tep** elliptic-obovate, 2–3 × 1.5–2 mm, scale-like, dirty whitish-yellow, translucent; **St** subequal, 2.5–3 mm; **Anth** medifixed, 1.2–1.5 mm; **Ov** ovoid, 2.5–3 × 2 mm, 3-locular with 1 ovule in each locule; **Sti** sessile, 3-lobed; **Fr** globose-ovoid, 8–9 × 6–7 mm, pale straw-brown, indehiscent; **Se** melon-shaped, 3–4 × 3 mm. — **Cytology:** 2n = 38 (Johnson & Gale 1983).

*B. hookeri* was first discovered around 1845. It was not described until 1859 when it was misidentified as *Dasyilirion hartwegianum* by Sir William Hooker at Kew. Rose (1906) established the monotypic genus *Calibanus* for this species, named for Shakespeare’s monster Caliban from the play “The Tempest”, presumably for the massive caudex. The plant is currently well known in cultivation as *Calibanus hookeri*. Most recently, Rojas-Piña & al. (2014) provided convincing molecular evidence that *Calibanus* is nested within *Beaucarnea* and hence not distinct at the

**Fig. 2** *Beaucarnea hookeri*. (Copyright: T. Wardhaugh)





generic level. *B. hookeri* is closely related to *B. compacta* and *B. glassiana*, characterised by having subglobose caudices and greatly reduced branches.

*B. hookeri* was rediscovered by Charlie Glass and Bob Foster in 1968 in San Luis Potosí, where it appears to be well camouflaged in habitat (Glass & Foster 1970: 269, ill.). Most of the material now widespread in cultivation originates from this introduction (ISI 688), since the plant has taken well to cultivation (Walker 2001). It has proved to be almost hardy, and easily propagated from seed. Johnson & Gale (1983) report successful artificial pollination with one-year old refrigerated pollen. Brand (2007) reports that seed-raised plants first flowered after 9 years.

*B. hookeri* is a remarkable caudiciform, eventually developing a large woody caudex, curious rather than attractive. It is known locally in Mexico as “Sacamecate” and its leaves are used for thatching and for scouring dishes.

**B. olsonii** V. Rojas & L. O. Alvarado (Phytotaxa 286(1): 15–18, ills., 2016). **Type:** Mexico, Puebla (*Olson & al.* 1044 [MEXU, MEXU, MO]). — **Distr:** Mexico (Puebla: Izúcar-Acatlán); dense tropical deciduous forest on steep slopes, 1300 m.

Trees 3–5 m; stem basally massively swollen, 2.4–4 m Ø, abruptly tapering into few slender **Br** 1–3 m long, dark grey and squamose forming irregular grooves along the length of the stem; **L** straight and terminally erect, 60–85 cm × 0.9–1.7 cm at the middle, green to bluish glaucous green, canaliculate, papillate, margin slightly irregular; **Inf** a thyrse with 3 orders of branching, last unit a reduced rhipidium, **Bra** narrowly triangular to triangular, apex acuminate to long caudate; **female Fl** with **Ped** 4–5 mm, articulated at  $\frac{2}{3}$  of the length below the flower; **Tep** ovate, whitish 1.5–1.7 × 1.3–2 mm; **male Fl** unknown; **Fr** (immature) obovate, 3-winged, 7–9 mm; **Se** (immature) 1 per fruit, brown, testa rugose.

Similar to *B. hiriartiae* but differs in its tessellated bark, straight leaves and short style. It is easily distinguished from other *Beaucarnea* species by its swollen base that abruptly tapers into a

slender stem and in its pedicel articulation that occurs at  $\frac{2}{3}$  of the length of the pedicel below the flower. *B. olsonii* is a very rare, localised species, known only from its type locality in SW Puebla with an extent of occurrence estimated to be <100 km<sup>2</sup>, and hence assessed as being critically endangered. This species is probably not in cultivation.

**B. pliabilis** (Baker) Rose (Contr. US Nation. Herb. 10: 89, 1906). **Type:** Mexico, Yucatán (*Schott* 892 [BM, MO]). — **Lit:** Lott & García-Mendoza (1994); Rojas-Piña & al. (2014). **Distr:** SE Mexico (Yucatán, Quintana Roo), Guatemala, Belize; deciduous forests on plains and hillsides. **I:** Trelease (1911: t. 10); Lundell (1939: fig. 1). — Fig. 3.

≡ *Dasyllirion pliabile* Baker (1880) ≡ *Nolina pliabilis* (Baker) Lundell (1939); **incl.** *Dracaena petenensis* Lundell (1935) ≡ *Beaucarnea petenensis* (Lundell) Lundell (1939); **incl.** *Beaucarnea ameliae* Lundell (1939).



**Fig. 3** *Beaucarnea pliabilis*. (Copyright: U. Eggli)

Trees 4–12 m, base swollen to 90 cm  $\varnothing$ , stem openly branched; **Br** slender; **L** linear, to  $100 \times 1.5$  cm, smooth, acuminate, strongly recurved, margin serrulate, tip entire, base amplexicaul; **Inf** compound-paniculate, primary divisions 30 cm, with few rather short spreading **Br** to 58 cm; **Bra** to 60 cm, bracteoles 6–7 mm, thin, ovate-lanceolate; **male Fl** in fascicles of 2–3; **Ped** 5–7 mm, articulated in the middle; **Tep** ovate-oblong or oblong-elliptic, pale yellowish-white,  $4 \times 3$  mm; **female Fl Ped** articulated 4–5 mm above the middle; **Tep**  $3\text{--}3.3 \times 1.8\text{--}2$  mm; **Fr** somewhat obovately round-ellipsoid,  $10\text{--}18 \times 11\text{--}12$  mm, apical notch 1–2 mm; **Se** irregularly 3-lobed, transversely wrinkled,  $3\text{--}4 \times 3$  mm, somewhat keeled, bright brown.

Resembling *B. guatemalensis*, but the latter has a finely scabrous leaf surface, whereas *B. pliabilis* has entirely smooth blades. Vernacular name: “Tzipil”. Only rarely cultivated.

**B. purpusii** Rose (Contr. US Nation. Herb. 10: 89, 1906). **Type:** Mexico, Puebla (Rose & al. 10156 [US, MEXU, NY]). — **Lit:** Rivera-Lugo & Solano (2012); Rojas-Piña & al. (2014). **Distr:** Mexico (Puebla, Oaxaca: Tehuacán-Cuicatlán valley); desert scrub, 1600–2200 m.

Trees 6–8 m; stem somewhat swollen at the base, little branched, trunk almost completely clothed by the reflexed and closely appressed old leaves; **L** at first erect, then spreading, and at last reflexed, long persisting, very pale, to  $50\text{--}60 \times 1\text{--}1.2$  cm, margin pale and entire.

A very poorly understood taxon, considered by Trelease (1911) to be a synonym of *B. stricta*, but accepted by Rivera-Lugo & Solano (2012) and reinstated as a distinct species by Rojas-Piña & al. (2014) based initially on molecular evidence. There are also apparently conspicuous inflorescence differences between *B. purpusii* and *B. stricta*; for example, the latter has more orders of branching. Further study is required of the reproductive characters of these two species.

The species is considered endangered, and Vadillo-Pro & al. (2016) established a successful micropropagation protocol on the base of vertical sections of seedlings.



**Fig. 4** *Beaucarnea recurvata*. (Copyright: C.C. Walker)

**B. recurvata** Lemaire (Ill. Hort. 8(Misc.): 58–59, fig. 1, 1861). **Type:** [lecto — icono]: l.c., Fig. 1, p. 58. — **Lit:** Contreras & al. (2008: conservation & use); Rojas-Piña & al. (2014). **Distr:** SE Mexico (Veracruz, Oaxaca); deciduous lowland forest and tropical deciduous forest, on hillsides with shallow, well-drained sandy or clayey soils. **I:** Lyons (1969); Rowley (1987: 89, as *Nolina*); Walker (2001: 214–216, figs. 1–3). — Fig. 4.

≡ *Nolina recurvata* (Lemaire) Hemsley (1884) ≡ *Dasyllirion recurvatum* (Lemaire) J. F. MacBride (1918); **incl.** *Nolina tuberculata* hort. (s.a.) (*nom. inval.*, Art. 29.1); **incl.** *Pincenectitia tuberculata* Lemaire (1861) (*nom. inval.*, Art. 34.1c) ≡ *Beaucarnea tuberculata* (Lemaire) Roezl (1883) (*nom. inval.*, Art. 34.1c); **incl.** *Beaucarnea recurvata* var. *intermedia* hort. ex Baker (1880); **incl.** *Beaucarnea recurvata* var. *rubra* hort. ex Baker (1880); **incl.** *Dasyllirion inerme* S. Watson (1891) ≡ *Beaucarnea inermis* (S. Watson) Rose (1906).

Trees to 9 m, stem basally moderately swollen, slender and few-branched above, caudex almost

globular when immature, later 4–6 m, 50 cm  $\varnothing$  and up to 2–3 m  $\varnothing$  at the base, bark smooth; **L** linear, 90–180  $\times$  1.5–2 cm, slightly tapering, recurved, thin, flat or slightly grooved, smooth, green, margin smooth; **Inf** to >1 m, nearly sessile, broadly ovoid-paniculate, primary **Br** to 30 cm, lower **Br** to 15 cm, branchlets 5 cm; **male Fl Ped** articulated above the middle; **Tep** 2–2.5 mm; **female Fl Tep** 2.5–4 mm; **Fr** ellipsoid to slightly obovate, 12–14  $\times$  9–10 mm, pale yellow, tip and base emarginate, apical notch 1–2  $\times$  1–2 mm; **Se** ellipsoid to ovoid, 3.5–4.5  $\times$  3–4 mm, lobes not prominent, testa rough to smooth, bright red-brown.

Similar to *B. sanctomariana*, but differing in the larger trunk bases, longer leaves, and larger ellipsoid fruits. Both species occur in the Isthmus of Tehuantepec, Oaxaca, where *B. recurvata* is restricted to the Pacific slopes, whereas *B. sanctomariana* occurs on the side facing the Gulf of Mexico (Hernández-Sandoval 2001). Most populations of *B. recurvata* are in a critical condition, resulting from the continued fragmentation and habitat destruction, caused by the expansion of agriculture, livestock grazing, removal of firewood, timber and urban expansion (Contreras & al. 2008). However, *B. recurvata* is readily grown from seed and therefore now extremely common in cultivation, and widely distributed through the commercial nursery trade. It retains its immature form of an almost globular caudex for many years before the stem tip starts to elongate, only branching after flowering. As a young plant, therefore, with the long narrow leaves emerging from the globose base it makes an unusual and attractive pot plant. First flowering of 15 year old pot-grown specimens has been reported at  $\pm$ 1 m tall and  $\pm$  20–25 cm basal diameter. At maturity it has a rather different form, basally swollen with a tapering main stem and a few terminal branches. A variegated cultivar is also sometimes encountered in cultivation and was named ‘Stripy Ponytail’ (Walker 2015). Vernacular name, especially in the USA: “ponytail palm”.

**B. sanctomariana** L. Hernández (Novon 11 (1): 50–53, ills., 2001). **Type:** Mexico, Oaxaca

(Wendt 5914 [MEXU ( $\dagger$ ?), CHAPA, LL ( $\dagger$ ?), MO ( $\dagger$ ?), UAT]). — **Lit:** Rojas-Piña & al. (2014). **Distr:** Mexico (Oaxaca); restricted to xerophytic vegetation on steep karstic rock outcrops that emerge from the surrounding tropical deciduous forest, 200–250 m.

Tree 4–7 m, stem profusely branched, base widely conical, 1–1.5 m  $\varnothing$ , bark fissured with rectangular to polyhedral pattern, brown-grey; **Br** elongate, slender, with leaf **Ros** spherical to widely ovoid; **L** linear, recurvate, very long acuminate, 75–85  $\times$  1.2–1.6 cm, smooth, bright green, margin pale green, denticulate; **Inf** ovoid to largely ellipsoid, 0.8–1 m  $\times$  1 cm  $\varnothing$  at the base; primary **Br** 10–15 cm, shorter **Br** 3–8 cm; **male Fl** fragrant; **Ped** 1.5–2.3 mm, articulated below the flower; **Tep** cream-yellow, ovate, 1.4–1.8 mm; **female Fl Ped** 1.5–2 mm, articulated at or above the middle; **Tep** cream-yellow, ovate, 1–1.5 mm; **Fr** ellipsoid to almost globose, 6–8  $\times$  5–7 mm, pale yellow at maturity; **Se** (immature) with apices of lobes very irregular, testa rugose, red-brown.

Morphologically similar to *B. hiriartiae* and *B. recurvata*. It shares with *B. hiriartiae* the recurved leaves, the undulate bracts, and the general colour of the inflorescence. It shares with *B. recurvata* the shape of the trunk base, and the recurved smooth leaves. Distinguishing features of *B. sanctomariana* are the short inflorescence branches and the small flowers and fruits. Its very limited distributional range characterises it as an endangered micro-endemic species.

**B. stricta** Lemaire (Ill. Hort. 8(Misc.): 61, 1861). **Type** [neo]: Mexico, Oaxaca (Hernández S. 2391 [MEXU, TEX, UAT]). — **Lit:** Matuda (1960); Rivera-Lugo & Solano (2012); Rojas-Piña & al. (2014). **Distr:** Mexico (Oaxaca); tropical deciduous forest on acid soils of volcanic origin, 1200–1500 m. **I:** Lyons (1969: 53–54); Walker (2001: 218, fig. 5). – Fig. 5.

$\equiv$  *Beaucarnea recurvata* var. *stricta* (Lemaire) Baker (1880)  $\equiv$  *Dasyllirion strictum* (Lemaire) J. F. Macbride (1918)  $\equiv$  *Nolina stricta* (Lemaire) Ciferri & Giacomini (1950); **incl.** *Pincenectitia glauca* Lemaire (1861) (*nom. inval.*, Art. 34.1c)  $\equiv$  *Beaucarnea glauca* (Lemaire) Hereman (1868) (*nom. inval.*, Art. 34.1c).





**Fig. 5** *Beaucarnea stricta*. (Copyright: U. Eggli)

Trees to 10 m; stem greatly swollen, circular in cross-section at the base, irregularly and modestly branched, bark corky, fissured; **L** linear, erect, to 55–80 × 0.8–1.5 cm, stiffly spreading, keeled, pale or glaucous grey, margin yellowish, usually minutely serrulate-scabrous; **Inf** short-stalked, ovoid-paniculate, primary divisions 20 cm, **Br** short, the lower with branchlets to 3 cm; **Ped** 2.8–3 mm; **Tep** 2.5 × 2 mm; **Fr** broadly ellipsoid, openly notched at tip and base, 12 × 8–10 mm; **Se** irregularly 3-lobed, smooth, 3.6 × 3.3 mm.

In the cladogram of Rojas-Piña & al. (2014), *B. stricta* occupies a distinct clade, separate from *B. purpusii*, that was until recently included as a synonym of *B. stricta*.

*B. stricta* is morphologically similar to *B. purpusii*, *B. hiriartiae* and *B. gracilis*, but is distinguished by the septal and distal nectaries; *B. stricta* also differs from *B. gracilis* in its larger leaves and bright yellow-green inflorescences (Rivera-Lugo & Solano 2012).

This is another tall tree, with a stem greatly swollen and circular in cross section at the base. Its specific name refers to the erect, straight leaves. It has a limited distribution in Oaxaca.

## References

- Brand, T. (2007) *Calibanus hookeri* in Blüte — leichter als gedacht? *Kakt. and. Sukk.* 58(10): 273–276, ills.
- Cardel, Y. [& al. 1997], Rico-Gray, V., García-Franco, J. G. & Thien, L. B. (1997) Ecological status of *Beaucarnea gracilis*, an endemic species of the semiarid Tehuacan Valley, Mexico. *Conservation Biol.* 11(2): 367–374. <https://doi.org/10.1046/j.1523-1739.1997.95322.x>
- Contreras, A. [& al. 2008], Osorio, M. L., Equihua, M. & Benítez, G. (2008) Conservación y aprovechamiento de *Beaucarnea recurvata*, especie forestal no maderable. *Cuad. Biodivers.* 28: 3–9.
- García-Franco, J. [& al. 1995], Rico-Gray, V. & Palacios-Rios, M. (1995) Parasitismo de *Psittacanthus calyculatus* (*Loranthaceae*) sobre *Beaucarnea gracilis* (*Nolinaceae*) en el Valle de Zapotitlán de las Salinas, Puebla, México. *Cact. Suc. Mex.* 40(3): 62–65, ill.
- Glass, C. & Foster, R. (1970) Mexican logbook. *Cact. Succ. J. (US)* 42(2): 73–77, (3): 107–112, 142, (4): 174–178, (5): 229–234, (6): 263–269.
- Hernández-Sandoval, L. G. (1993) *Beaucarnea*, un genero amenazado? *Cact. Suc. Mex.* 38(1): 11–13, ill.
- Hernández-Sandoval, L. G. (2001) *Beaucarnea sanctomariana* (*Nolinaceae*), a new micro-endemic species of Ponytail Palm from the Isthmus de Tehuantepec, Oaxaca, Mexico. *Novon* 11(1): 50–53, ills. <https://www.jstor.org/stable/3393207>
- Hernández-Sandoval, L. G. & Zamudio, S. (2003) Two new remarkable *Nolinaceae* from Central Mexico. *Brittonia* 55(3): 226–232, ills. <https://www.jstor.org/stable/3218443>
- Hernández-Sandoval, L. G. [& al. 2012], Osorio Rosales, M. L., Pérez Farrera, A., Contreras Hernández, A., Malda Barrera, G., Espadas Manrique, C., Almanza Rodríguez, K. E., Castillo Gómez, H. A. & Félix Álvarez, A. (2012) Manejo y conservación de las especies con valor comercial de Pata de Elefante (*Beaucarnea*). Querétaro (MX): Ediciones Universitarias, Universidad Autónoma de Querétaro.
- Johnson, M. A. T. & Gale, R. M. O. (1983) Observations on the leaf-anatomy, pollen, cytology and propagation of *Calibanus hookeri* (Lem.) Trelease. *Bradleya* 1: 25–32, ills. <https://doi.org/10.25223/brad.n1.1983.a4>
- Lott, E. J. & García-Mendoza, A. (1994) *Agavaceae*. In: Davidse, G. & al. (eds.): *Flora Mesoamericana*, Volumen 6, *Alismataceae a Cyperaceae*; pp. 35–47, keys. México (MX): UNAM, Instituto de Biología / St. Louis (US): Missouri Botanical Garden / London (GB): Natural History Museum. <https://www.tropicos.org/Project/FM>

- Lundell, C. L. (1939) Studies of Mexican and Central American plants. VIII. Bull. Torrey Bot. Club 66(9): 583–604. <https://doi.org/10.2307/2480801>
- Lyons, G. W. (1969) The Huntington Desert Garden today. Cact. Succ. J. (US) 41(2): 51–56, (3): 120–123, (4): 151–154, (5): 221–224, ills.
- Martínez, M. [ & al. 2014], Hernández-Sandoval, L. & Carrillo, L. (2014) Foliar anatomy of *Beaucarnea Lemaire* (*Nolinaceae* s.s.). Pl. Syst. Evol. 300(10): 2249–2258, ills., key. <https://doi.org/10.1007/s00606-014-1048-2>
- Matuda, E. (1960) *Beaucarnea stricta*. Cact. Suc. Mex. 5 (4): 93–94, ill.
- Rivera-Lugo, M. & Solano, E. (2012) Flora del Valle de Tehuacán-Cuicatlan. Fascículo 99. *Nolinaceae* Nakai. México D.F. (MX): Instituto de Biología UNAM.
- Rojas-Piña, V. [ & al. 2014], Olson, M. E., Alvarado-Cárdenas, L. O. & Eguiarte, L. E. (2014) Molecular phylogenetics and morphology of *Beaucarnea* (*Ruscaceae*) as distinct from *Nolina*, and the submerision of *Calibanus* into *Beaucarnea*. Taxon 63(6): 1193–1211, ills., key. <https://doi.org/10.12705/636.9>
- Rose, J. N. (1906) Studies of Mexican and Central American plants. No. 5. *Liliaceae*. *Dasyliirion* and its allies. Contr. US Nation. Herb. 10(3): 87–92, tt. 23–25. <https://www.biodiversitylibrary.org/page/41739857#page/193>
- Rowley, G. D. (1987) Caudiciform and pachycaul succulents. Pachycauls, bottle-, barrel- and elephant-trees and their kin: A collector's miscellany. Mill Valley (US): Strawberry Press.
- Spee, B. (2007) *Calibanus hookeri*, geen plant om mee te nemen. Succulenta 86(3): 123–126, ills.
- Thiede, J. (2012) Nomenclatural status of unranked names published by Trelease (1911) in *Beaucarnea*, *Dasyliirion*, and *Nolina* (*Asparagaceae* — *Nolinoideae*). Phytoneuron 2012(77): 1–4. <https://www.phytoneuron.net/77PhytoN-Beaucarnea.pdf?>
- Trelease, W. (1911) The desert group *Nolineae*. Proc. Amer. Philos. Soc. 50(200): 404–443, tt. 1–17. <https://www.jstor.org/stable/983932>
- Vadillo-Pro, M. C. [ & al. 2016], Hernández-Sandoval, L., Malda-Barrera, G., Osorio-Rosales, M. L. & Mata-Rosas, M. (2016) In vitro regeneration from longitudinal sections of seedlings of *Beaucarnea purpusii* Rose, an endemic and endangered species. HortScience 51(3): 279–284, ills.
- Walker, C. C. (2001) Introducing the *Nolinaceae*. Brit. Cact. Succ. J. 19(4): 214–221, ills.
- Walker, C. C. (2015) *Beaucarnea* updated. CactusWorld 33(4): 267–272, ills.





## Dasyilirion RUSCACEAE

C. C. Walker

**Dasyilirion** Zuccarini (Allg. Gartenzeitung 6(33): 258, 1838). **Type:** *Dasyilirion graminifolium* Zuccarini. — **Nolinoideae** — **Lit:** Trelease (1911: synopsis); Bogler (1994a: systematics); Bogler (1994b: phylogeny); Bogler (1995: systematics, phylogeny); Hochstätter (2011: synopsis); Hochstätter (2012: synopsis). **Distr:** S USA to Mexico. **Etym:** Gr. ‘dasys’, dense, rough, shaggy; and Gr. ‘leirion’, lily; presumably for the long and untidy appearance of the leaves.

**Incl.** *Dasyilirium* Lemaire (1865) (*nom. inval.*, Art. 61.1).

Dioecious, short arborescent perennial shrubs with thick unbranched stems crowned with dense rosettes, sometimes rosettes  $\pm$  stemless; **L** serrulate or prickly, or unarmed, linear, hard and fibrous; **Inf** paniculate, elongate, conspicuously bracteate, to 6 m; **Ped** jointed at the base of the flowers; **Per** small, whitish, persistent; **St** 6, vestigial in female flowers; **Ov** 1-celled, ovules 2 or 3 but only 1 developing; **Sty** very short, erect; **Sti** 3; **Fr** 1-seeded (occasionally 2-seeded) small capsules, 3-winged, thin-walled. — **Cytology:**  $2n = 38$  (Satô 1935, 1942; Gómez-Pompa & al. 1971).

A genus of  $\pm 20$  species, many poorly understood. All are xerophytic shrubs and not truly succulent, but some are sometimes cultivated in succulent plant collections. Several species, commonly known by the Indian vernacular name “SotoI”, have various uses. Their stems were used for building and for fuel. The leaves are trimmed off and the remaining stump is roasted or boiled. The heads are often baked in pits dug in the ground. The roasted stems are also allowed to ferment to produce an alcoholic beverage. The leaves are much used for thatching, mats, baskets, rough hats etc., and their fibres for rough cordage. Dried and varnished expanded leaf bases, called “Desert Spoons”, are widely used in flower arrangements etc.

Trelease (1911) divided the genus into 2 unranked groups: *Eudasyilirion* and *Quadrangulatae*. Krause (1930) cited “*Dasyilirion* Sek. II *Quadrangulatae* Trelease” with full reference, and this was accepted by Thiede (2012d) as a valid, albeit unintended, new combination. Hochstätter (2011) published an additional sect. *Glaucophyllum* for some species previously placed in sect. *Dasyilirion*. This sectional classification is adopted here:

[1] Sect. *Dasyilirion* (= *Eudasyilirion* Trelease 1911, *nom. inval.* ICN Art. 21.3): **L** 2-edged, usually somewhat concave and irregularly keeled, margins prickly and usually rough with minute intervening denticles. — 9 species.

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- [2] Sect. *Quadrangulatae* (Trelease) Kraus 1930: L 4-sided, unarmed. — 4 species.  
 [3] Sect. *Glaucophyllum* Hochstätter 2011: L waxy-glaucous. — 9 species.

Only selected species of these xerophytes are dealt with here, namely those that have a long history, are of particular interest or are widely distributed. Many species not treated here are either very localised and rare or recently recognised.

The following name is of unresolved application but is referred to this genus:

*Dasylyrion robustum* hort. (s.a.) (*nom. inval.*, Art. 29.1).

**D. acrotrichum** (Schiede) Zuccarini (Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 3: 226, 228, t. 1: Fig. 4, 1840). **Type:** Mexico, Puebla (*Schiede* s.n. [B †?]). — **Distr:** Mexico (Hidalgo, Puebla, Querétaro, San Luis Potosí); dry rocky slopes, in grassland or among shrubs or in oak-pine forest or open oak woodland, sometimes on limestone, 1800–2600 m. **I:** Curtis's Bot. Mag. 84: t. 5030, 1858; McVaugh (1989: 175, Fig. 28); Hochstätter (2011: 115).

≡ *Yucca acrotricha* Schiede (1829); **incl.** *Roulinia gracilis* Brongniart (1840) ≡ *Barbacenia gracilis* (Brongniart) Brongniart (1840) (*nom. inval.*, Art. 34.1c) ≡ *Bonapartea gracilis* (Brongniart) Otto (1841) (*nom. inval.*, Art. 34.1c) ≡ *Yucca gracilis* (Brongniart) Otto (1841) (*nom. illeg.*, Art. 53.1) ≡ *Dasylyrion gracile* (Brongniart) Zuccarini (1845) ≡ *Littaea gracilis* (Brongniart) Verschaffelt (1864).

[1] Stem to 1 m; outer L recurved, linear, green and glossy or somewhat glaucous and dull, 60–100 × 0.9–1.8 cm, tip split into 20–30 spreading fibres, margin distinctly and finely toothed between the prickles, prickles 5–10 (–15) mm apart, to 2 mm long, rather straight, pale yellowish with slightly brown tips; **Inf** paniculate, 3–5 m; **Bra** ovate, entire; **Top** 2–3 mm; **Fr** round-cordate, shallowly notched, wings broadening upwards, 8–9 × 6–7 mm; **Se** 3.5 × 3 mm. — **Cytology:** 2n = 38 (Satô 1942).

McVaugh (1989) argued that the correct spelling of the epithet should be 'acrotriche', since this

is seemingly a bastard word, neither a noun in apposition to the generic name nor a proper Latin adjectival form. In contrast, most authors since Zuccarini transferred this species to *Dasylyrion* from *Yucca*, have used the form 'acrotrichum', and this usage is here followed.

This species is widely distributed in S-C Mexico. Plants are robust, short- to tall-stemmed. Leaves characteristically have a matt or dull surface with coarsely brushy tips (Hochstätter 2011).

**D. glaucophyllum** Hooker (Curtis's Bot. Mag. 84: t. 5041 + text, 1858). **Type:** K. — **Distr:** E-C Mexico (Hidalgo); dry rocky slopes, 1900–3000 m. **I:** Riha & Subik (1981: Fig. 225); Hochstätter (2012: 162–163).

**Incl.** *Bonapartea glauca* hort. (s.a.) (*nom. inval.*, Art. 29.1); **incl.** *Dasylyrion glaucum* Carrière (1872).

[3] Stem short; L linear, acuminate, intensely glaucous, bluish-green, 60–120 × 1.2–1.8 cm, tip entire, marginal prickles 1–2 mm long, horny, deep yellow, margin finely toothed between the prickles; **Inf** densely paniculate, to 1.2 m; **Top** greenish-white, red-tipped, 2 mm; **Fr** subellipsoid, 9–10 × 6 mm; **Se** 4 × 2.5 mm.

This species was described by Hooker (1858) based on a single staminate specimen that flowered at Kew in the unusually warm summer of 1857. Hooker observed that, compared to *D. acrotrichum*, the leaves of his new species were held more erect and rigid, were very glaucous and the tips were not broken into tufts or brushes. This species is the type of the new sect. *Glaucophyllum* Hochstätter. It develops a robust short stem, with characteristic waxy-glaucous leaves. It is apparently very rare, and geographically isolated in E-C Mexico.

**D. graminifolium** (Zuccarini) Zuccarini (Allg. Gartenzeitung 6(33): 259, 1838). **Type:** not typified. — **Distr:** Mexico (San Luis Potosí). **I:** Hochstätter (2011: 106).

≡ *Yucca graminifolia* Zuccarini (1837).

[1] Stem short, <80 cm; L linear, long-acuminate, bright green, smooth, glossy, 90–120 × 1.2–1.4 cm, tip with 6–8 spreading fibres, marginal prickles 5–10 mm apart,

1–2 mm long, horny, yellow or tips slightly darkened; **Inf** paniculate, 2.4–2.7 m; **Tep** 2 mm; **Fr** ellipsoid, 8–9 × 6 mm.

One of the earliest species described, but currently the most poorly known. The description is based on a staminate greenhouse-grown plant. The source of the seed from which the type specimen was grown is not known for certain. Hence Bogler (1994b) treated the name *D. graminifolium* as a confused name. It is, however, accepted by Hochstätter (2011) and Thiede (2012d); according to Hochstätter it occurs very localised in E-C Mexico.

**D. leiophyllum** Engelman *ex* Trelease (Proc. Amer. Philos. Soc. 50(200): 433, ill., t. 12, 1911). **Type:** USA, Texas (*Havard* s.n. [MO, MO]). — **Distr:** USA (Texas, New Mexico), Mexico (Chihuahua, Coahuila); hillsides, in deciduous woodlands, and in grasslands of desert regions, often in limestone soils, 1200–1600 m. **I:** Lamb & Lamb (1974: t. 17); Hochstätter (2011: 109).

**Incl.** *Dasyilirion stewartii* I. M. Johnston (1943).

[1] Stem short, < 80 cm, **Ros** to 1.3 m Ø; **L** linear, smooth, glossy green or somewhat glaucous, 100 × 2.5–3 cm, tip fibrous, marginal prickles 10–15 mm apart, 3–4 mm long, recurved, becoming orange or reddish; **Inf** paniculate, to 3 m; **Tep** greenish, 2 mm; **Fr** broadly ellipsoid, openly and deeply notched at the tip, 6–9 × 2–6 mm; **Se** 3 × 2 mm.

Easily recognised by the downward-curving, retrorse prickles on the leaf margins that distinguishes it from all other species of the genus (Bogler 1994b).

The fire ecology of *D. leiophyllum* is summarised by Tesky (1993: accessed 23. 2. 2015). This species occurs in desert and semi-desert communities subject to naturally occurring fires. Young plants are usually only slightly scorched by fire. In contrast, mature plants with dense sheaths of dead leaves surrounding the trunk are especially susceptible to fire damage. Plants surviving fire regain most of their pre-fire leaf cover within 3 years, but can take up to 15–20 years to accumulate the shaggy bases of dead leaves.

**D. longissimum** Lemaire (Ill. Hort. 3(Misc.): 91, 1856). **Type** [neo]: Mexico, Hidalgo (*Quintero* 3329 [MEXU, ARIZ, CAS, F, GH, MO, NY, RSA, TEX, US]). — **Lit:** Alanis Flores & al. (1994); Bogler (1998b). **Distr:** Mexico (Tamaulipas, San Luis Potosí, Hidalgo, Querétaro); dry rocky hillsides with substrates of caliche, limestone or volcanic ash, or in open thorn-scrub forests, 1500–1900 m. **I:** Curtis's Bot. Mag. 126: t. 7749, 1900; Bogler (1998b: 82, Fig. 10D); Hochstätter (2011: 119). — Figs. 1 and 2.

**Incl.** *Dasyilirion juncifolium* Rehnelt (1906).

[2] Stem solitary, upright or partially reclining, 2 (–4) m; **L** very numerous, spreading in all directions, long and arching, lower ones recurved against the stem, all leaves narrowly linear, green, dull, smooth, rhombic or square in cross-section, upper and lower surfaces raised to low keels, leaf bases spoon-shaped, 10–12 × 4.5–6 cm, lamina 80–140 × 1–1.2 cm at the base, tip entire, margin minutely granular-roughened or smooth; **Inf** paniculate, 3–4 m, elongate; **male FI** on short



**Fig. 1** *Dasyilirion longissimum*. (Copyright: U. Eggli)



**Fig. 2** *Dasyilirion longissimum*. (Copyright: U. Eggli)

pedicels, **Tep** spatulate,  $2.4 \times 2$  mm; **female Fl** on short pedicels, **Tep** denticulate-laciniate,  $1.6\text{--}1.8 \times 1.4$  mm; **Fr** tan-coloured, broadly obovoid or ellipsoid, scarcely notched,  $4\text{--}6 \times 3.5\text{--}5$  mm; **Se** single, trigonous, turbinate, smooth,  $3\text{--}3.5 \times 2.5$  mm. — **Cytology**:  $2n = 38$  (Satô 1942).

*D. longissimum* is very similar to *D. quadrangulatum* in habit, both having tall trunks with dense rosettes of gracefully arching, quadrangulate leaves. They have long been confused, but differ in that the leaves of *D. longissimum* are somewhat flatter and broader than those of *D. quadrangulatum* (Bogler 1998b).

**D. quadrangulatum** S. Watson (Proc. Amer. Acad. Arts 14: 250, 1879). **Type**: Mexico, Tamaulipas (Palmer s.n. [GH, MO]). — **Distr**: Mexico (Tamaulipas, Nuevo León); dry limestone or caliche hillsides and arroyos or open, brushy chaparral vegetation, 1800–2000 m. **I**: Bogler (1998b):

81, Fig. 9, 82, Fig. 10A-B); Hochstätter (2011: 118).

[2] Stem solitary, upright, to 3 m; **L** very numerous, spreading in all directions, long and arching, lower ones recurved against the stem, all leaves narrowly linear, green, dull, smooth, quadrangulate in cross-section, upper and lower surfaces raised to low keels, leaf bases spoon-shaped,  $13\text{--}14 \times 5\text{--}6$  cm, lamina  $80\text{--}90 \times 0.8\text{--}0.9$  cm at the base, tip entire, smooth, margin minutely papillate; **Inf** paniculate, 3–6 m, elongate; **male Fl** on short pedicels, **Tep** obovate,  $2.4 \times 1.5\text{--}2$  mm; **female Fl** on short pedicels, **Tep** oblanceolate, denticulate,  $2\text{--}2.5$  ( $\text{--}3$ )  $\times 1.5$  mm; **Fr** purple-red, broadly ellipsoid-ovoid, scarcely notched,  $4\text{--}6 \times 3.5\text{--}5$  mm; **Se** single, occasionally 2, trigonous, turbinate, smooth,  $2.5 \times 2$  mm.

Vegetatively a very distinctive species since few other dasyilirions become as massive under natural conditions. The trunk is always upright, never reclining on the ground with age as in most other species. Its closest relative is *D. longissimum*, with which it was confused for a long time until resolved by Bogler (1998b).

**D. serratifolium** (Karwinsky ex Schultes fil.) Zuccarini (Allg. Gartenzeitung 6(33): 258, 1838). **Type** [lecto]: Mexico, Oaxaca (Karwinsky s.n. [K]). — **Lit**: Rivera-Lugo & Solano (2012). **Distr**: Mexico (Oaxaca, Veracruz (Acultzingo): endemic to the S part of the Tehuacán-Cuicatlán valley); arid limestone or volcanic ash hillsides and open rocky areas, in xeric shrubby woodlands; 1300–2700 m. **I**: Gómez-Pompa & al. (1971: 216, Fig. 8); Hochstätter (2011: 112).

≡ *Yucca serratifolia* Karwinsky ex Schultes fil. (1830) ≡ *Roulinia serratifolia* (Karwinsky ex Schultes fil.) Brongniart (1840); **incl.** *Dasyilirion laxiflorum* Baker (1872).

[1] Subcaulescent, short or with stem 1–2 m; **L** arching and curving, dull, not waxy, finely roughened on one or both faces with sharp papillae, very scabrous,  $60\text{--}100 \times 1.5\text{--}3$  cm, tip fibrous, marginal prickles hooked, 20–30 mm apart, 1–3 mm long, horny, deep yellow; **Inf**



loosely paniculate; **Tep** 2 mm; **Fr**  $\pm$  globose, broadly winged, tip deeply notched,  $6\text{--}8 \times 6\text{--}8$  mm; **Se**  $4 \times 3$  mm. — **Cytology**:  $2n = 38$  (Gómez-Pompa & al. 1971: 214).

Recognised by its scabrous-papillate, dull leaves with whitish-yellow prickles. The surfaces of the leaves have a rough feel, like fine sandpaper. Close examination reveals the surface to be covered by large, sharp papillae, and although the leaves appear glaucous because of the papillae, they are actually wax-free (Bogler 1994b).

*D. laxiflorum* Baker 1872 (also erroneously attributed to a 1881-publication) is a confused taxon that is sometimes listed as synonym of *Beaucarnea stricta*.

**D. wheeleri** S. Watson (in Rothrock, Rep. US Geogr. Surv. Wheeler, 6: 378, 1878). **Type** [lecto]: USA, Arizona (*Rothrock* 655 [GH, F, NY, US]). — **Lit**: Laferrière (1991). **Distr**: SW USA (Arizona, New Mexico, Texas), Mexico (Sonora, Chihuahua); grassland, open woodlands and shrublands 1000–1800 m. **I**: Gentry (1972: 176, Fig. 69); Folsom & al. (1995: 67); Hochstätter (2012: 166). — Figs. 3 and 4.

**Incl.** *Dasyilirion wheeleri* [?] *wislizeni* Trelease (1911)  $\equiv$  *Dasyilirion wheeleri* var. *wislizeni* (Trelease) Trelease (1912).

[3] Perennial bushy shrubs, 0.5–1.5 m tall, **Ros** in shrubby groups, skirted by persistent dry recurved leaves; **L** numerous, glaucous, nearly smooth,  $60\text{--}100 \times 1.5\text{--}2$  (–2.5) cm, tip attenuate, margin armed with sharp slender straight to antrorse teeth, teeth yellow to brownish, 2–5 mm; **Inf** paniculate, slender, 3–4 m, peduncle extending above the leaves, with numerous short ascending lateral **Br** subtended by broad scarious fimbriate bractlets; **Fr** round-obovate,  $7\text{--}9 \times 6\text{--}7$  mm, remains of style normally about equalling the  $\pm 1$  mm deep apical notch, tips of the wings acute to obtuse, distal wing tips extending  $<1.5$  mm above the base of the style; **Se** brownish, 3.5–4 mm. — **Cytology**:  $2n = 38$  (Satô 1935).

Characterised by its very large habit, waxy glaucous leaves with serrated margins and brushy leaf apices. It is probably the most widely distributed



**Fig. 3** *Dasyilirion wheeleri*. (Copyright: C. C. Walker)

species, ranging from S USA to Sonora and Chihuahua (Hochstätter 2012). This species reaches its E limit in the Franklin Mts. N of El Paso, Texas, where plants are especially large and robust (Bogler 1994b). Laferrière (1991) reports a great deal of phenotypic variation within individual populations of *D. wheeleri*. He recognizes var. *durangense* as distinct, based on a statistical analysis, which shows a consistent difference in fruit notch depth between specimens from the southern part of the range and those from further north. Hochstätter (2012) re-established *D. durangense* Trelease as a distinct but rare species found in a restricted area in Durango and Zacatecas.

*D. wheeleri* is commonly known by the Indian name “Soto!”. Native Americans have many uses for it — after removal of the teeth! — including thatching, mats, baskets. Stems are used for posts in houses and corals. The alcoholic beverage “Soto!” is distilled from the fermented soft meristematic tissue whilst the roots are pit-baked (Hodgson 2001).



**Fig. 4** *Dasylyrion wheeleri*. (Copyright: C. C. Walker)



## References

- Alanis Flores, G. J. [& al. 1994], Rocha Domínguez, L. & Marroquín de la Fuente, J. S. (1994) Datos fenológicos de *Dasylyrion longissimum* en un jardín botánico. *Cact. Suc. Mex.* 39(2): 43–47, ill.
- Bogler, D. J. (1994a) Systematics of *Dasylyrion* (*Nolinaceae*). *Amer. J. Bot.* 81(6: Suppl.): 142 [abstract 399]. <https://www.jstor.org/stable/2445447>
- Bogler, D. J. (1994b) Taxonomy and phylogeny of *Dasylyrion* (*Nolinaceae*). Austin (US): University of Texas, unpublished Ph.D. thesis.
- Bogler, D. J. (1995) Systematics of *Dasylyrion*. Taxonomy and molecular phylogeny. *Bol. Soc. Bot. México* 56: 69–76.
- Bogler, D. J. (1998b) Three new species of *Dasylyrion* (*Nolinaceae*) from Mexico and a clarification of the *D. longissimum* complex. *Brittonia* 50(1): 71–86, ills. <https://doi.org/10.2307/2807720>
- Folsom, D. B. [& al. 1995], Trager, J. N., Folsom, J., Clements, J. & Scott, N. (1995) Dry climate gardening with succulents. New York (US): Pantheon Books, Knopf Publishing Group.
- Gentry, H. S. (1972) The *Agave* family in Sonora. Agricultural handbook No. 399. Washington D.C. (US): US Department of Agriculture. <https://naldc.nal.usda.gov/download/CAT87209091/PDF>
- Gómez-Pompa, A. [& al. 1971], Villalobos-Pietrini, R. & Chimal, A. (1971) Studies in the *Agavaceae* I. Chromosome morphology and number of seven species. *Madroño* 21(4): 208–221, ills. <https://www.jstor.org/stable/41423783>
- Hochstätter, F. (2011) *Dasylyrion* Zucc. (*Nolinaceae*). Revisión del género [parte 1] / le specie [parte 2]. *Piante Grasse* 31(1): 25–30, (3): 106–122, ills., key.
- Hochstätter, F. (2012) *Dasylyrion*: le specie / the species. Parte / Part 3. Sezione / section *Glaucophyllum* Hochstätter. *Piante Grasse* 31(4): 162–181, ills., map.
- Hodgson, W. C. (2001) Food plants of the Sonoran Desert. Tucson (US): University of Arizona Press.
- Hooker, W. J. (1858) *Dasylyrium glaucophyllum*. *Curtis's Bot. Mag.* 84: t. 5041 + text. <https://www.biodiversitylibrary.org/item/14224#page/56>
- Krause, K. (1930) *Liliaceae*. In: Engler, A. & Prantl, K. (eds.): *Die natürlichen Pflanzenfamilien*, ed. 2, 15a: 227–385, key, ills. Leipzig (DE): W. Engelmann.
- Laferrière, J. E. (1991) *Dasylyrion wheeleri* var. *durangense*: A new combination in the *Nolinaceae*. *Ann. Missouri Bot. Gard.* 78: 516–520, ills., map. <https://www.biodiversitylibrary.org/item/89022#page/522>
- Lamb, E. & Lamb, B. (1974) Colourful cacti and other succulents of the desert. London (GB): Blandford Press.
- McVaugh, R. (1989) Flora Novo-Galiciana. A descriptive account of the vascular plants of Western Mexico. Vol. 15: *Bromeliaceae* to *Dioscoreaceae*. Ann Arbor (US): University of Michigan Herbarium.
- Riha, J. & Subik, R. (1981) Illustrated encyclopedia of cacti and other succulents. London (GB): Octopus Books.
- Rivera-Lugo, M. & Solano, E. (2012) Flora del Valle de Tehuacán-Cuicatlan. Fascículo 99. *Nolinaceae* Nakai. México D.F. (MX): Instituto de Biología UNAM.
- Satô, D. (1935) Analysis of the karyotypes in *Yucca*, *Agave* and the related genera with special reference to the phylogenetic significance. *Jap. J. Genet.* 1: 272–278.
- Satô, D. (1942) Karyotype alteration and phylogeny in *Liliaceae* and allied families. *Jap. J. Bot.* 12: 57–161.
- Testy, J. L. (1993) *Dasylyrion leiophyllum*. In: Fire Effects Information System. Washington D.C. (US): US

- Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Services Laboratory. <https://www.fs.fed.us/database/feis/>
- Thiede, J. (2012d) Nomenclatural status of unranked names published by Trelease (1911) in *Beaucarnea*, *Dasyllirion*, and *Nolina* (*Asparagaceae* — *Nolinoideae*). *Phytoneuron* 2012(77): 1–4. <http://phytoneuron.net/77PhytoN-Beaucarnea.pdf?>
- Trelease, W. (1911) The desert group *Nolineae*. *Proc. Amer. Philos. Soc.* 50(200): 404–443, tt. 1–17. <https://www.jstor.org/stable/983932>





## Dracaena RUSCACEAE

C. C. Walker

**Dracaena** Vandelli *ex* Linné (Syst. Nat., ed. 12, 2: 246, 1767). **Type:** *Asparagus draco* Linné. — **Dracaenoideae** — **Lit:** Marrero & al. (1998: systematics Canary Islands); Walker (1999: introduction); Lu & Morden (2014: molecular phylogeny); Lebrun & Stork (2014: 213–227, synopsis tropical Africa). **Distr:** Predominantly tropical Africa, Macaronesia, S Arabia, Socotra, Madagascar, SE Asia, 2 spp. in C America and Cuba. **Etym:** Lat. ‘draco, draconis’, female dragon (from Gr. ‘drakon’, dragon); from the vernacular name of *D. draco*, “Dragon’s Blood Tree”, which is based on the red exudate of the bruised stems.

**Incl.** *Pleomele* Salisbury (1796). **Type:** *Aletris fragrans* Linné [lectotype, selected by N. E. Brown, Kew Bull. 1914(8): 274, 1914].

**Incl.** *Nemampsis* Rafinesque (1838). **Type:** *Nemampsis ternifolia* Rafinesque [*nom. illeg.*, = *Dracaena surculosa* Lindley, fide ING].

Woody shrubs or trees, sometimes with massive trunks; bark smooth, often with prominent leaf scars; **R** usually bright orange; **L** usually spirally arranged, often in dense **Ros** at branch tips, tough and fibrous to coriaceous, smooth, often variegated, sessile or petiolate, ensiform or oblong, entire; **Inf**

terminal, racemose, often paniculate; **Ped** articulated at the middle; **Fl** 1 to few in fascicles, nocturnal and usually highly fragrant; **Per** to 5 cm long, white or greenish with purple tinges, basally tubular with 6 free lobes; **St** 6, inserted at the throat of the perianth tube; **Ov** superior, ovoid, sessile, 3-locular; **Sti** capitate; **Fr** globose, baccate, fleshy; **Se** 1–3, testa thick, sometimes pulpy.

A genus of  $\pm 80$  species, but apparently with hundreds of redundant synonyms. According to Bos (1984) and Bos (1998), *Dracaena* is close to and probably not separable from *Sansevieria*; this proposal was confirmed by Lu & Morden (2014). Several species are extremely widely cultivated as houseplants, particularly attractive as variegated cultivars. The genus is of minor interest to succulent plant growers since small plants of the few xerophytic species are relatively uninspiring and slow-growing, in contrast to the impressive bulky specimens of mature trees. Only a few species with pachycaul stems are covered here, and of these, only *D. draco* is frequently cultivated. *D. draco* and *D. cinnabari* are the “Dragon’s Blood Trees”, the dried red resinous sap (used in varnishes etc.) of which was of economic importance and at one time Socotra’s major export item.

The small group of dragon tree species, consisting of *D. draco* and its allies, has an interesting disjunct distribution in Macaronesia, NE Africa and Arabia (see Walker (1999: Fig. 2)). The recently described 16 million-year-old fossil, *D. tayfunii*, has characters in common with modern-day dragon trees: terminal leaf rosettes,

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ensiform leaves with conspicuously dilated bases, and strongly papillate leaf epidermis with sunken stomata. This fossil originated from Miocene deposits in W Anatolia, from which it was postulated that modern-day dragon trees with xeromorphic features may have originated from a W Eurasian mesic lineage (Denk & al. 2014).

Jankalski (2008) divided the genus into three subgenera:

- [1] Subgen. *Dracaena*: **Fl** stellate with a very short tube to 2 mm; **Inf** an erect panicle; **Fil** thickened near the middle. ±14 spp. but not all considered succulent. In the phylogenetic tree of Lu & Morden (2014), the dragon tree species are not clustered into a single clade, suggesting the relationship is not as close as previously indicated.
- [2] Subgen. *Pleomele* (Salisbury) Jankalski 2008 (≡ *Pleomele* Salisbury 1796): **Fl** salverform with a slender tube, white or greenish, often purple tinged; **Inf** an erect to pendent bracteate panicle or thyrses; **Fil** terete. Over 60 spp. (only 1 treated here with borderline succulence).
- [3] Subgen. *Chrysodracon* Jankalski 2008: **Fl** tubular-funneliform with a broad tube, yellow; **Inf** a pendent foliaceous panicle; **Fil** flattened, subulate. About 7 spp. (none treated here). Lu & Morden (2014) elevated this group to generic status as *Chrysodracon* (Jankalski) P.-L. Lu & Morden.

**D. aletriformis** (Haworth) Bos (in Leistner & al. (ed.), Fl. South Afr. 5(3): 3, 1992). **Type** [neo]: RSA, Eastern Cape (*Drège* 4494a [K, G, MO, P]). — **Lit**: Bos (1992: 3). **Distr**: RSA (Eastern Cape, KwaZulu Natal, Mpumalanga, Limpopo), Swaziland, Moçambique, Kenya, Tanzania; coastal bush to montane evergreen to semi-deciduous forests. **I**: Wyk & Wyk (1997: 55); Jaarsveld (2016).

≡ *Yucca aletriformis* Haworth (1831); **incl.** *Cordyline rumphii* Hooker (1847) (*nom. illeg.*, Art. 52.1); **incl.** *Dracaena hookeriana* K. Koch (1861) ≡ *Draco hookeriana* (K. Koch) Kuntze (1891) ≡ *Pleomele hookeriana* (K. Koch) N. E. Brown (1914); **incl.** *Dracaena latifolia* Regel (1871); **incl.** *Dracaena rumphii* Regel (1871); **incl.** *Sansevieria*

*paniculata* Schinz (1894) (*nom. inval.*, Art. 34.1b?); **incl.** *Dracaena transvaalensis* Baker (1904).

[2] Small tree, not always branched, to 5 m; **L** in terminal **Ros**, narrow to broadly strap-shaped, with a short flaring sheath, 50–100 × 2.5–11 cm, bright to greyish-green, margins white, cartilaginous; **Inf** erect, to >1 m; **Fl** in groups of 1–4, greenish-white, 25–35 (–42) mm; **Ped** 5–10 mm; **Tep** ± 1.5× as long as the tube; **Fr** globose, usually 1-seeded, lobed when 2- or 3-seeded, 7–19 mm Ø, red or orange.

Widely distributed in S Africa, but of limited interest here in terms of its borderline succulence. Wyk & Wyk (1997) and Jaarsveld (2016) argue that *D. transvaalensis* should be accepted as separate species, being confined to exposed arid places in the Limpopo and Mpumalanga provinces, differing from *D. aletriformis* s.s. by greyish stiff leaves and papillate fruits.

**D. cinnabari** Balfour *fil.* (Trans. Roy. Soc. Edinburgh 30: 623, 1882). **Type**: not typified. — **Lit**: Beyhl (1995b); Miller & Morris (2004: 51, 235); both with ill.; Brown & Mies (2012: conservation). **Distr**: Yemen (Socotra); endemic. **I**: Walker (1999: 171, Fig. 1). – Fig. 1.

[1] Trees with stout trunks to 10 m, dichotomously branched with regular semiglobose dense crown; **L** 30–60 × 2–3 cm, erect, rigid, ensiform with broadened base, sessile, dark green; **Inf** paniculate, well-branched; **Fl** in groups of 2–4; **Ped** 5 mm; **Per** to 5 mm long, cup-shaped, cream; **St** slightly shorter than the perianth; **Sty** filiform; **Sti** capitate; **Fr** globose, fleshy, 10–15 mm Ø, ripening red to black.

This species belongs to an informally recognized group within the genus, the “dragon trees”. They are all thick-stemmed trees with dichotomous branching. Leaves are crowded into dense rosettes at the branch tips. *D. draco* differs from *D. cinnabari* in its compressed ensiform leaves, smaller bracteoles, greenish perianth segments, and shorter anthers. *D. ombet* and *D. serrulata* have a less robust habit, more slender panicle branches, and longer pedicels. However, the assumed close relationship is not confirmed by Lu & Morden (2014), who showed that only *D. draco*, *D. ellenbeckiana* and





**Fig. 1** *Dracaena cinnabari*. (Copyright: A. Miller)

*D. serrulata* are in a common clade, together with several shrubby taxa.

*D. cinnabari* is the most famous and distinctive plant on Socotra, where it has a widespread but fragmented distribution, forming dense forests on the high plateaux, notably the Haggeher mountains. Its distribution pattern closely matches areas receiving frequent low cloud, rain and drizzle during the monsoon (Miller & Morris 2004). Studies of population age structure and plant growth estimates indicate that the species is not regenerating to any significant extent — referred to as “population overmaturity” (Adolt & Pavlis 2004; Habrova & al. 2009; Adolt & al. 2012). This has led to an extrapolation of a 45% loss of populations by 2080 (Attorre & al. 2007). Consequently the species can be considered to be severely endangered.

It has an extensive range of uses: food for humans and livestock, timber, fibre, etc. Commercially it is the famed dragon’s blood resin for which the plant is renowned with uses as a dye, in medicines and cosmetics. The specific name meaning

cinnabar red refers to the colour of the stem exudate: scarlet with a slight hint of orange. Outside of Socotra this species is rarely cultivated, in contrast to *D. draco*.

***D. draco*** (Linné) Linné (Syst. Nat., ed. 12, 2: 246, 1767). **Type:** [lecto — icono:] Clusius, Rar. Pl. Hist. 1: 1, “Draco”, 1601. — **Distr:** Canary Islands, Madeira, Cape Verde Islands, Morocco.

≡ *Asparagus draco* Linné (1762); **incl.** *Yucca draco* Carrière (1859).

***D. draco* ssp. *ajgal*** Benabid & Cuzin (Compt. Rend. Acad. Sci. Paris, Sér. 3, Sci. Vie 320: 270, 1997). **Type:** Morocco (Benabid & Cuzin s.n. [RAB]). — **Distr:** Morocco (W Anti-Atlas); mixed open woodland, quartzite cliffs in gorges. **I:** Plant Talk 12: 18, 1998; Audissou (1999); Bensusan & al. (2015).

[1] Differs from ssp. *draco*: **L** smaller, 60 × 3 cm; **Ped** of **Fl** shorter, 1–4 mm; **Per** yellowish-white, tube campanulate, shorter, 1–2 mm; **Tep** shorter, 7–8 mm; **Anth** yellow.

This taxon was only discovered in 1996 as a population consisting of thousands of trees on quartzite cliffs in inaccessible gorges in the W part of the Anti-Atlas mountains in Morocco E of Tiznit. This discovery is highly significant, in view of the severely endangered status of ssp. *draco* in the Canary Islands.

***D. draco* ssp. *caboverdeana*** Marrero Rodriguez & R. S. Almeida (Int. J. Geobot. Res. 2: 36, ill. (pp. 39–40), 2012). **Type:** Cape Verde Islands, Santo Antão (Marrero & al. s.n. [LPA, LPA]). — **Distr:** Cape Verde Islands (Santo Antão, São Nicolau, Fogo); sclerophyllous forests, windward slopes of the islands, 50–1400 m.

[1] Differs from ssp. *draco*: Stem with low aspect and short trunk, 4–6 m, crown dense; **L** shorter and narrower, 67.4 ± 14.6 × 3.6 ± 0.48 cm, blue-glaucous, lamina flat to slightly canaliculate, hardly flexible; **Fr** larger, 14.94 ± 0.62 mm Ø.

This taxon was recognised as distinct following a study of qualitative and quantitative characters of a sampling of plants in the 3 main areas of distribution of *D. draco*: Canary Islands/Madeira, Anti-Atlas Mts. of Morocco, and the Cape Verde

**Fig. 2** *Dracaena draco*  
ssp. *draco*. (Copyright:  
C. C. Walker)



Islands. Key features of ssp. *caboverdeana* are the shape of the plant, with a short trunk but densely branched canopy, esp. the colour and size of the leaves, and the size of the fruit. This leaves ssp. *draco* restricted to the Canary Islands and Madeira.

**D. draco** ssp. *draco* — **Lit:** Beyhl (1995a); Lodé (2010b); both with ill. **Distr:** Canary Islands (Tenerife, Gran Canaria, La Palma), Madeira. **I:** Bramwell & Bramwell (2001: 395); Leroy (2004); Lodé (2010b: 191, 193, 195). – Fig. 2.

[1] Trees to  $\pm 20$  m tall; trunk silvery-grey, smooth; **Br** dichotomously branched forming a semiglobose crown; **L** linear-lanceolate, sessile, glaucous, coriaceous, to 110 cm  $\times$  4 cm, in dense terminal **Ros**; **Inf** paniculate; **Fl** in groups of 4–5; **Ped** 5–10 mm; **Per** white, pink, crimson to greenish-white, tube campanulate, 1.5–4 mm; **Top** 7–11 mm; **Anth** greenish; **Fr** globose berries, to  $13.59 \pm 0.85$  mm  $\varnothing$ , red-orange.

See *D. cinnabari* for relationships. This is the “Dragon Tree” of the Canary Islands, critically endangered in the wild. Almeida Pérez (2003a) confirms the existence of both *D. draco* and *D. tamaranae* on Gran Canaria, where *D. draco* is confined to canyons in the NE, with specimens estimated to be 210–220 years old. A healthy

population still remains in the Barranca del Infierno, Tenerife (Lodé 2010a). *D. draco* is now extensively cultivated in gardens in frost-free climates, but is slow growing as a pot plant. Leroy (2004) provides advice on cultivation, notably on raising the plant from seed. Mature specimens are presumed to be of great age and a famous specimen at Orotava on Tenerife, blown down by a storm in 1868, was 21 m tall and 15 m  $\varnothing$  at the base of the trunk, and was estimated to be 6,000 years old. Mägdefrau (1975) has shown, however, that an age of a few hundred years is much more reasonable. Krawczynszyn & Krawczynszyn (2016) investigated the effect of sunlight on photomorphogenesis in *D. draco* and concluded that this is a key environmental factor in growth, flowering and shaping of these trees with unidirectional light producing deformed trees.

Marrero (2013) reports a fossil with an estimated age of 3–3.9 million years from Gran Canaria.

**D. ellenbeckiana** Engler (Bot. Jahrb. Syst. 32: 95, 1903). **Type:** Ethiopia, Harar Prov. (*Ellenbeck* 1232 [B]). — **Distr:** E Ethiopia, Kenya, N Uganda; semi-evergreen bushland or open dry forest on rocky slopes, 1050–2100 m. **I:** Bally (1967: Figs. 1–2); Mwachala & Mbugua (2007: 5); Sebsebe Demissew & Nordal (2010: 277–278).

**Incl.** *Dracaena ellenbeckii* hort. (s.a.) (*nom. inval.*, Art. 61.1).

[1] Large shrubs 3–6 m tall, dichotomously branching to form many-stemmed clumps; **Br** 4–8 cm Ø; **L** 35–55 × 1–2.2 cm, often restricted to the branch tips, ensiform, coriaceous, glabrous, entire, base amplexicaul, sessile; **Inf** paniculate; **Fl** 2–7 together in cymose groups; **Ped** 3–5 mm; **Per** to 10 mm, **Tep** linear-oblong, 10 × 1.8–2 mm; **St** slightly shorter than the perianth; **Ov** longitudinally ribbed; **Sty** cylindrical, 3 × 0.5 mm; **Sti** capitate; **Fr** subglobose, 4–10 × 4–10 mm, turning from green over red to dark purple; **Se** globose, 4–5 mm Ø, ivory-white.

Best described as a woody xerophyte rather than a succulent. Vernacular name: “Ol Kedong”. The Kedong Valley in Kenya is named after this locally abundant *Dracaena*. Used by the Masai for arrow quivers.

**D. jayniana** Wilkin & Suksathan (Kew Bull. 67 (4): 698–703, ills., 2012). **Type:** Thailand, Korat Prov. (*Kerr* 9989 [K, BM, C, L, P]). — **Distr:** C & NE Thailand; hilltops of limestone karsts, in seasonally deciduous vegetation.

[1] Trees to 5 (–8) m tall, stems to 10 cm Ø at the base, bark pale brown to grey-brown; **Br** basal with 3–5 erect stems; **L** in dense terminal clusters, coriaceous, sheath elliptic to ovate to 6 × 4 cm, lamina linear-acuminate, dark green, 40–75 × 0.5–1.3 cm, all but the youngest leaves curved near the base, apex pendent; **Inf** erect to ascending, paniculate, fertile axis to 50 cm long with 4 orders of branching; **Fl** in groups of up to 5; **Ped** 1.9–4.6 mm; bracteoles to 2 mm; **Per** dull golden-yellow, membranous and translucent towards the margins, central vein darker; **Tep** fused at the base to form a very short tube, narrowly ovate to oblong, free part 5.6–6 × 1.5–2.1 mm, **ITep** slightly broader than the **OTep**; **St** basally fused to the tepals; **Anth** pale yellow, to 1.2 × 0.4 mm; **Ov** fusiform-cylindrical, 3.4–3.6 × 1.3–1.5 mm; **Sty** cylindrical, to 2.4 × 0.7 mm; **Sti** capitate, trilobulate; **Fr** (sub-) globose berries, dull red when ripe, to 12.7 mm Ø; **Se** subglobose, to 8.5 × 7.5 mm.

Morphologically this new species is related to the traditional dragon tree group of *D. draco* and its

allies, although it is not truly xeromorphic. In Lu & Morden (2014) this was included as *Dracaena* sp. 1. Geographically, it is remote from *D. draco* and other arborescent taxa, being endemic to C and NE Thailand where it is known as “Chan daeng”. It occurs in association with *Pandanus*, succulent spiny *Euphorbia* and *Cycas* spp. A preliminary assessment of its conservation status is as endangered. A tonic drink is made from the dried red sap and it is used in horticulture in Thailand (Wilkin & al. 2012).

**D. ombet** Kotschy & Peyritsch (Pl. Tinn., 47, 1867). **Type:** [lecto — icono]: l.c., frontispiece. — **Lit:** Bos & Teketay (1997); Sebsebe Demissew & Nordal (2010). **Distr:** SE Egypt, Sudan, Eritrea, Ethiopia, Djibouti, Somalia.

≡ *Draco ombet* (Kotschy & Peyritsch) Kuntze (1891).

**D. ombet** ssp. **ombet** — **Distr:** SE Egypt, Sudan, Eritrea, N Ethiopia, Djibouti, Somalia; bushland and woodland, usually on limestone, 1000–1800 m. **I:** Sebsebe Demissew & Nordal (2010: 281, Fig. 123).

[1] Trees to 4 m; **Br** thick, dichotomously branched, forming a semiglobose crown; **L** crowded, to 60 × 3 cm, often restricted to the branch tips, rigid, glabrous throughout, ensiform, succulent and to 1 cm thick, margins smooth, entire, tip acute, lamina widened abruptly to a clasping amplexicaul base ±2× as wide as long; **Inf** paniculate, much branched, glabrous, to 0.5 m; **Fl** 2–7 together in cymose groups; **Ped** glabrous or pubescent, 2–4 mm; **Per** to 10 mm; **Tep** linear-oblong, almost free, whitish, to 10 × 2 mm; **St** somewhat shorter than the perianth; **Fil** flattened; **Ov** oblong, shortly stipitate; **Sty** cylindrical; **Sti** capitate; **Fr** subglobose berries, 10–12 mm Ø; **Se** globose, 6 mm Ø.

Differs from the rest of the species in the genus in having succulent leaves. In Ethiopia and Eritrea this subspecies grows in open *Olea europaea* forest on limestone, and in semi-desert grassland with scattered *Acacia* scrub (Sebsebe Demissew & Nordal 2010).

**D. ombet** ssp. **schizantha** (Baker) Bos (SINET Ethiopian J. Bot. 1997: 20, 1997). **Type:** Somalia



(Hildebrandt 1472 [K, B?, BM, HBG, K, WAG]). — **Distr:** Djibouti, S & SE Ethiopia, Somalia. **I:** Thulin (1995: t. 1E, as *D. ombet*); Bos & Teketay (1997: 78, Fig. 187.6).

≡ *Dracaena schizantha* Baker (1877); **incl.** *Dracaena rhabdophylla* Chiovenda (1952).

[1] Differs from ssp. *ombet*: Trees to 8 m; **L** margins scabrid, lamina widened abruptly to a clasping amplexicaul base  $\pm 3\text{--}4\times$  as wide as long; terminal branches of the **Inf** pubescent.

In Ethiopia this subspecies grows on mountain slopes, in *Acacia*–*Commiphora* bushland on limestone, and also in evergreen bushland (Sebsebe Demissew & Nordal 2010). The red resin is used in traditional medicine (Bos & Teketay 1997).

**D. serrulata** Baker (Bull. Misc. Inform. Kew 1894: 342, 1894). **Type:** Yemen (Lunt 206 [K]). — **Distr:** Saudi Arabia, Yemen, Oman.

**D. serrulata** ssp. *dhofarica* T. A. McCoy & Lavranos (Avonia 35(1): 58–60, ills. (pp. 54, 56–60), 2017). **Type:** Oman, Dhofar (McCoy 4897 [FT]). — **Distr:** Oman (Dhofar). **I:** Miller & Morris (1988: 17, as *D. serrulata*). – Fig. 3.

[1] Differs from ssp. *serrulata*: **L** dark green, margins entire with hyaline edge; **Tep** light pink.

The Dhofar population of *D. serrulata* is separated from the nearest known representatives of ssp. *serrulata* by  $\pm 500$  km (McCoy & Lavranos 2017). In Oman this unusual and distinctive tree is

restricted to the highest dry plateaux. It appears to be under extreme pressure with little regeneration because of overgrazing, esp. by camels and leaf harvesting for fibres. McCoy & Lavranos report that only plants on steep cliffs retain their normal growth habit, and that flowering is very irregular in the wild. Resin production was not traditionally important, but fibres extracted from the leaves are used for rope making (Miller & Morris 1988).

**D. serrulata** ssp. *mccoyorum* Lavranos (Cact. Succ. J. (US) 89(4): 149–151, ills., 2017). **Type:** Saudi Arabia, Asir Prov. (McCoy 5112 [FT]). — **Distr:** Saudi Arabia (Asir); rocky mountain.

[1] Differs from ssp. *serrulata*: Large many-branched umbrella-shaped tree 7–8 m; **L** very light grey, margins entire with hyaline edge; **Tep** tan/beige.

The sole, northerly population of ssp. *mccoyorum* is separated from the nearest known population of ssp. *serrulata* by about 250 km (Lavranos 2017). Endemic to Saudi Arabia where it occurs near the summit of a single mountain with unusual geology (tonalite). During 30 years of observation this population has declined significantly and only a few mature specimens remain, leading to the imminent danger of extinction. Threats recorded are mostly due to human activities: overgrazing, removal of terminal leaves for fodder and removal of larger branches for hollowing out to make bee hives.

**Fig. 3** *Dracaena serrulata* ssp. *dhofarica*. (Copyright: B. Jonkers)



**D. serrulata** ssp. **serrulata** — **Lit:** Beyhl (1999: with ills.). **Distr:** Saudi Arabia, Yemen. **I:** Collenette (2000: 33, 36–37).

[1] Trees to 5 m (but mostly smaller) with a single stem, branched above but without well-defined semiglobose crown; **L** to 50–100 × 2–5 cm, glaucous-grey, linear-lanceolate, flat in section above, convex beneath, margins serrulate, tip acute; **Inf** large erect branched panicles, to 1.5 m; **Per** 4 mm long, tube cylindrical; **Tep** fused at the base, narrow, spreading, white; **Sty** filiform; **Sti** capitate; **Ov** ovoid, 3-celled, with a solitary basal ovule in each; **Fr** fleshy, globose, ±6 mm Ø, 1- to 3-seeded.

Similar to *D. cinnabari* (see there for details). It was first described from specimens collected in the Wadi Hadramawt, Yemen. It occurs W-wards, extending N along the Great Arabian Escarpment of Saudi Arabia. Plants tend to be sparingly branched with rather thin, linear, glaucous-grey leaves with the distinctive, finely toothed leaf margins for which it was named. Collenette (2000) states that plants in Saudi Arabia appear to be very slow growing and that the trees are frequently felled as the hollow trunks make excellent bee hives.

**D. tamaranae** A. Marrero & al. (Bot. J. Linn. Soc. 128: 294–297, ills., 1998). **Type:** Canary Islands, Gran Canaria (Marrero & al. 18525 [MA, K, LPA, TFC]). — **Lit:** Marrero (2000); Lodé (2010a: 191, 197, with ills.). **Distr:** Canary Islands (SW Gran Canaria); slopes and cliffs, 300–1300 m. **I:** Bramwell & Bramwell (2001: 395).

[1] Trees 6–10 m tall, bark yellow-grey, slightly glossy; **Br** trichotomous; **L** subulate, canaliculate, rather falcate, glaucous, basally swollen with a sub-amplexicaul pseudosheath, lamina 40–80 (–110) × 3–4.5 cm, margins hyaline-white, entire; **Inf** paniculate, 80–100 cm long; **Fl** in groups of 2–5; **Ped** 2.25–3.25 mm; bracteoles minute; **Per** bright greenish-white, 9.5–11 mm; **Tep** oblong-linear, **ITep** narrower than **OTep**, joined at the base to form a very short tube; **St** shorter than the tepals; **Anth** yellow-greenish, 2 mm; **Ov** trilobular, 3.6 × 2.4 mm; **Sty** filiform, 5.8 mm; **Sti** capitate, trilobulate; **Fr** globose berries, greenish, glaucous, orange when ripe; **Se** globose to broadly ovoid, 6–7 mm.

*D. tamaranae* seems closely related to the species from the Horn of Africa and Arabia *D. ombet* and

*D. serrulata*. All these species have glaucous leaves, minute bracteoles and are not densely branched. In contrast to *D. tamaranae*, *D. draco* and *D. cinnabari* have flat, non-glaucous, ensiform leaves and complex inflorescences with several orders of branching.

*D. tamaranae* is extremely rare. It grows in crevices of inaccessible cliffs and canyons in the arid S and SW of Gran Canaria. The census of Almeida Pérez (2003b) indicates a total of <100 individuals: 63 juveniles, 12 adults and 1 very mature specimen; 10 dead specimens were also observed, but no seedlings. This confirms the earlier assessment and status as a critically endangered species (Marrero & al. 1998).

## References

- Adolt, R. & Pavlis, J. (2004) Age structure and growth of *Dracaena cinnabari* populations on Socotra. *Trees* (Berlin) 18: 43–53, ills. <https://doi.org/10.1007/s00468-003-0279-6>
- Adolt, R. [ & al. 2012], Habrova, H. & Madera, P. (2012) Crown age estimation of a monocotyledonous tree species *Dracaena cinnabari* using logistic regression. *Trees* (Berlin) 26: 1287–1298, ills. <https://doi.org/10.1007/s00468-012-0704-9>
- Almeida Pérez, R. S. (2003a) Sobre la presencia de *Dracaena draco* (L.) L. en Gran Canaria (Islas Canarias): Aportación corológica, estado actual y significación biogeográfica. *Bot. Macaronés.* 24: 17–38, map, ills.
- Almeida Pérez, R. S. (2003b) Censo, distribución, hábitat y estado de conservación de *Dracaena tamaranae* A. Marrero, R. S. Almeida & M. González-Martín, Gran Canaria, Islas Canarias. *Bot. Macaronés.* 24: 39–56, maps, ills.
- Attorre, F. [ & al. 2007], Francesconi, F., Taleb, N., Scholte, P., Saed, A., Alfo, M. & Bruno, F. (2007) Will Dragonblood survive the next period of climate change? Current and future potential distribution of *Dracaena cinnabari* (Socotra, Yemen). *Biol. Conservation* 138: 430–439, ills., maps. <https://doi.org/10.1016/j.biocon.2007.05.009>
- Audissou, J.-A. (1999) The Dragon Tree in Morocco. *Dracaena draco* ssp. *ajgal* Benabid & Cuzin. *Cact.-Avent.* 41: 23–25, ills.
- Bally, P. R. O. (1967) Miscellaneous notes on the flora of Tropical East Africa, including description of new taxa, 35–37. *Candollea* 22(2): 255–263, ills., maps.
- Bensusan, K. [ & al. 2015], Gdaniec, A., Guillem, R. & Taheri, A. (2015) Chasing Atlas dragons. *Cact. Succ. J. (US)* 87(3): 136–144, ills., map. <https://doi.org/10.2985/015.087.0307>
- Beyhl, F. (1995a) Der Drachenbaum und seine Verwandtschaft. I. Der Kanarische Drachenbaum, *Dracaena draco* L. *Palmengarten* 59(1): 70–74, ills.



- Beyhl, F. (1995b) Der Drachenbaum und seine Verwandtschaft: II. Der Echte Drachenbaum, *Dracaena cinnabari*, von der Insel Sokotra. *Palmengarten* 59(2): 140–145, ills.
- Beyhl, F. E. (1999) Der Südarabische Drachenbaum (*Dracaena serrulata* Baker). *Palmengarten* 63(1): 28–31, ills.
- Bos, J. J. (1984) *Dracaena* in West Africa. *Agric. Univ. Wageningen Pap.* 84-1: 126 pp., ills., maps, key. <http://edepot.wur.nl/283694>
- Bos, J. J. (1992) *Dracaena*. In: Leistner, O. A. (ed.): *Flora of Southern Africa*, 5(3): 1–4. Pretoria (ZA): National Botanical Institute.
- Bos, J. J. (1998) *Dracaenaceae*. In: Kubitzki, K. (ed.): *The families and genera of vascular plants*; 3: 238–241, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_30](https://doi.org/10.1007/978-3-662-03533-7_30)
- Bos, J. J. & Teketay, D. (1997) *Dracaenaceae*. In: Edwards, S. & al. (eds.): *Flora of Ethiopia and Eritrea*, 6: 76–82, ills., keys. Addis Ababa (ET): University of Addis Ababa / Uppsala (SE): Uppsala University.
- Bramwell, B. & Bramwell, Z. (2001) *Wild flowers of the Canary Islands*. Madrid (ES): Editorial Rueda.
- Brown, G. & Mies, B. A. (2012) *Vegetation ecology of Socotra*. Dordrecht (NL): Springer Netherlands. <https://doi.org/10.1007/978-94-007-4141-6>
- Collenette, S. (2000) *Dracaena* in Saudi Arabia. *Brit. Cact. Succ. J.* 18(1): 33–37, ills., map.
- Denk, T. [et al. 2014], Tuncay Güner, H. & Grimm, G. W. (2014) From mesic to arid: Leaf epidermal features suggest preadaptation in Miocene dragon trees (*Dracaena*). *Rev. Palaeobot. Palynol.* 200: 211–228, ills. <https://doi.org/10.1016/j.revpalbo.2013.09.009>
- Habrova, H. [et al. 2009], Cermak, Z. & Paulis, J. (2009) Dragon's Blood Tree — Threatened by overmaturity, not by extinction: Dynamics of a *Dracaena cinnabari* woodland in the mountains of Soqotra. *Biol. Conservation* 142(4): 772–778. <https://doi.org/10.1016/j.biocon.2008.12.022>
- Jaarsveld, E. J. van (2016) *Dracaena transvaalensis* Bak. (*Dracaenaceae*), the dragon tree of the Limpopo Province, South Africa. *Bradleya* 34: 230–236, ills. <https://doi.org/10.25223/brad.n34.2016.a11>
- Jankalski, S. (2008) Subgenera and new combinations in *Dracaena*. *Sansevieria* 18: 17–21, ills.
- Krawczynszyn, J. & Krawczynszyn, T. (2016) Photomorphogenesis in *Dracaena draco*. *Trees* (Berlin) 30: 647–664, ills. <https://doi.org/10.1007/s00468-015-1307-z>
- Lavranos, J. J. (2017) A new, arborescent subspecies of *Dracaena* from Saudi Arabia. *Cact. Succ. J. (US)* 89(4): 148–152, ills., map. <https://doi.org/10.2985/015.089.0402>
- Lebrun, J.-P. & Stork, A. L. (2014) *Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (Anthericaceae – Palmae)*. Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Leroy, A. (2004) *Dracaena draco*. Una parte di storia delle Isole Canarie. A part of the history of Canary Islands. *Cactus & Co.* 8(1): 4–17, ills.
- Lodé, J. (2010a) *Plantas suculentas de las Islas Canarias. Guía de identificación fácil. Succulent plants of the Canary Islands. Identification easy guide. Plantes succulentes des Îles Canaries. Guide d'identification facile. Sukkulenten auf den Kanarischen Inseln. Führer für die leichte Bestimmung der Arten. Santa Cruz de Tenerife (ES): Turquesa.*
- Lodé, J. (2010b) *Succulent plants of Socotra*. Barcelona (ES): Todograf / published by the author.
- Lu, P.-L. & Morden, C. W. (2014) Phylogenetic relationships among *Dracaenoid* genera (*Asparagaceae: Nolinoideae*) inferred from chloroplast DNA loci. *Syst. Bot.* 39(1): 90–104. <https://doi.org/10.1600/036364414X678035>
- Mägdefrau, K. (1975) Das Alter der Drachenbäume auf Tenerife. *Flora* 164: 347–357.
- Marrero, A. (2000) *Dracaena tamaranae*, el género *Dracaena* y otros afines: Análisis morfológico para una aproximación filogenética. *Mus. Canario* 55: 301–332. <http://dialnet.unirioja.es/servlet/oiart?codigo=2523131>
- Marrero, A. (2013) Aportaciones a la flora pliocena de la isla de Gran Canaria: Avances a los estudios florísticos y paleoambientales. *Vieraea* 41: 371–384, ills.
- Marrero, A. [et al. 1998], Almeida, R. S. & González-Martín, M. (1998) A new species of the wild dragon tree, *Dracaena (Dracaenaceae)* from Gran Canaria and its taxonomic and biogeographic implications. *Bot. J. Linn. Soc.* 128: 291–314, ills., map. <https://doi.org/10.1006/bojl.1998.0193>
- McCoy, T. A. & Lavranos, J. (2017) Beobachtungen zu drei neuen Arten bzw. Unterarten von Dhofar-Xerophyten und ihre Beschreibungen. *Observations on three new species of Dhofari xerophytes and their descriptions*. *Avonia* 35(1): 54–67, ills.
- Miller, A. G. & Morris, M. (1988) *Plants of Dhofar. The southern region of Oman. Traditional, economic and medicinal uses*. Sultanate of Oman (OM): Government of Oman.
- Miller, A. G. & Morris, M. (2004) *Ethnoflora of the Soqotra Archipelago*. Edinburgh (GB): Royal Botanic Garden Edinburgh.
- Mwachala, G. & Mbugua, P. (2007) *Dracaenaceae*. In: Beentje, H. J. & Ghazanfar, S. A. (eds.): *Flora of Tropical East Africa*. Richmond (GB): Royal Botanic Gardens, Kew.
- Sebsebe Demissew & Nordal, I. (2010) *Aloes and lilies of Ethiopia and Eritrea*. Ed. 2. Addis Ababa (ET): Shama Books.
- Thulin, M. (ed.) (1995) *Flora of Somalia. Volume 4. Angiospermae (Hydrocharitaceae – Pandanaceae)*. Richmond (GB): Royal Botanic Gardens Kew.
- Walker, C. C. (1999) A tale of dragons — the pachycaul species of *Dracaena*. *Brit. Cact. Succ. J.* 17(4): 171–177, ills., map.
- Wilkin, P. [et al. 2012], Suksathan, P., Keeratikiat, K., van Welzen, P., & Wiland-Szymanska, J. (2012) A new threatened endemic species from central and northeastern Thailand, *Dracaena jayniana (Asparagaceae: tribe Nolinoideae)*. *Kew Bull.* 67(4): 697–705, ills, map. <https://doi.org/10.1007/s12225-012-9412-2>
- Wyk, B. van & Wyk, P. van (1997) *Field guide to trees of southern Africa*. Cape Town (ZA): Struik Nature.



## Nolina RUSCACEAE

C. C. Walker

**Nolina** Michaux (Fl. Bor.-Amer. 1: 207, 1803).  
**Type:** *Nolina georgiana* Michaux. —  
**Nolinoideae** — **Lit:** Trelease (1911: synopsis);  
Walker (2001: introduction); Hess (2002: Fl. N  
America); Hochstätter (2010: monograph). **Distr:**  
S USA (California, Arizona, Texas to Florida),  
Mexico. **Etym:** For Abbé P. C. Nolin (fl. 1803),  
French agriculturalist and horticultural author.

Dioecious (or rarely polygamo-dioecious),  
acaulescent or arborescent perennial shrubs,  
stems sometimes basally swollen, occasionally  
with extensive underground rhizomes; **L** linear,  
hard, fibrous, margins rough or serrulate; **Inf**  
paniculate, diffuse and racemose, **Br** subtended  
by **Bra**; **Ped** jointed; **Fl** usually functionally uni-  
sexual;  **Tep** 6, in 2 groups of 3, small, persistent,  
spreading; **St** 6, usually abortive in fertile female  
flowers; **Fil** short, slender; **Ov** 3-lobed, sessile or  
shortly stipitate, abortive in male flowers; **Fr**  
papery 3-celled capsules, dehiscent; **Se** 1–3, glo-  
bose to oblong.

A genus of c. 30 species. As the genus is here  
circumscribed, and separated from *Beaucarnea*  
(incl. *Calibanus*), it consists of xerophytic shrubs,  
not truly succulent, but some species have mas-  
sive pachycaul stems. Most taxa occur in Mexico,  
but several species grow across the S USA from

California to Florida. Many are poorly known.  
Gentry (1972) notes that the genus possesses  
few striking morphological characters, with  
flowers being monotonously similar and fruits  
varying only in size and dehiscence. He suggests  
leaf characters to be the most useful for determin-  
ing the nature of closely related entities.

Hochstätter (2010) published a synopsis of the  
genus, which is largely followed here with the  
addition of more recently described species. He  
included a key to the 26 species recognised at  
that time.

In Mexico species have several common  
names, including “Zacate Cortador”, “Zacate de  
Armazón” and “Palmilla”. In the USA, species are  
commonly known as “Beargrass”, and as the  
name suggests, plants resemble coarse grass  
when not in flower. Leaves are tough and have  
been used for thatching, brooms, baskets, hats,  
mats etc. In the Sonoran Desert, flower stalks of  
*N. beldingii*, *N. bigelovii* and *N. macrocarpa* are  
roasted and eaten (Hodgson 2001: 64).

Trelease (1911) divided the genus into  
4 unranked groups. Hochstätter (2010), in his  
synopsis of *Nolina*, cited these names as being  
published at sectional rank. Since he also cited  
the full references from Trelease, Thiede (2012)  
treated Hochstätter’s sectional names as validly  
published, albeit unintended, new combinations.  
This sectional classification is adopted here:

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- [1] Sect. *Nolina* (= *Graminifoliae* Trelease 1911, *nom. inval.*, Art. 22.1): Acaulescent, **L** thin and grass-like but hard and fibrous, linear, rarely > 0.5 cm wide, rather flat, usually not brush-like at the tip. — 6 spp. (no taxa treated here).
- [2] Sect. *Erumpentes* (Trelease 1911) Hochstätter 2010: **L** rather thick, linear or narrowly oblong-triangular, to 1.2 cm wide, green, ± concave, tip often fibrous-lacerate; **Fr** small, not inflated. — 7 spp., of which 2 are included as representatives of this xerophytic but non-succulent group.
- [3] Sect. *Microcarpae* (Trelease 1911) Hochstätter 2010: **L** rather thick, linear or narrowly oblong-triangular, to 1.2 cm wide, green, ± concave, tip often fibrous-lacerate; **Fr** moderately sized, somewhat inflated. — 4 spp. (no taxa treated here).
- [4] Sect. *Arborescentes* (Trelease 1911) Hochstätter 2010: Mostly trees or more rarely with underground branching rhizome; **L** relatively thin, 1.5–4 cm wide, tip usually not brush-like; **Fr** large, inflated. — 11 spp., all treated here because of their mainly pachycaul habit.

**N. azureogradiata** D. Donati (Piante Grasse 31(2): 54, ill. (pp. 52–57), 2011). **Type:** Mexico, Oaxaca (Hinton & al. 29252 [Herb. G. B. Hinton, MEXU]). — **Distr:** Mexico (S Oaxaca: Sierra Madre del Sur); dense moist woodlands, 1800–2400 m. — Fig. 1.

[4] Arborescent, stem up to 4 m, 15–20 cm Ø, often modestly branched; **L** arranged into terminal **Ros**, linear, tapering, to 130 × 4 cm, glaucous-pruinose, deep blue, slightly flexible, tip over 8 cm, dried and intact, erect, pointed; **Inf** conical, paniculate, 2–3 m, well branched, primary **Br** 30–60 cm; **Fl** 4–8 mm Ø, white, highly scented.

Closest to *N. parviflora*, but differing principally in the larger inflorescence, smaller highly scented flowers, but especially in the deep blue glaucous-pruinose leaves, contrasting with the green leaves of the former species.

**N. beldingii** Brandege (Zoe 1(10): 305–306, 1890). **Type:** Mexico, Baja California (*Brandegee*



**Fig. 1** *Nolina azureogradiata*. (Copyright: D. Donati)

583 [not recorded]). — **Distr:** Mexico (Baja California: Cape region); 300–1500 m. **I:** Hochstätter (2010: 34–35).

**Incl.** *Nolina beldingii* [?] *deserticola* Trelease (1911) ≡ *Nolina beldingii* var. *deserticola* (Trelease) Trelease (1912).

[4] Tree, stem 3–6 m, openly branched, with a large crown of stiff **L** forming **Ros**; **Br** 8–10 cm, often again branched with branchlets 1–2 cm; **L** rigid, erect to recurving, 50–100 × 1–2 cm, flexible, blue-green, margin serrulate; **Inf** erect, paniculate, 1–2 m × 20–50 cm; **Fl** 2 × 2 mm Ø, cream; **Fr** depressed, retuse at the base, 5–10 × 15 mm; **Se** globose to ovate, brownish, 4 × 5 mm.

This Baja Californian endemic is a small tree, with its type locality in the mountain tops of the Cape Region. Its appearance is similar to *N. nelsonii*, but the leaves are less rigid. Superficially it looks like *Yucca rostrata*. It is frost hardy to –10°C.

**N. bigelovii** (Torrey) S. Watson (Proc. Amer. Acad. Arts 14: 247, 1879). **Type:** USA, Arizona

(*Bigelow* s.n. [NY, GH]). — **Distr:** USA (California, Nevada, Arizona), Mexico (Sonora, N Baja California); rocky hillsides and flats of the S Mojave and Sonoran Deserts, 300–1500 m. **I:** Gentry (1972: 181, fig. 71); Hochstätter (2010: 32–33).

≡ *Dasylyrion bigelovii* Torrey (1857) ≡ *Beaucarnea bigelovii* (Torrey) Baker (1872).

[4] Stem 1–3 m with a large crown of stiff **L** persisting dry and reflexed on the trunk; **L** linear, 80–120 × 1.5–3.5 cm, tip entire, margins at first serrulate then filiferous; **Inf** paniculate, 60–100 cm; **Bra** deltoid-lanceolate, thin, 4–10 × 1–2 cm, attenuate, soon deciduous, primary **Br** slender, 10–20 cm, ascending, glabrous, smooth; **Tep** oblong-linear, 2.5–3 mm; **OTep** introrsely shortly apiculate, reflexed in female flowers; **ITep** erect or ascending; **Fr** narrowly emarginate at tip and base, 8–12 × 9–12 mm; **Se** ovoid to oblong, grey to white-tawny, wrinkled, 2.5–3.5 mm.

This is the most distinctive and widespread member of Sect. *Arborescentes*. The filiferous leaves are diagnostic. Gentry (1972) anticipated that the taxon should also occur in adjacent Mexico (Sonora) and this range extension has been confirmed (Hochstätter 2010). Common names: “Bigelow’s Nolina”, “Bigelow’s Beargrass”.

**N. cismontana** Dice (Novon 5(2): 162–164, 1995). **Type:** USA, California (*Dice & Oberbauer* 650 [SD 121705, ARIZ, NY, RSA, UC]). — **Lit:** Dice (1988). **Distr:** USA (cismontane S California); chaparral on sandstone and shales, 200–1300 m. **I:** Hochstätter (2010: 43).

[4] Stem 0.5–1.5 m, with woody caudex, branching above and below ground, mature **Ros** with 30–90 **L**; **L** lanceolate-linear, 50–140 × 1.2–3 cm, base expanded, margin serrulate; **Inf** 1–3 m, with rather narrow **Br** 13–35 cm long and spreading; **Bra** large, papery, persistent; **Tep** cream-white, ovate, 3–5 × 1.5–2.5 mm; **Fr** orbicular, papery, emarginate at base and tip, 8–12 mm tall and slightly broader; **Se** ovoid to oblong, reddish-brown, 4–5 × 3–4 mm. — **Cytology:** 2n = 38.

Close to *N. parryi* and for a long time confused with it (Hess & Dice 1995). Endemic to S California, and geographically isolated. It is endangered and threatened throughout most of its range by residential and commercial development. Vernacular names: “Chaparral Beargrass”, “Chaparral Nolina”.

**N. excelsa** García-Mendoza & E. Solano (Bot. Sci. 90(1): 22, ill. (p. 23), 2012). **Type:** Mexico, Oaxaca (*Redonda-Martínez & al.* 481 [MEXU, FEZA]). — **Lit:** Rivera-Lugo & Solano (2012). **Distr:** Mexico (Oaxaca: Mixteca Alta); ecotone between oak forests and desert scrub, slopes, 2300–2700 m.

[4] Tree, stem 8–13 m, 40–50 cm Ø, basally swollen, outer bark fissured, grey-blackish, with 8–16 **Br**; **L** linear, (60–) 70–85 × 1.4–2.1 cm, chartaceous, glaucous, apex attenuated, margin denticulate; **Inf** paniculate, erect, lax, 1.2–1.6 (–2.5) m; **Br** 12–14 cm; **Bra** 35–40 × 3–6 cm, lanceolate, appressed, papery; bracteoles 3–9 × 2–5 mm, ovate to deltoid; **Fl** unisexual; **Ped** 3.5–4 mm; **Tep** 3–4 × 1.8–2 mm, free, nearly equal, elliptic to obovate, with apiculate apex, papillate, in male flowers reflexed, concave in female flowers, whitish with a longitudinal median purple stripe; **Fr** narrowly emarginate at tip and base, 7–8.5 × 7–9 mm Ø, rounded, distally inflated, with thin pericarp; **Se** subglobose, dark brown, muriculate, 3.5–4.2 × 3–3.8 mm.

This species, with stems up to 13 m tall, is the largest in the genus and hence its very appropriate epithet. Its closest relative is *N. parviflora*, from which it is distinguished by its greater height, shorter and less glaucous leaves, whitish tepals with the distinct purple mid-stripe, smaller fruits, and in the shape, size and ornamentation of the seeds (muriculate in *N. excelsa*; reticulate in *N. parviflora*). Additionally both species flower and fruit at different times. *N. excelsa* is endemic to a small region E and N of Huajuapán. It is known by the name “Sotol”. The leaves are used to thatch roofs of houses.

**N. hibernica** Hochstätter & D. Donati (Piante Grasse 30(2): 73–74, ill., 2010). **Type:** Mexico, Tamaulipas (*Hinton & al.* 29065 [Herb. G. B.





**Fig. 2** *Nolina hibernica*. (Copyright: D. Donati)

Hinton, MEXU)]. — **Distr:** Mexico (Tamaulipas, Nuevo León); dense pinon woodland on humid and shady slopes, 2400–3200 m. **I:** Hochstätter (2010: 40). — Fig. 2.

[4] Tree-like, stem to > 6 m, 25 cm Ø, basally swollen, modestly branched; **L** linear, tapering to 120 × 4 cm, pale green, very flexible, with slightly curling tip 15 cm long, dead leaves forming a dense covering of the branches below the terminal rosette; **Inf** paniculate, >2.3 m tall, elongate, branched, primary **Br** 15–30 cm; **Fl** 20 mm Ø, white; **Fr** and **Se** not known.

One of the largest and hardiest members of the genus. It is adapted to alpine conditions, where temperatures below  $-15^{\circ}\text{C}$  are not infrequent. It grows sympatrically with *N. nelsonii*, but no hybrids have yet been observed (Hochstätter & Donati 2010).

**N. interrata** Gentry (Madroño 8: 181, fig. 1, t. 1, 1946). **Type:** USA, California (*Gentry* 7330 [SD]). — **Distr:** USA (S California: San Diego County), Mexico (N Baja California); rocky hillsides, chaparral, 200–700 m; very rare. **I:** Hochstätter (2010: 44–45).

[4] Plants with underground branching rhizome to 3 m × 30 cm Ø, above-ground stems

not obvious, mature **Ros** with < 45 **L**; **L** linear, glaucous, 70–100 × 0.8–1.5 cm, base barely expanded, tip dry, slender, not filiferous, margin minutely and persistently serrate, armed with denticles of 2 sizes; **Inf** open compound panicles 1.5–2 m, base of peduncle 0.5–1.8 cm Ø; **Bra** persistent, 20–40 cm; **female Fl** with staminodes inserted on the **Tep**; **Fr** large, broader than long, 12–15 mm wide; **Se** reddish-brown to yellowish, wrinkled, 5 × 4 mm.

Distinguished by the glaucous leaves with coarse armature. The horizontal underground stem or rhizome is especially noteworthy, but this structure may be present in other species assumed to be acaulescent, since this feature may be readily overlooked. Known locally in San Diego County as “Dehesa Nolina” and “Dehesa Beargrass”. *N. interrata* is very rare and hence one of the most endangered plant species in California, occurring in only two small stands. The populations are stable but are slowly being affected by land clearance for housing development. Three additional populations are known in Baja California.

**N. matapensis** Wiggins (Contr. Dudley Herb. 3: 65, 1940). **Type:** Mexico, Sonora (*Wiggins* 7515 [DS]). — **Distr:** Mexico (Sonora, Chihuahua); mountain woodland, gravelly slopes, 900–1700 m. **I:** Walker (2001: 221, figs. 11–12); Hochstätter (2010: 40).

[4] Small trees, stem to 3–10 m, basally swollen, simple or modestly branched, bark fissured; **Ros** small; **L** linear, 70–120 × 1–1.5 cm, recurved, hard, striate, greenish-yellow, somewhat glaucous, margin finely serrulate; **Inf** paniculate, 1.5–3 × longer than the **L**, primary **Br** 15–35 cm, branchlets 10–15 cm; **Tep** oblong-linear, 2 mm; **Fr** broadly ellipsoid, depressed, deeply notched at both ends, tardily dehiscent, 8–9 × 5 mm; **Se** pale brown, nearly globose, 2.5–3 mm Ø.

This species has a narrow distribution range. The leaves are used for basket-making, the stems for posts. A relatively unknown species, first introduced into cultivation in 1976 as ISI 982. Plants from this introduction are now multi-headed specimens at the Huntington Botanical



Garden. The species is recommended as an attractive landscape plant for subtropical areas such as S California. Local vernacular names: “Palmito”, “Tuya”.

**N. nelsonii** Rose (Contr. US Nation. Herb. 10: 92, 1906). **Type:** Mexico, Tamaulipas (*Nelson* 4489 [US]). — **Distr:** Mexico (Tamaulipas), dry bush, 1200–2500 m. **I:** Hochstätter (2010: 39).

[4] Tree, stem to 4.5 m, openly branched, with a large crown of stiff **L** forming small **Ros**; **L** rigid, erect to recurving, 50–70 × 3–4 cm, flexible, blue to blue-green, margin serrulate; **Inf** erect, paniculate, 2–3 m × 20–60 cm; **Bra** scarious, lacerate; **Fl** 3 mm × 3 mm Ø, cream; **Fr** papery, 8–10 mm Ø; **Se** globose to ovate, brownish, 2–3 mm Ø.

This is a small tree similar to *N. parryi*, but the leaves differ in size and form. Superficially it looks like *Yucca rostrata*. Reported as frost hardy to –12 °C.

**N. parryi** S. Watson (Proc. Amer. Acad. Arts 14: 247, 1879). **Type:** USA, California (*Parry* s.n. [GH, MO]). — **Lit:** Mitich (1982); Hess & Dice (1995). **Distr:** USA (California); rocky slopes in desert and pinyon-juniper woodland, 900–2100 m. **I:** Hochstätter (2010: 30–31). – Fig. 3.

≡ *Nolina bigelovii* var. *parryi* (S. Watson) L. D. Benson (1945) ≡ *Nolina bigelovii* ssp. *parryi* (S. Watson) E. Murray (1983); **incl.** *Nolina parryi* ssp. *parryi*; **incl.** *Nolina parryi* ssp. *wolfii* Munz (1950) ≡ *Nolina bigelovii* var. *wolfii* (Munz) L. D. Benson (1954) ≡ *Nolina wolfii* (Munz) Munz (1974) ≡ *Nolina bigelovii* ssp. *wolfii* (Munz) E. Murray (1983).

[4] Arborescent, stem 1–2 (–6) m, basally branching, mature **Ros** with up to 200 **L**; **L** linear, 50–150 × 2–4 cm, almost pungent, rather thick, concave, keeled, margin serrulate-scabrous, base strongly expanded; **Inf** to 4 m, with rather narrow **Br** 15–30 cm long and spreading, densely flowered branchlets < 4 cm; **Bra** large, papery, persistent; **Fl** large; **Tep** 4 mm, creamy-white; **Fr** very large, orbicular, deeply notched at both ends, 12–15 mm Ø; **Se** reddish-brown, 4 × 3 mm.



**Fig. 3** *Nolina parryi*. (Copyright: U. Eggli)

*N. parryi* is differentiated from *N. cismontana* by the taller stems, larger number of leaves per rosette and broader leaf bases (Dice 1988, Hess & Dice 1995). It is endemic to California. Mitich (1982) records spectacular specimens in the Kingston Mountains, Mojave Desert. Here some individuals reach a height of over 6 m with stems 1 m Ø, and with leaves 1.5 m long; the plants are 4 m across. Inflorescences are enormous too, being 4 m long with the fertile portion 2 m in length. He reports that *N. parryi* grows readily from seed, requiring a mild climate for outdoor cultivation. In such conditions plants flower after 7–8 years. Common names: “Parry’s Nolina”, “Giant Nolina”.

**N. parviflora** (Kunth) Hemsley (Biol. Centr.-Amer., Bot. 3: 372, 1884). **Type:** Mexico, México (*Humboldt & Bonpland* 4031 [P]). — **Lit:** McVaugh (1989: 242–244, with ills.); Rivera-Lugo & Solano (2012); Ruiz-Sanchez & Specht (2013); Ruiz-Sanchez & Specht (2014). **Distr:**

Mexico (Chihuahua?, Durango, Zacatecas, Nayarit, Jalisco, Michoacán, Querétaro?, Hidalgo, Mexico, Puebla, Veracruz, Oaxaca); widely distributed in the pine forest, pine-oak-juniper forests, xerophytic scrub and tropical dry forest localities of the Trans-Mexican Volcanic Belt, Sierra Madre Occidental, Sierra Madre Oriental and Sierra Madre del Sur mountain ranges: steep slopes, mountainsides, barrancas, sandy or rocky soils, 1300–2400 m. **I:** Rowley (1990: figs. 1–2, 4, as *N. longifolia*); Folsom & al. (1995: 104–105, as *N. longifolia*); Hochstätter (2010: 36; 41–42, as *N. longifolia*).

≡ *Cordylina parviflora* Kunth (1815) ≡ *Dracaena parviflora* (Kunth) Willdenow (1829) ≡ *Beaucarnea parviflora* (Kunth) Baker (1872); **incl.** *Yucca longifolia* Karwinsky ex Schultes fil. (1830) ≡ *Dasyllirion longifolium* (Karwinsky ex Schultes fil.) Zuccarini (1840) ≡ *Beaucarnea longifolia* (Karwinsky ex Schultes fil.) Baker (1872) ≡ *Nolina longifolia* (Karwinsky ex Schultes fil.) Hemsley (1884); **incl.** *Roulinia humboldtiana* Brongniart (1840); **incl.** *Roulinia karwinskiana* Brongniart (1840); **incl.** *Dasyllirion humboldtii* Kunth (1844); **incl.** *Nolina altamiranoana* Rose (1905); **incl.** *Nolina elegans* Rose (1906).

[4] Arborescent, stem 1–3 (rarely >5) m, swollen at base, with 1–6 **Br**, bark thick, corky and rough, with a large crown forming **Ros** of several hundred **L**; **L** initially rigid, later flexible, long-attenuate, erect to recurving, ultimately drooping, to 1–1.5 m × 1.5–2.5 cm, broadened to 5 cm at the base, pale green, smooth and ribbed on both surfaces, margin serrulate, tip entire; **Inf** erect, paniculate, widely-branched, 0.8–2 m; primary **Br** to 30 cm, spreading; **Bra** very long and narrow above a dilated base, foliaceous, to 60 cm; **Fl** very numerous; **Tep** 2.5–3 (–4) mm, white-creamy or with green-brown midline; **Fr** globose, 8–12 mm × 8–12 mm Ø; **Se** ovoid to nearly globose, light brown, 3.5–4 × 3–3.5 mm.

McVaugh (1989) substantially broadened the concept of *N. parviflora* to include *N. longifolia* and *N. elegans*, giving the species a very widespread distribution from (?) Chihuahua S to Oaxaca. In contrast, Trelease (1911) and Hochstätter (2010) maintained their separation.

*N. elegans* has been of uncertain status since its original description by Rose as “probably acaulescent”. Characteristic features of *N. parviflora* are the short, broad, widely branched panicles with short very showy long bracts and dense, numerous flowers. It is a small tree similar to *N. parryi*, but the leaves differ in size and form, being generally longer and more flexible in *N. parviflora*, initially erect, then spreading and drooping. Easily mistaken for *Beaucarnea recurvata*, but in contrast *N. parviflora* has a more arborescent habit and the leaves are long, lax, and not significantly thicker at the base. Superficially it also looks like *Yucca filifera*. Plants flower annually, but there are mass flowering cycles that last up to three years. Bees, wasps and flies are pollinators (Ruiz-Sanchez & Specht 2013). It is surprisingly little-known and seldom cultivated. It is frost-hardy to –10 °C.

**N. pollyjeanneae** Hochstätter (Acta Succ. 1 (1): 7, ills. (pp. 4–8), 2013). **Type:** USA, Oklahoma (Hochstätter 523.50 [SRP, HEID]). — **Distr:** USA (Oklahoma); isolated gentle limestone slopes, on dry rocky hills in open woodland 1300 m.

[2] Low-growing acaulescent spreading shrubs forming dense clumps 1–2 m Ø; **L** thin, grass-like, quite flexible, 40–80 × 0.2–0.4 cm, deep green, convex at the base then concave, tip fibrous and tapered, upper surface smooth, lower surface rough, margin finely denticulate; **Inf** paniculate, 40–80 cm, branched, generally exceeding the leaves; **Fl** 2–3 mm Ø, white to greenish; **Fr** capsules 3–4 mm Ø, unilocular, light brown to almost transparent; **Se** globose, 2–3 mm Ø.

Closest geographically and ecologically to the grass-like species *N. greenei* (not treated here) and *N. texana*, but endemic to Oklahoma.

**N. texana** S. Watson (Proc. Amer. Acad. Arts 14: 248, 1879). **Type:** USA, Texas (*Lindheimer* 712 [MO]). — **Distr:** USA (Texas, C New Mexico), adjacent Mexico (?); rocky hillsides (limestone, granite), grasslands and shrublands, 200–2800 m. **I:** Small (1916); Gentry (1972: 183, fig. 72); Hochstätter (2010: 15).

≡ *Beaucarnea texana* (S. Watson) Baker (1880); **incl.** *Nolina erumpens* [?] *compacta* Trelease (1911) ≡ *Nolina erumpens* var. *compacta* (Trelease) Trelease (1912) ≡ *Nolina texana* var. *compacta* (Trelease) I. M. Johnston (1943).

[2] Low-growing acaulescent spreading shrubs; **L** narrowly linear, 70–120 × 0.3–0.4 cm, deeply rounded below, margins somewhat serrulate or smooth; **Inf** paniculate, slender, 30–60 cm, primary **Br** 10–15 cm; **Bra** caudate-attenuate, surpassing the branches, dry, yellowish, persisting; **Fl** 2.5–3.5 mm, white to creamy; **Fr** 5–7 × 4–5 mm, round-ovate; **Se** globose, 2.5–4 mm Ø. — **Cytology:** 2n = 38.

In contrast to other members of Sect. *Erumpentes*, the inflorescence of *N. texana* is longer. It has a wide geographical range in the USA, and Gentry (1972) anticipates localities being found in NW Mexico (Sonora). This is one of the hardiest species in the genus and can tolerate temperatures below –20 °C and hence is winter-hardy in Europe. Common names: “Texas Sacahuiste”, “Bunchgrass”.

## References

- Dice, J. C. (1988) Systematic studies in the *Nolina bigelovii* — *N. parryi* (*Nolinaceae*) complex. San Diego (US): San Diego State University, unpubl. M. Sc. thesis.
- Folsom, D. B. [ & al. 1995], Trager, J. N., Folsom, J., Clements, J. & Scott, N. (1995) Dry climate gardening with succulents. New York (US): Pantheon Books, Knopf Publishing Group.
- Gentry, H. S. (1972) The *Agave* family in Sonora. Agricultural handbook No. 399. Washington D.C. (US): US Department of Agriculture. **URL:** <http://naldc.nal.usda.gov/download/CAT87209091/PDF>
- Hess, W. J. (2002) *Nolina* Michaux. In: Flora of North America Editorial committee (eds.): Flora of North America North of Mexico, Volume 26: *Magnoliophyta: Liliidae: Liliales* and *Orchidales*; pp. 415–421, ills., key. New York (US)/Oxford (GB): Oxford University Press.
- Hess, W. J. & Dice, J. C. (1995) *Nolina cismontana* (*Nolinaceae*), a new species name for an old taxon. *Novon* 5(2): 162–164, key. **URL:** <http://www.jstor.org/stable/3392239>
- Hochstätter, F. (2010) Il genere / The genus *Nolina* (*Nolinaceae*). *Piante Grasse* 30 (1: Suppl.): 1–48, ills., map, key.
- Hochstätter, F. & Donati, D. (2010) Una nuova specie appartenente al genera *Nolina*. A new species belonging to genus *Nolina*: *Nolina hibernica* Hochstätter & Donati. *Piante Grasse* 30(2): 72–77, ills.
- Hodgson, W. C. (2001) Food plants of the Sonoran Desert. Tucson (US): University of Arizona Press.
- McVaugh, R. (1989) Flora Novo-Galiciana. A descriptive account of the vascular plants of Western Mexico. Vol. 15: *Bromeliaceae* to *Dioscoreaceae*. Ann Arbor (US): University of Michigan Herbarium.
- Mitich, L. W. (1982) Parry's *Nolina* (*Nolina parryi*). *Cact. Succ. J. Gr. Brit.* 44: 67–68, ill.
- Rivera-Lugo, M. & Solano, E. (2012) Flora del Valle de Tehuacán-Cuicatlan. Fascículo 99. *Nolinaceae* Nakai. México D.F. (MX): Instituto de Biología UNAM.
- Rowley, G. D. (1990) *Nolina* en culture. *Cact.-Avent.* 5: 2–4.
- Ruiz-Sanchez, E. & Specht, C. D. (2013) Influence of the geological history of the Trans-Mexican Volcanic Belt on the diversification of *Nolina parviflora* (*Asparagaceae: Nolinoideae*). *J. Biogeogr.* 40: 1336–1347. <https://doi.org/10.1111/jbi.12073>
- Ruiz-Sanchez, E. & Specht, C. D. (2014) Ecological speciation in *Nolina parviflora* (*Asparagaceae*): Lacking spatial connectivity along of the Trans-Mexican Volcanic Belt. *PLoS One* 9(6): e98754, 11 pages, maps, ills. <https://doi.org/10.1371/journal.pone.0098754>
- Small, J. K. (1916) *Nolina texana*. *Addisonia* 2: 1–2, t. 41.
- Thiede, J. (2012) Nomenclatural status of unranked names published by Trelease (1911) in *Beaucarnea*, *Dasyllirion*, and *Nolina* (*Asparagaceae* — *Nolinoideae*). *Phytoneuron* 2012(77): 1–4. <http://www.phytoneuron.net/77PhytoN-Beaucarnea.pdf>
- Trelease, W. (1911) The desert group *Nolineae*. *Proc. Amer. Philos. Soc.* 50(200): 404–443, tt. 1–17. **URL:** <http://www.jstor.org/stable/983932>
- Walker, C. C. (2001) Introducing the *Nolinaceae*. *Brit. Cact. Succ. J.* 19(4): 214–221, ills.





## Sansevieria RUSCACEAE

L. E. Newton

**Sansevieria** Thunberg (Prodr. Fl. Cap., 65, 1794). **Type:** *Sansevieria thyrsiflora* Thunberg [*nom. illeg.*, = *Aloe hyacinthoides* Linné (ICBN 2006: 280)]. — **Dracaenoideae** — **Lit:** Brown (1915: synopsis); Binojkumar (2002: synopsis India); Chahinian (2005a: ill. synopsis); Mbugua (2007: Flora Tropical E Africa); Carlquist & Schneider (2007: anatomy); Croix (2010: Flora Zambesiaca); Newton (2012b: with key to arborescent spp.); Mansfeld (2013a: ill. synopsis); Mansfeld (2014c: synopsis fieldnumbers); Lebrun & Stork (2014: 228–252, synopsis tropical Africa). **Distr:** Africa, Arabian Peninsula (Yemen, Oman), Comores, Madagascar, India, Sri Lanka, Myanmar. **Etym:** For Pietro Antonio Sanseverino, Count of Chiaromonte (1724–1771), Italian patron of horticulture in Naples and founder of a private botanical garden.

**Incl.** *Cordyline* Adanson (1763) (*nomen rejiciendum*, Art. 56.1). **Type:** *Aloe hyacinthoides* Linné.

**Incl.** *Acyntha* Medikus (1786) (*nomen rejiciendum*, Art. 56.1). **Type:** *Aloe hyacinthoides* Linné.

**Incl.** *Sanseverinia* Petagna (1787) (*nomen rejiciendum*, Art. 56.1). **Type:** *Sanseverinia thyrsiflora* Petagna.

Acaulescent or caulescent perennials, sometimes branching near the base, with subterranean rhizomes or stolons above ground; **L** solitary, few or many, distichous or in **Ros**, succulent or leathery, lanceolate, linear or lorate and flat, or cylindrical or semi-cylindrical and usually with a groove on the upper surface, sessile, sometimes narrowed at the base to resemble a petiole, apex often a pungent spine, green, often with lighter blotches, scattered or in transverse bands; **Inf** terminal, paniculate or unbranched, the fertile portion a dense or lax thyrses, elongated or sometimes capitate, with extrafloral nectaries associated with the bracts; **Fl** solitary or (usually) in a dense helicoid cyme, bracteate, pedicellate, actinomorphic, usually nocturnal and sweetly scented; **Ped** articulated; **Te**p united at the base to form a tube with 6 free lobes that curl back at anthesis, mostly whitish; **St** 6, extended beyond the perianth tube, exposed at anthesis by curling back of tepals; **Sty** simple, as long as the stamens or slightly longer; **Ov** with 3 locules, but often only 1 or 2 seeds mature; **Fr** resembling berries, but seeds covered with a fibrous endocarp. — **Cytology:** The few published chromosome numbers suggest that there is some polyploidy, with base numbers of  $x = 20$  or  $21$ . Early counts were summarised by Darlington & Wylie (1955).

The genus has been variously included in the families Agavaceae, Asparagaceae, Dracaenaceae, Haemodoraceae, Liliaceae, and Ruscaceae. In the latest general classification it is placed in the Asparagaceae (APG 2009, 2016), though Nyffeler & Eggl (2010) proposed recognition of Ruscaceae

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s.l. Menale & al. (2013) argue that the name should be attributed to Petagna, since Thunberg merely used an erroneous spelling (*Sansevieria*, now a conserved name) for Petagna's *Sanseverinia*. Symoens (2014) resolved the etymology of the name.

Following morphological studies, Bos (1984) suggested that *Sansevieria* should be included in *Dracaena*. In a later publication (Bos 1998) *Dracaena* does include *Sansevieria*, but no transfers of individual species were made. Molecular studies by Lu & Morden (2014) supported this sinking of *Sansevieria*. Consequently new combinations were published by Mabberley (2017: 1101) and Christenhusz & al. (2018), transferring the species to *Dracaena*. Whilst the genus could be included in *Dracaena* eventually, Christenhusz & al. (2018) missed out several species, and some of their new names (e.g. for *S. pinguicula* fa. *disticha*, see there) are unacceptable, and so they are not followed in this account.

Seedlings of species with cylindrical leaves, as well as young plants raised from cuttings, have short, flat leaves, and they look different from mature plants. In the descriptions below, leaf dimensions are length and width, plus thickness from front to back in the case of cylindrical and laterally compressed leaves. Although often referred to as "spike-like racemes", the fertile (flowering) portions are neither spikes nor racemes — they are compound structures with flower clusters arranged along an axis, and not opening from the base upwards (Newton 2007). Jankalski (2009a) regarded the inflorescence as a thyrses, interpreting the flower clusters as axillary fascicled cymes, stating that the central flower in each cluster is the first to open. It was shown by Newton (2011) that the central flower is not the first to open, at least in some species examined, and so the neutral term glomerule was proposed. Budweg (2016) agreed that the inflorescences are simple or branched thyrses, but with helicoid cymes, confirming that the central flower is not the first to open.

Useful diagnostic characters, such as whether leaf surfaces are rough or smooth, and the colour of rhizomes, are often not mentioned in protologues. Earlier literature stated that the seeds

have a fleshy covering, the sarcotesta, and no pericarp. Budweg (2014) discussed past interpretations of the fruit, and has shown that the seeds are covered with a fibrous endocarp.

Many of the species included in Brown's account were described from cultivated plants of undocumented wild origin, and in some cases even the country of origin was unknown. Many species are poorly represented in herbaria, and more field work is required to determine distribution and variation.

**Classification:** An infra-generic classification was suggested by Pfennig, but it was not presented formally with names for the groups (Pfennig 1977a; Newton 2005a). Mbugua (2007) gave subgeneric names to the groups proposed by Pfennig, but without valid publication. Jankalski (2009a) published names for the same groups proposed by Pfennig, at the rank of section. Mansfeld (2013a) took this further by proposing subsections. Jankalski (2015) proposed an alternative classification within Sect. *Sansevieria*, with 16 species groups, without formal names. — The following synopsis is based on Pfennig's scheme, with slight modification:

- [1] **Inf** branching (Sect. *Dracomima* Jankalski 2009)
- [2] **Inf** unbranched, fertile portion capitate (Sect. *Cephalantha* Jankalski 2009)
- [3] **Inf** unbranched, fertile portion elongated (Sect. *Sansevieria*)
  - [3a] Plants with stolons above ground.
  - [3b] Plants with underground rhizomes;
    - L** cylindrical or semicylindrical, upper surface often grooved.
  - [3c] Plants with underground rhizomes;
    - L** flattened or folded.

**Succulence:** Although most flat-leaf species appear more leathery than succulent, it has been shown by Koller & Rost (1988a) and Koller & Rost (1988b) that leaves of all *Sansevieria* species have succulent tissue. This occupies a central mesophyll and is unusual in having a branched network of living cells and solitary or grouped dead water storage cells, called tracheids by Carlquist & Schneider (2007). In all other succulent plants examined the water-storage cells are living.

**Ecology:** With nocturnal white flowers, emitting a strong sweet scent, sansevierias are typically phalaenophilous, specifically sphingophilous. This pollination syndrome was observed by Newton (1994) and photographs of hawkmoths visiting flowers were shown by Rulkens & Baptista (2009a) and Mansfeld (2013b). An early morning visit to *Sansevieria* flowers by a sunbird was not regarded as effecting pollination (Newton 2004).

It has been reported that some wild animals chew leaves of sansevierias without swallowing them, perhaps for moisture content, including baboon (Newton & Mbugua, 1993), elephant (Newton 2009b) and rhinoceros (Newton 2003b), or possibly even for medicinal purposes (Newton 2003b).

**Ethnobotany:** Some species have been used at a local level as a source of cordage fibre, giving rise to such vernacular names as “Bowstring hemp” and “African sisal”. Hybrids with improved fibre quality have been produced in the USA (Joyner & al. 1951; Wilson 1962). Arising from their popularity as ornamentals, numerous cultivars have been described, especially with varying degrees of variegation, and some cases of small-growing (“dwarf”) variants. Jankalski (2009b) compiled a list of known hybrids and cultivars. Several other uses were documented by Khalumba & al. (2008), Takawira-Nyenyema & Stedje (2011), and Takawira-Nyenyema & al. (2014).

The following names are of unresolved application but are referred to this genus: *Sansevieria cylindrica* Baum (1903) (*nom. illeg.*, Art. 53.1); *Sansevieria ehrenbergii* K. Schumann (1900) (*nom. illeg.*, Art. 53.1); *Sansevieria fulvocincta* Haworth (1819); *Sansevieria glauca* Haworth (1812); *Sansevieria guineensis* var.  $\gamma$  Schultes (1829); *Sansevieria laetevirens* Haworth (1812); *Sansevieria polyphylla* Haworth (1812); *Sansevieria pumila* Spin (1818) (*nom. illeg.*, Art. 53.1); *Sansevieria stenophylla* Link (1821); *Sansevieria striata* G. Don *ex* Steudel (1841) (*nom. inval.*, Art. 32.1c); *Sansevieria venosa* G. Don *ex* Steudel (1841) (*nom. inval.*, Art. 32.1c).

**S. aethiopica** Thunberg (Prodr. Fl. Cap., 65, 1794). **Type:** RSA, Eastern Cape (*Thunberg* s.n. [UPS]). — **Dist:** Botswana, Namibia,



**Fig. 1** *Sansevieria aethiopica*. (Copyright: L. E. Newton)

Malawi, Moçambique, Zimbabwe, RSA (Northern Cape, North-West Prov., Eastern Cape, Gauteng); dry open places or bushland on well-drained soil. **I:** Obermeyer & al. (1992: 6). – Fig. 1.

≡ *Dracaena aethiopica* (Thunberg) Byng & Christenhusz (2018); **incl.** *Alettris hyacinthoides* var. *zeylanica* Aiton (1789) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria zeylanica* Redouté (1809) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria glauca* Gérôme & Labroy (1903) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria thunbergii* Mattei (1918) (*nom. illeg.*, Art. 52.1); **incl.** *Sansevieria caespitosa* Dinter (1926); **incl.** *Sansevieria scabrifolia* Dinter (1932); **incl.** *Sansevieria transvaalensis* hort. *ex* Morgenstern (1979) (*nom. inval.*, Art. 36.1, 37.1).

[3c] Acaulescent, rhizomatous; rhizome  $\pm 1$  cm  $\varnothing$ ; **L** 13–30, rosulate, ascending-spreading, linear or linear-lanceolate, 13–43  $\times$  1–2 cm, upper surface concave, base sometimes slightly narrowed, gradually narrowed above the middle

to a subulate green tip 1.6–2.5 mm long, soon becoming white, otherwise dark green with bluish hue,  $\pm$  glaucous, sometimes with paler green transverse bands, margin red or whitish, surface slightly rough; **Inf** 35–75 cm, simple, elongate, fertile portion dense, 4–6 **Fl** per cluster; **Bra** ovate-lanceolate, acute, 0.5–1 mm; **Ped** to 5 mm; **Fl** white, sometimes purple or cream, tube 20–35 mm, lobes 15–20 mm.

Croix (2010) includes Malawi and Moçambique in the distribution as new records. Mbugua (2007) described a plant in Kenya as *S. aethiopica* ssp. *itumei* (as ‘itumea’), but this is now regarded as a separate species (see *S. itumei*) (Newton 2016).

**S. arborescens** Cornu ex Gérôme & Labroy (Bull. Mus. Hist. Nat. (Paris) 9: 170, 172–173, ills., 1903). **Type** [neo]: Kenya, Coast Prov. (Ngwiri s.n. in Newton 5884 [EA]). — **Lit**: Newton (2009a). **Distr**: Kenya, N Tanzania; lowland *Acacia* bushland, 40–375 m. **I**: *Sansevieria* J. 3(1): 36–37, 1994.

$\equiv$  *Dracaena arborescens* (Cornu ex Gérôme & Labroy) Byng & Christenhusz (2018).

[1] Caulescent, rhizomatous, rhizome 1 cm  $\varnothing$ , pale brown; stem erect, to 20–150  $\times$  2–2.5 cm; **L** many, densely spiralled, spreading or recurved, lanceolate or linear-lanceolate, upper surface concave, 15–22  $\times$  2–4.5 cm, base scarcely or slightly narrowed, green with whitish or reddish slightly wavy margin, surface smooth, with a 8.5–25.4 mm pale brown stout pungent subulate tip; **Inf** 50 cm, paniculate, lower branches to 8 cm, fertile portion subdense, 4–6 **Fl** per cluster; **Bra** triangular, 2 mm; **Ped** 3 mm; **Fl** white, tube 6 mm, lobes 9 mm.

Originally described with flowers unknown. Cornu labelled living plants with the name, but did not publish it. Brown (1915) erroneously applied this name to the plants later described as *S. dumetescens* and *S. ascendens*.

**S. ascendens** L. E. Newton (Bradleya 28: 19–21, ills., 2010). **Type**: Kenya, Coast Prov. (Newton 5842 [K, EA]). — **Distr**: S Kenya, N Tanzania; dry bushland, 160–350 m.

$\equiv$  *Dracaena ascendens* (L. E. Newton) Byng & Christenhusz (2018).

[1] Caulescent, rhizomatous; rhizome 2 cm  $\varnothing$ , yellow-buff in colour; stem unbranched, to 1.5 m, erect or becoming decumbent; **L** spiral, spreading, to 60  $\times$  3 cm, 10–15 mm thick, canalliculate above, narrowed to a pungent 1 cm red-brown spine-like tip, mid-green, lower surface with 10–15 dark green longitudinal lines for most of the length, margin 1 mm, red-brown with whitish fraying edge, both surfaces smooth; **Inf** to 1 m  $\times$  35 cm, paniculate with  $\pm$ 20 ascending branches, lower ones to 40 cm with secondary branching, fertile portion erect, to 21 cm, subdense, 4–6 **Fl** per cluster; **Bra** rounded, 1  $\times$  2 mm, base brownish, white above; **Ped** 3 mm, pale green; **Fl** white, finely speckled brown, tube 5  $\times$  3 mm, lobes 8  $\times$  1.5 mm.

Suggested to be the hybrid *S. dumetescens*  $\times$  *S. ehrenbergii* by Jankalski (2015), but this is unlikely, as *S. ascendens* is known from 3 distinct populations, and *S. ehrenbergii* is not recorded from anywhere near this area (Newton 2016).

**S. aubrytiana** Carrière (Rev. Hort. (Paris) 33: 448–449, 1861). **Type**: Gabon (*Aubry le Comte* s.n. [P]). — **Distr**: Angola, Gabon, Tanzania; dry areas.

$\equiv$  *Dracaena aubrytiana* (Carrière) Byng & Christenhusz (2018); **incl.** *Sansevieria bracteata* Baker (1878).

[3c] Acaulescent, rhizomatous; **L** erect, lanceolate, 38–60  $\times$  5–7 cm, base narrowed from the middle or below into a channelled petiole, dark green with wide pale green irregular bands or blotches on both surfaces, glaucous, narrowed above to a  $\geq$ 6.4 mm tip, margin hard, brownish-red, sometimes with whitish edge; **Inf** 45–60 cm, simple, elongated, fertile portion 5–6 cm, dense; **Bra** lanceolate or oblong-lanceolate, acute, 1.3–1.9 mm; **Ped** 2–3 mm; **Fl** white, tube 88–114 mm, lobes  $\pm$ 25–32 mm.

The first edition of this handbook, as well as Mbugua (2007) treat this as *S. bracteata*, but the name *S. aubrytiana* has priority. Treated as a doubtful species by Lebrun & Stork (2014), though accepted by Chahinian (2005a) and Mansfeld (2015a). Lebrun & Stork (2014) also treat *S. bracteata* as distinct.

**S. bacularis** Pfennig *ex* A. Butler & Jankalski (Sansevieria 22: 3–4, ills. (pp. 3–7), 2010). **Type:** Democratic Republic of the Congo [Zaire], Kivu Prov. (*Bequaert* 5367 [BR]). — **Distr:** E Democratic Republic of the Congo [Zaire] (Sud-Kivu). **I:** Mansfeld (2015b).

≡ *Dracaena bacularis* (Pfennig *ex* A. Butler & Jankalski) Byng & Christenhusz (2018); **incl.** *Sansevieria cylindrica* De Wildemans (1921) (*nom. illeg.*, Art. 53.1).

[3b] Acaulescent, rhizomatous; **L** 1–2, usually upright, cylindrical or slightly compressed, 125–170 × 1.1–1.5 cm, apex soft, dark green with lighter cross banding, verrucose, somewhat rough, base sheathed in 2.5 × 2–3 cm cataphylls, deep purple, pale brown when dry; **Inf** to 115 cm, simple, elongated, fertile portion 30–45 × 7.5 cm, semidense, 2–8 **Fl** per cluster; **Bra** lanceolate, 5–10 mm; **Ped** 6–7 mm; **Fl** white with purple stripes, tube 5 × 2.5 mm, lobes 15–17 × 2–2.5 mm.

The name was proposed by Pfennig and appeared in print by other authors without validation until 2010.

**S. bagamoyensis** N. E. Brown (Bull. Misc. Inform. Kew 1913: 306, 1913). **Type:** Tanzania, Bagamoyo Distr. (*Sacleux* 672 [P]). — **Lit:** Newton (2012b: with ills.). **Distr:** N Tanzania; half-shade of coastal bushland, 100–200 m.

≡ *Dracaena bagamoyensis* (N. E. Brown) Byng & Christenhusz (2018).

[1] Caulescent, rhizomatous; rhizome 1–1.5 cm Ø, pale brown; stem erect to 2 m; **L** spiralled, recurved or recurved-spreading, linear-lanceolate or linear, upper surface concave, 34–40 × 1.6–2.5 cm, dark green, narrowed to a ≥4.2 mm brown hard spine-like tip, margin narrowly red-brown with white membranous edge, surface smooth; **Inf** 40–55 cm, paniculate, fertile portion lax, ± 6 **Fl** per cluster; **Bra** lanceolate-acute, 2–3 mm; **Ped** to 6 mm; **Fl** cream-white, tube 6–7 mm, lobes ±6.5 mm.

**S. ballyi** L. E. Newton (Brit. Cact. Succ. J. 22(1): 11–13, ills., 2004). **Type:** Kenya, Coast Prov. (*Newton* 5594 [K, EA]). — **Lit:** Mansfeld (2016a: history of discovery, with ills.); Jankalski

(2016: synopsis cultivars). **Distr:** Kenya, Tanzania.

≡ *Dracaena ballyi* (L. E. Newton) Byng & Christenhusz (2018).

**S. ballyi** var. **ballyi** — **Lit:** Newton (2010). **Distr:** S Kenya, N Tanzania; rocky areas, often in shade, 65–975 m.

**Incl.** *Sansevieria tsavoensis* Pfennig *ex* Heitz & Zeller (1990) (*nom. inval.*, Art. 36.1, 37.1).

[3a] Acaulescent, stoloniferous; branching freely above ground; stolons to 18 cm; **L** 6–10, rosulate, spreading, almost cylindrical, 6–12 × 6–9 cm, with a groove on the upper surface from the base to  $\frac{2}{3}$ – $\frac{3}{4}$  of the leaf length, narrowed to a pungent 7 mm red-brown spine-like tip, with alternating bands of dark and light green, margins of the groove with red-brown line and narrow white edge, surface rough; **Inf** to 15.5 cm, simple, elongated, fertile portion to 8 cm, subdense, 2 **Fl** per cluster; **Bra** triangular, 3 × 3 mm; **Ped** 1–2 mm; **Fl** pale pink, tube 18–22 × 2–2.7 mm, lobes 10–13 × 1.5 mm, whitish inside.

For many years cultivated as *Sansevieria* ‘Bally 12681’. No herbarium specimen was deposited by Bally, but the type was collected at the same locality. *S. gracilis* var. *humbertiana* in the sense of Mbugua (2007) belongs here.

Mansfeld & Budweg (2015a) describe a cross with *S. parva* (male), and report that the reciprocal cross was not possible.

**S. ballyi** var. **robertsoniae** L. E. Newton (Sansevieria 33: 11–12, ill., 2015). **Type:** Kenya, Coast Prov. (*Newton & al.* 5981 [EA]). — **Distr:** S Kenya (Coast Prov.); savanna woodland, in shade, 100 m.

≡ *Sansevieria ballyi* ‘Ann Robertson’ L. E. Newton (2010).

[3a] Differs from var. *ballyi*: **L** with paler colour and very smooth surface.

First described in 2010 as the cultivar *S. ballyi* ‘Ann Robertson’.

**S. bella** L. E. Newton (Cact. Succ. J. (US) 72 (4): 224–226, ills., 2000). **Type:** Kenya, Rift Valley Prov. (*Newton* 3945 [K, EA]). — **Distr:** S



Kenya; under shrubs or amongst rocks in dry bushland, 1700–2030 m.

≡ *Dracaena bella* (L. E. Newton) Byng & Christenhusz (2018).

[3a] Caulescent, with runners, branching freely above ground; runners spreading or ascending, to 15 cm; **L** up to 8, ± distichous, ascending, cylindrical with a groove on the upper surface from the base to ±¼ of their length, to 70 cm, to 3.5 cm thick, with distinct dark and light green transverse bands and darker green narrow longitudinal lines, tip a red-brown spine to 5 mm, pungent or relatively blunt, margins with a red-brown line and a narrow colourless flange, surface very rough; **Inf** to 60 cm, simple, elongated, peduncle light green with a slight bloom, fertile portion to 55 cm, dense, up to 7 **Fl** per cluster; **Bra** triangular, 3 × 2 mm; **Ped** to 5 mm; **Fl** white, tube 10–15 mm, lobes 13–18 mm.

Close to *S. suffruticosa* and possibly better treated as a variety of that.

**S. bhitalae** R. H. Webb & L. E. Newton (Sansevieria 37: 12–15, ills., 2018). **Type:** Tanzania, Iringa Region (*Bhitala* 1000 [MO]). — **Distr:** Tanzania (Iringa Region); in deep shade on hill-slopes and on old anthills, 1360 m.

[2] Rhizomatous, acaulescent; **L** 1–3, erect, laterally compressed (folded) with a dorsal broad U-shaped groove 1.2 cm deep, 40–90 × 5–7 cm, yellow-green to blue-grey-green, with yellow-green mottling that ranges from prominent to very faint, and upper surface with faint longitudinal striations (up to 8 near the base) nearly the entire leaf length, surface smooth; **Inf** capitate; peduncle reddish, 15 cm, clusters with 2–3 flowers; **Bra** broadly ovate, 16 × 5 mm; **Fl** white to lilac with a purple-violet blush, tube 75 mm, lobes 28 mm.

There is a juvenile form, possibly persistent for a few years, with 2–6 leaves, ovate-elliptical to oblanceolate, blue-green to grey-green, mottled with yellow-green markings and lines, rigid and nearly prostrate to spreading with a pointed tip and a red leaf margin with some shredding white fibres.

**S. braunii** Engler & K. Krause (Bot. Jahrb. Syst. 45: 153–154, 1911). **Type:** Tanzania,

Kigoma (*Braun* s.n. [EA]). — **Distr:** SW Tanzania; woodland in deep shade, 500–1160 m.

≡ *Dracaena testudinea* Byng & Christenhusz (2018).

[2] caulescent, rhizomatous, rhizome 3 cm Ø, brownish-orange; **L** usually 2, lanceolate-oblong, 50–70 × 7–11 cm, base slightly narrowed, green with few whitish bands or blotches, tip acuminate, margin hardened, red-brown; **Inf** 45 cm, simple, cylindrical, peduncle reddish, fertile portion 15 cm Ø, dense; **Bra** lanceolate-acute, 20 × 6 mm; **Ped** 10 mm; **Fl** white, tube ±82 mm, lobes ±25–30 mm.

The plants treated as *S. braunii* by Mbugua (1998) are *S. frequens*.

**S. burdettii** Chahinian (Brit. Cact. Succ. J. 18 (3): 132–133, ills., 2000). **Type:** Malawi, Southern Region (*Burdett* s.n. in *Chahinian* 318 [K, MO]). — **Lit:** Rulken & Baptista (2013); Thiede & Campbell-Barker (2015). **Distr:** C to S Malawi, NE Moçambique; rocky woodland, 100–500 m.

≡ *Dracaena burdettii* (Chahinian) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; rhizome to 4 cm Ø, orange; **L** 3–6, distichous, slightly spreading, cylindrical with a groove on the upper surface from the base to ⅓ to ½ of the leaf length, to 90 cm, base 2.5 cm wide, dark green with several longitudinal lines, sometimes with faint transverse bands on young leaves, margins green with a withered non-fibrous flange, tip a withered spine, surface smooth, waxy; **Inf** 16–20 cm, simple, elongated, peduncle green with small white spots, fertile portion 12–14.75 cm, dense, 4–6 **Fl** per cluster; **Bra** 1–2 mm; **Ped** 4 mm; **Fl** white tinged pinkish-brown, tube 20–25 mm, lobes 18–20 mm.

Type cited erroneously as *Chahinian* 316 in the protologue.

**S. burmanica** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 228–230, Fig. 12, 1915). **Type:** Myanmar, Mandalay Prov. (*Clayton* s.n. [K]). — **Lit:** Mansfeld & Ott (2015). **Distr:** N Myanmar, S India (Tamil Nadu); scrub forest, ± 100 m. **I:** Mansfeld (2016b).



≡ *Dracaena burmanica* (N. E. Brown) Byng & Christenhusz (2018); **incl.** *Sansevieria roxburghiana* Hooker *fil.* (1896) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria maduraiensis* Binojkumar (2002).

[3c] Acaulescent, rhizomatous; rhizome 1.25–1.8 cm Ø; **L** 8–18, rosulate, erect, linear or linear-lanceolate, flat or upper surface concave, 45–76 × 1–3.2 cm, green with paler transverse bands, upper surface with 1–3 longitudinal striations, lower surface with 6–9 striations, narrowed above to a 2.5–10 cm green soft subulate tip, margin green, becoming whitish with age, surface smooth; **Inf** 60–76 cm, simple, elongated, fertile portion lax, 2–5 **Fl** per cluster; **Bra** lanceolate, acute, 2–4 mm; **Ped** 7.5–8.5 mm; **Fl** greenish-white, tube 7.5–8.5 mm, lobes 8.5 mm.

After being lost in cultivation for many years, this species was rediscovered in habitat in 1982 (Mansfeld & Ott 2015).

**S. canaliculata** Carrière (Rev. Hort. (Paris) 33: 449, 1861). **Type** [neo]: Comores, Mayotte (*Boivin* 3079 [P, BM]). — **Distr:** Madagascar, Comores, N Moçambique, Tanzania; sandstone outcrops, 50–100 m. **I:** Brown (1915: 224).

≡ *Dracaena canaliculata* (Carrière) Byng & Christenhusz (2018); **incl.** *Sansevieria sulcata* Bojer *ex* Baker (1875) (*nom. inval.*, ICN Art. 36.1c); **incl.** *Sansevieria sulcata* Baker (1887); **incl.** *Sansevieria schimperi* Baker (1898); **incl.** *Sansevieria livingstoniae* Rendle (1932); **incl.** *Sansevieria pfennigii* Mbugua (2007).

[3b] Acaulescent, rhizomatous; rhizome 1–1.25 cm Ø; **L** 1–2, to 5 cm apart along the rhizome, erect or slightly curved, cylindrical or slightly laterally compressed, with 5–6 shallow longitudinal grooves, 15–76 cm, 1–2 cm thick, dark green, narrowed shortly to a whitish hard acute tip, surface almost smooth; **Inf** 5–16 cm, simple, elongated, fertile portion lax, **Fl** usually 3 per cluster, solitary near the tip; **Bra** ovate-acute, ± 4 mm; **Ped** 1–1.6 mm; **Fl** white tinged green, tube 25 mm, lobes 17 mm. — **Cytology:** 2n = 42 (Sharma & Chaudhuri 1964).

Described from a cultivated plant of unknown origin. Brown (1915) cited a specimen from

Somalia, but Thulin (1995) found no material agreeing with the description. The species was reported by Perrier (1938) to be naturalized in Madagascar.

**S. caulescens** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 200, Fig. 2A–B, 1915). **Type:** Kenya (*Powell* s.n. [K]). — **Distr:** Kenya.

≡ *Dracaena caulescens* (N. E. Brown) Byng & Christenhusz (2018).

[3a] Caulescent; stem erect, to 60 × 2.5–3.8 cm, branching at the base; **L** many, densely spiralled, spreading and slightly recurved, cylindrical with a groove along the upper face almost to the tip, 45–84 × 2–3.4 cm, 1.3–1.8 cm thick, dark green, lower surface with 9–12 dark longitudinal striations, with whitish edges, when young with indistinct transverse dark green bands, gradually narrowed to a firm green tip becoming pale brown or whitish, surface slightly rough; **Inf** 60–70 cm, simple, elongated, fertile portion ±40–46 cm, dense, 6–12 **Fl** per cluster; **Bra** very small, inconspicuous; **Ped** 7.4–9.5 mm; **Fl** whitish, tube 15 mm, lobes 19 mm.

I am not aware of any recent field gatherings matching this description. Lebrun & Stork (2014) followed Mbugua (2007) in treating this as a synonym of *S. gracilis*, but that species has stems that rarely exceed 8 cm in length.

**S. chahinianii** R. H. Webb & Myklebust (Sansevieria 37: 6–7, ills., 2018). **Type:** Somalia (*Specks* 14026 [MO]). — **Distr:** E Somalia (W of Eyl); mixed savanna, 180 m.

[3c] Acaulescent, rhizomatous, rhizomes to 20 cm; **L** (1–) 2 (–4), ascending to spreading, oblanceolate, 10–25 × 6–7 cm, grey-green with dark green irregular transverse bands, with a shallow central channel bearing longitudinal lines that are more prominent towards the base, tip 5 mm, white, chartaceous, margin entire, with outer thin white line adjacent to a thin red line, upper surface smooth, lower surface very rough; **Inf** 33 cm, simple, fertile portion to 15 cm, subdense, with 2 flowers per cluster; **Bra** triangular, scarious, 2 × 5 mm; **Ped** 1–2 mm; **Fl** yellow-white, tube 20–22 mm, lobes ±15 mm.

**S. concinna** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 233–234, Fig. 14, 1915). **Type:** Moçambique, Sofala Prov. (*Dawe* 1 [K]). — **Distr:** Moçambique, Tanzania, Zimbabwe, NE RSA (KwaZulu-Natal); in the shade of coastal forest in sandy soil. **I:** Jaarsveld (1994).

≡ *Dracaena spathulata* Byng & Christenhusz (2018) ≡ *Sansevieria subspicata* var. *concinna* (N. E. Brown) Mbugua (2007).

[3c] Acaulescent, rhizomatous; rhizome ±1.25 cm Ø; **L** ± 5, rosulate, ascending-spreading, lanceolate, 15–25 × 1.25–3 cm, base shortly narrowed to a 3.8–8.9 cm channelled petiole, green with pale green transverse bands, with a 4.2–8.5 mm green subulate tip, margin scarcely hardened, green, surface smooth; **Inf** 15–30 cm, simple, elongate, peduncle green, tinged and dotted purple, fertile portion subdense, 1 or 2 **Fl** per cluster; **Bra** lanceolate-acuminate, 6–8.5 mm; **Ped** 3–4 mm; **Fl** white, tube 45 mm, lobes 21 mm.

Treated as a variety of *S. subspicata* by Lebrun & Stork (2014), but accepted by Chahinian (2005a) and Mansfeld (2015a).

**S. conspicua** N. E. Brown (Bull. Misc. Inform. Kew 1913: 306, 1913). **Type:** Kenya, Coast Prov. (*Powell* 12 [K]). — **Distr:** Kenya, Malawi, Tanzania; coastal thicket and grassland, to 375 m. **I:** Powys (1996). – Fig. 2.

≡ *Dracaena conspicua* (N. E. Brown) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome 1.7–1.9 cm Ø; **L** 3–5, rosulate, ascending-spreading, lanceolate, 23–76 × 5–8.3 cm, base narrowed from below the middle, dull green, upper surface with darker longitudinal striations, with a 2.1–3.2 mm hard tip, margin hardened, reddish-brown and edged white, surface smooth; **Inf** to 60 cm, simple, elongated, peduncle greyish-green tinged dull purple, fertile portion 25.5–30 cm, dense, 1–3 **Fl** per cluster; **Bra** linear-lanceolate, 0.6–1.3 mm; **Ped** 0.4–0.6 mm; **Fl** greenish-white below, white above, tube 38–42 mm, lobes 25–32 mm.

**S. cylindrica** Bojer ex Hooker (Curtis's Bot. Mag. 85: t. 5093 + text, 1859). **Type:** Angola



**Fig. 2** *Sansevieria conspicua*. (Copyright: L. E. Newton).

(*Welwitsch* 3749 [K, P]). — **Distr:** Angola, Zambia, Zimbabwe.

**S. cylindrica** var. *cylindrica* — **Distr:** Angola, Zambia, Zimbabwe.

**Incl.** *Sansevieria angolensis* Welwitsch ex Hooker (1858) (*nom. inval.*, Art. 32.1d) ≡ *Dracaena angolensis* (Welwitsch ex Carrière) Byng & Christenhusz (2018); **incl.** *Sansevieria guineensis* Weiner (1887) (*nom. illeg.*, Art. 53.1).

[3b] Acaulescent, rhizomatous; rhizome 2.5–3.8 cm Ø; **L** 3–4, distichous, erect, cylindrical or slightly laterally compressed, 60–150 cm, 2–3 cm thick, green or whitish-green, with dark green transverse bands, gradually narrowed to a 4.2–6.4 mm hard whitish acute tip, surface slightly rough; **Inf** 60–90 cm, simple, elongated, fertile portion 38–75 cm, 5–6 **Fl** per cluster; **Bra** lanceolate or ovate-lanceolate, 4–10 mm; **Ped** 4–8.5 mm; **Fl** white or tinted, tube 17–25 mm, lobes 17–19 mm. — **Cytology:** 2n = 40 (Roy

1956), 92 (Sharma & Chaudhuri 1964), 102–104 (Darlington & Wylie 1955).

**S. cylindrica** var. **patula** N. E. Brown (Bull. Misc. Inform. Kew 1915 (5): 218–219, Fig. 5D, 1915). **Type:** Angola (*Anonymus* s.n. [K]). — **Distr:** Angola.

[3b] Differs from var. *cylindrica*: **L** 3–6, diverging, recurved or spreading; **Fl** tube 11.5–19 mm, lobes 15–19 mm.

Not recognised by Croix (2010), who suggests that it should probably be treated only as a cultivar.

**S. dawei** Stapf (J. Linn. Soc., Bot. 37: 529, 1906). **Type:** Uganda, Central Distr. (*Dawe* 109 [K]). — **Lit:** Mbugua (2003). **Distr:** Kenya, Uganda, Burundi; open woodland, 600–1300 m.

≡ *Dracaena dawei* (Stapf) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome to  $\geq 2.5$  cm  $\varnothing$ , pale brown; **L** 2–3, ascending or suberect, lanceolate, 60–150  $\times$  5.7–11 cm, base narrowed from below the middle to a long or short channelled petiole, dull dark green and glaucous, narrowed above the middle to an acute tip, margin reddish-brown, upper surface smooth, lower surface slightly rough; **Inf** 45–75 cm, simple, elongated, dense, 3–4 **Fl** per cluster; **Bra** ovate or ovate-oblong, acute or subobtusate, 8.5–17 mm; **Ped** 4–6 mm; **Fl** white, tube 19–25 mm, lobes 17–22 mm.

Mansfeld (2014b) suggests that *S. dawei* should be included in the synonymy of *S. forskaoliana*, though he did not examine material from the type locality, in Uganda.

**S. dhofarica** T. A. McCoy & Lavranos (Avonia 35(1): 65, ill. (pp. 64–67), 2017). **Type:** Oman, Dhofar (*McCoy* 5014 [FT]). — **Distr:** Oman (Dhofar); limestone hills,  $\pm$  80 m.

[1] Acaulescent, rhizomatous, forming large clumps; rhizome 2–2.3 cm  $\varnothing$ , greyish-tan; **L** 4–5, distichous, ascending, laterally compressed, deeply channelled low down, 50–60  $\times$  5–6 cm, 5–7 cm thick at the base, with 4–7 deep grooves on the flattened sides, light to dark green, surface slightly rough, margin entire,

reddish-brown, with thin membranous edge, tip acute, pungent; **Inf** 100 cm, with 6–12 **Br**, peduncle green or reddish-green; fertile portion 6–8 cm, 4–7 **Fl** per cluster; **Bra** attenuate-acute, 0.2  $\times$  0.1 mm, green; **Ped** 0.3 mm; **Fl** tube 12 mm, colour and lobe size not given in the protologue.

**S. dooneri** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 231–233, Fig. 13A–B, 1915). **Type:** Kenya, Rift Valley Prov. (*Dooner* s.n. [K]). — **Lit:** Newton (2003a). **Distr:** Kenya, Tanzania; shade in dry forest,  $\pm$  2000–2100 m.

≡ *Dracaena dooneri* (N. E. Brown) Byng & Christenhusz (2018).

[3c] Acaulescent or shortly caulescent, rhizomatous or with runners; rhizome 0.6–0.85 cm  $\varnothing$ ; stem to 5 cm, concealed by leaf bases; **L** to 20, in lax rosettes, lanceolate or lorate, base erect or ascending, recurved-spreading above, 10–43  $\times$  1.5–3 cm, base gradually narrowed from near or above the middle, dark green, lower surface slightly paler, both surfaces with faint and irregular pale green transverse bands, shortly narrowed to a 6–50 mm green soft subulate tip, margin green, surface smooth; **Inf** 30–38 cm, simple, elongated, peduncle green, fertile portion 15–19 cm, lax, 2–3 **Fl** per cluster; **Bra** ovate-lanceolate, acute, 2–4 mm; **Ped** 3–4 mm; **Fl** dull pink or pale purplish, whitish inside, tube  $\pm$  12 mm, lobes 11.6–12.7 mm.

Similar to, and possibly conspecific with, *S. parva*, whose type locality is only  $\pm$  55 km away from that of this species. Included in *S. parva* by Mbugua (2007), Lebrun & Stork (2014) and Mansfeld (2015a), though regarded as distinct by Chahinian (2005a).

**S. downsii** Chahinian (Brit. Cact. Succ. J. 18 (3): 133–135, ill., 2000). **Type:** Malawi, Northern Region (*Downs* 1/75 [K, MO]). — **Lit:** Thiede & al. (2009: with ill.). **Distr:** N Malawi, NE Zambia; dry woodland, 1000–1500 m.

≡ *Dracaena downsii* (Chahinian) Byng & Christenhusz (2018).

[3a] Acaulescent, with runners, runners to 2 cm  $\varnothing$ , covered with leaf sheaths; **L** 6–14, rosulate, spreading-recurved, cylindrical with a groove on

the upper face from the base to  $\frac{1}{4}$ – $\frac{4}{5}$  of the leaf length, 14–45 cm, base 3.2 cm wide, medium bluish-green with sparse grey-green transverse bands and dark green longitudinal lines, margins with a chestnut-brown line and a narrow colourless flange, tip a spine, sometimes chestnut-brown, surface slightly rough, somewhat shiny, waxy; **Inf** to 1.6 m, simple, elongated, peduncle medium green, speckled, fertile portion  $< \frac{2}{3}$  of the peduncle length, lax, 3–5 **Fl** per cluster; **Bra** 1–2 mm; **Ped** 3 mm; **Fl** white tinged green, tube  $\pm 10$  mm, lobes  $\pm 12$  mm.

The plants reported from Malawi as possibly being *S. gracilis* by Thiede (1993) are *S. downsii*.

**S. dumetescens** L. E. Newton (Bradleya 27: 156–158, ills., 2009a). **Type:** Kenya, Kilifi Distr. (Newton 3761 [K, EA]). — **Distr:** S Kenya; dry bushland, 100–200 m.

≡ *Dracaena dumetescens* (L. E. Newton) Byng & Christenhusz (2018).

[1] Caulescent, rhizomatous, forming dense clumps to 2 m  $\varnothing$  or more; rhizome 1.8–2.3 cm  $\varnothing$ , pale brown; stem erect, to 1.6 m  $\times$  2–2.5 cm; **L** spiral, spreading or recurved, lanceolate or linear-lanceolate, 40–55  $\times$  3–4.5 cm, narrowed to a pungent 13–17 mm pale brown spine-like tip, green with whitish or reddish slightly wavy margin, both surfaces smooth; **Inf** to 55 cm, paniculate, with up to 18 **Br**, the lowest to 20 cm with secondary branching, fertile portion subdense, 4–6 **Fl** per cluster; **Bra** triangular, 1–2  $\times$  1 mm, colourless; **Ped** 3 mm; **Fl** white, tube 6  $\times$  2.5 mm, lobes 9  $\times$  1.8 mm.

Here belongs *S. arborescens* in the sense of Brown (1915).

**S. ebracteata** (Cavanilles) C. R. Suresh (in Nicolson, Interpret. Van Rheede's Hort. Malab., 271, 1988). **Type:** [icono] Rheede, Hort. Malab. 11: 83, t. 42, 1692. — **Lit:** Mansfeld & Ott (2015). **Distr:** S India (Kerala, Karnataka, Tamil Nadu, Hyderabad); sandy places.

≡ *Salmia ebracteata* Cavanilles (1795) ≡ *Dracaena ebracteata* (Cavanilles) Byng & Christenhusz (2018); **incl.** *Aletris zeylanica* var.  $\beta$  Lamarck (1783); **incl.** *Sansevieria lanuginosa* Willdenow (1797) (*nom. illeg.*, Art. 52.1) ≡ *Acynta*

*lanuginosa* (Willdenow) Kuntze (1891) (*nom. illeg.*, Art. 52.1).

[3b] Acaulescent, rhizomatous; rhizome stout; **L** 3–5, erect, semiterete with concave channel down the upper surface and several grooves down the lateral and lower surfaces, 45–90  $\times$  1.7–2 cm, narrowed to an acute tip, green with “woolly” grooves, surface rough; **Inf**  $\pm 60$  cm, simple, elongated, density unknown, 2–5 **Fl** per cluster; **Ped**  $\pm 4.2$  mm; **Fl** whitish-green, tube 8.5–10 mm, lobes 10–15 mm.

**S. ehrenbergii** Schweinfurth ex Baker (J. Linn. Soc., Bot. 14: 549, 1875). **Type:** Sudan (*Schweinfurth* 31 [B?, K, P]). — **Distr:** Yemen, Djibouti, Eritrea, Ethiopia, Kenya, Somalia, Sudan, Tanzania, Uganda; rocky ground, usually in the shade of thickets or small trees, 400–1100 m. **I:** Teketay (1995).

[1] Acaulescent or caulescent, rhizomatous; rhizome 3 cm  $\varnothing$ ; stem erect, to 25 cm; **L** 5–9, distichous, erect or spreading, laterally compressed with a groove along the upper surface, 76–180 cm, 3–4.5 cm thick, narrowed to an abrupt 6.5–20 mm hard spine-like tip, dark green with 5–12 blackish-green shallow longitudinal grooves, margin reddish-brown with white membranous edge, surface slightly rough; **Inf** to 2 m, paniculate, fertile portion with 4–7 **Fl** per cluster; **Ped** 2–4 mm; **Fl** purple to white, tube 5–6.5 mm, lobes 7–18 mm. — **Cytology:**  $2n = 40$  (Sharma & Chaudhuri 1964).

Often confused with *S. robusta*, and possibly not as widespread as shown above (from literature records). The species is quite variable. Some more robust variants reported in Yemen (Vrskovy 2009) are probably *S. dhofarica*.

**S. eilensis** Chahinian (*Sansevieria* J. 4(1): 9–11, ills., 1995). **Type:** Somalia, Nugaal Distr. (*Lavranos & Horwood* 10178 [MO, UPS]). — **Distr:** E Somalia; shaded limestone,  $\pm 120$  m. **I:** Lavranos (1994: as *S. sp.*). — Fig. 3.

≡ *Dracaena eilensis* (Chahinian) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; **L** 2–3, mostly distichous, cylindrical, sometimes with a groove on the upper surface, 7–18 cm, 1.9–2.5 cm thick,





**Fig. 3** *Sansevieria eilensis*. (Copyright: J. Trager).

narrowed from the middle to the base, narrowed abruptly to a 5 mm acute spine-like tip, medium grey-green, with light grey-green transverse bands and up to 12 medium green longitudinal lines, margin green becoming brown edged white, surface rough; **Inf** 34 cm, simple, spike-like, peduncle light green, fertile portion 23 cm, lax, 2–4 **Fl** per cluster; **Bra** 2–6 × 1–3 mm; **Ped** 4–5 mm; **Fl** greenish-white, tube ±8 mm, lobes ±14 mm.

The type citation *Lavranos* 10179 in the protologue is an error.

**S. elliptica** (Chiovenda) Chiovenda ex Guidotti (Agric. Colon. 26: 549, 1932). **Type**: not typified. — **Distr**: Somalia, Kenya.

≡ *Acyntha elliptica* Chiovenda (1932); **incl.** *Acyntha abyssinica* var. *sublaevigata* Chiovenda (1932) ≡ *Sansevieria abyssinica* var. *sublaevigata* (Chiovenda) Cufodontis (1971).

[3c] Acaulescent, rhizomatous; rhizome 2 cm Ø; **L** 1–3, erect or slightly spreading-recurved,

elliptic or oblong-elliptic, 16–30 × 9–14 cm, 4–5 mm thick in the middle, distinctly canaliculate, tip broadly and shortly attenuate and acute, margins sometimes undulate, both surfaces dark green with irregular transverse bands of pale grey-green blotches, sometimes irregularly reticulate, margins purple-brownish with narrow white edge, upper surface slightly rough, lower surface very rough; **Inf** 20–35 cm, simple, with 1–2 basal bracts, elongated, fertile portion 15 cm, 3–5 **Fl** per cluster; **Bra** 15–20 × 7–8 mm, lanceolate, acuminate, membranous, whitish; **Fl** unknown.

The protologue does not include details of flowers. Included in *S. forskaoliana* by Thulin (1995) and Mbugua (2007), but Jankalski (2007c) argues for its recognition as a distinct species, with spreading leaves smooth above and rough below, and foliaceous bracts on the peduncle (though see note after *S. forskaoliana*). Included in *S. forskaoliana* by Lebrun & Stork (2014) and Mansfeld (2015a).

**S. erythraeae** Mattei (Boll. Stud. Inform. Reale Giardino Colon. [Palermo] 4: 170, 1918). **Type** [lecto]: Eritrea (*Schweinfurth & Riva* 1468 [K, FT]). — **Lit**: Jankalski (2004). **Distr**: Eritrea, N Ethiopia, Sudan; semi-arid areas along rivers, 1200–2100 m.

≡ *Dracaena erythraeae* (Mattei) Byng & Christenhusz (2018); **incl.** *Sansevieria schweinfurthii* Täckholm & Drar (1954) (*nom. inval.*, Art. 36.1); **incl.** *Sansevieria cylindrica* Schweinfurth (1894) (*nom. illeg.*, Art. 53.1).

[3b] Acaulescent, rhizomatous; **L** 6–8, erect, cylindrical with a short groove on the upper surface and 5 furrows on the lower surface, 40–50 cm; **Inf** to 50 cm, simple, elongated, fertile portion dense, 3–5 **Fl** per cluster; **Bra** ovate-lanceolate, acute; **Ped** 7–8 mm; **Fl** white, tube 5–7 mm, lobes >7 mm.

**S. fasciata** Cornu ex Gêrôme & Labroy (Bull. Mus. Hist. Nat. (Paris) 9: 170, 172–173, Fig. 3, 1903). **Type**: Congo Free State [Democratic Republic of the Congo [Zaire]] (*Dybowski / Lecomte* s.n. [P, K]). — **Distr**: Democratic Republic of the Congo [Zaire].



≡ *Dracaena fasciata* (Cornu ex Gérôme & Labroy) Byng & Christenhusz (2018); **incl.** *Sansevieria lasciata* L. Gentil (1907) (*nom. inval.*, Art. 61.1).

[3c] Acaulescent, rhizomatous; **L** 2–5, recurved-spreading, lanceolate, 38–84 × 3.8–11.5 cm, narrowed from about the middle to the channelled petiole, with a 2.1–6.4 mm green acute tip, upper surface pale green broken into patches by irregular transverse zigzag dark green bands, lower surface whitish-green with irregular narrow transverse dark green bands, margin green, becoming reddish or whitish, surface smooth; **Inf** and **Fl** not known.

Regarded as a plant of uncertain status by Lebrun & Stork (2014).

**S. fischeri** (Baker) Marais (Kew Bull. 41(1): 58, 1986). **Type:** Tanzania, Kilimanjaro Distr. (*Fischer* 9 [B?, K [fragment]]). — **Distr:** S Ethiopia, Kenya, Somalia, Tanzania; sandy soils at edges of thickets and in dense bush, 260–900 m. **I:** Rauh (1963: 126, as *S. singularis*).

≡ *Buphane fischeri* Baker (1898); **incl.** *Sansevieria singularis* N. E. Brown (1911) ≡ *Dracaena singularis* (N. E. Brown) Byng & Christenhusz (2018).

[2] Acaulescent, rhizomatous; rhizome to 4.5 cm Ø; **L** solitary, erect, cylindrical with 4–6 longitudinal furrows, 45–240 cm, narrowed slightly upwards to near the tip, then narrowing shortly to a whitish stout acute tip, dull greyish-green or bluish-green, brighter green with pale green transverse bands when young, surface slightly rough; **Inf** to 10 cm, simple, capitate, peduncle subterranean, fertile portion dense; **Bra** acute, 3–5 × 3 mm; **Ped** 12.7 mm; **Fl** tube 20–50 mm, whitish sometimes tinged with violet, lobes 5–10 mm, white with violet venation outside.

In growth habit and leaves this is very similar to *S. stuckyi*, and as both were described without inflorescences and flowers unknown, the two taxa have been confused in cultivation. Rauh (1963) first described the inflorescence and flowers of *S. fischeri*, and those of *S. stuckyi* were described by Jumelle (1923) and Pfennig (1981), confirming that the two species are distinct. Takawira-Nyenywa (2006) cites specimens from Zimbabwe, but states that it is now extinct there.

**S. formosa** Chahinian (*Sansevieria* 26: 2–5, *ills.*, 2012). **Type:** Malawi (*Burdett* s.n. in *Chahinian* 319 [K, MO]). — **Distr:** Malawi; ecology not described, 140 m.

≡ *Dracaena malawiana* Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome 1.8–2.6 cm Ø; **L** 1–2 or more, margins curved upwards to form a channel, to 50 × 5 cm, tip obtuse, dark greyish-green, sometimes with faint green banding, margins with narrow chestnut-coloured line, surface smooth; **Inf** simple, ± capitate, to 21 cm, fertile portion 10–15 cm Ø, 2–4 **Fl** per cluster; **Bra** triangular, 16–20 × 4–7 mm; **Fl** grey-white, with purple tinge near the base, tube 80–82 × 2 mm, lobes 32–33 × 3 mm.

Examination of specimens from N Malawi (Thiede et al., in press) suggests that the leaves may be up to 100 cm long, slightly spotted or distinctly spotted.

**S. forskaoliana** (Schultes *fil.*) Hepper & Wood (Kew Bull. 38(1): 83, 1983). **Type:** Yemen (*Forskål* 9 [C]). — **Lit:** Hepper & Friis (1994); Friis (1995). **Distr:** Yemen, Sudan, Djibouti, Democratic Republic of the Congo [Zaire], Eritrea, Ethiopia, Somalia, Kenya; dry rocky slopes and river beds, usually in shade, 550–2000 m. **I:** Teketay (1995: 53).

≡ *Smilacina forskaoliana* Schultes *fil.* (1829) ≡ *Dracaena forskaoliana* (Schultes & Schultes *fil.*) Byng & Christenhusz (2018); **incl.** *Convallaria racemosa* Forsskål (1775) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria guineensis* Schweinfurth (1894) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria guineensis* var. *angustior* Engler (1902) ≡ *Sansevieria abyssinica* var. *angustior* (Engler) Cufodontis (1971); **incl.** *Sansevieria abyssinica* N. E. Brown (1913) ≡ *Acyntina abyssinica* (N. E. Brown) Chiovenda (1916).

[3c] Acaulescent, rhizomatous; rhizome ≥2 cm Ø; **L** erect, lanceolate, ≥60 × 6.3–7.5 cm, narrowed from the middle to a channelled petiole 1/5–1/3 as long as the lamina, green, with a ≥ 2.1 mm brown hardened tip, margin wavy, hard, reddish-brown, 0.1 mm, upper surface smooth, lower surface rough, minutely papillose; **Inf** to ≥95 cm, simple, elongated, fertile portion

with 4–5 **Fl** per cluster; **Ped** to 10 mm; **Fl** white, details not known.

The spelling of the epithet is still frequently seen as *forskaliana*, but the form here used is mandatory according to ICN Art. 60.6. Originally described from a fruiting specimen without leaves, bracts and flowers. Status still uncertain: Thulin (1995) and Mbugua (2007) include *S. elliptica* here, but Jankalski (2007c) treats that as a distinct species, with leaves smooth above and rough below, in contrast to *S. forskaoliana* with both leaf surfaces rough. However, a plant collected recently from the *S. forskaoliana* type locality has leaves smooth above and rough below, and there is no mention of leaf surfaces in the protologue. Further studies of field-collected material are needed to resolve this.

**S. francisii** Chahinian (Sansevieria J. 4(1): 12–14, ills., 1995). **Type:** Kenya, Coast Prov. (Horwood 432 [MO, UPS, ZSS]). — **Distr:** S Kenya (Coast Prov., Tana River Distr.); ecology not described. **I:** Speirs (1984: as *S. sp.*); Mansfeld & Rosigkeit (2016).

≡ *Dracaena francisii* (Chahinian) Byng & Christenhusz (2018).

[3a] Caulescent, with runners; stem erect, to ≥30 cm; runners to 16 × 0.8–1.4 cm; **L** to 40, spiralled in 5 rows, cylindrical with a groove on the upper surface for ¼ to ¾ of the length, 8–15 cm, narrowed gradually to a 5 mm acute spine-like tip, dark green with grey-green transverse bands and 4–6 dark green longitudinal lines, margin brownish-red with a white edge on the basal ½, green above, surface slightly rough; **Inf** 12–25 cm, simple, elongated, fertile portion dense, 1–2 **Fl** per cluster; **Bra** triangular, ± 6 × 3 mm; **Ped** ± 2 mm; **Fl** greenish-white to brownish-green, tube 16–19 mm, lobes 8–10 mm.

**S. frequens** Chahinian (Cact. Succ. J. (US) 72 (3): 130–132, ills., 2000). **Type:** Kenya, Laikipia Distr. (Chahinian 785 [MO, NY]). — **Lit:** Mbugua (1998: as *S. braunii*). **Distr:** Ethiopia, Kenya, Uganda; mostly rocky areas in grassland or open bush, 600–1750 m.

≡ *Dracaena frequens* (Chahinian) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome to 5 cm Ø, yellow-buff coloured; **L** 4–8 (usually 6), rosulate, erect, leathery, oblanceolate, 90 or more × 15 cm, dull grass-green, sometimes with a bloom, base slightly narrowed, tip obtuse, margins fibrous, chestnut-brown, surface smooth; **Inf** 60–90 cm, simple, elongated, peduncle green, fertile portion dense; **Bra** 3.35–8 × 2.5–3 mm; **Ped** shorter or longer than the bracts; **Fl** greenish-white, tube 18–20 mm, lobes 26–28 mm.

**S. gracilis** N. E. Brown (Bull. Misc. Inform. Kew 1911: 96, 1911). **Type:** Kenya, Coast Prov. (Powell 11 [K]). — **Distr:** Kenya, Tanzania; dry bushland and thicket, 30–600 m. **I:** Brown (1915: 204).

≡ *Dracaena serpenta* Byng & Christenhusz (2018).

[3a] Caulescent, with runners; stem erect, to 8 cm; runners slightly ascending, to 90 × 0.8 cm; **L** 8–12, densely spiralled, ascending or spreading, cylindrical with a groove on the upper surface for up to 12.5 cm from the base, 23–80 cm, to 0.6–1 cm thick, deep grass-green, sometimes with inconspicuous narrow transverse darker bands and slightly darker longitudinal lines, narrowed gradually to a 2.1–6.4 mm brown or whitish spine-like tip, margin membranous, white, surface smooth; **Inf** to 30 cm, simple, elongated, peduncle light green, fertile portion lax, 2 **Fl** per cluster; **Bra** lanceolate or linear-lanceolate, acute, 2.1–3.2 mm; **Ped** 1–1.6 mm; **Fl** white, tube 19–25 mm, lobes 10.5–12.7 mm.

Widespread in the Coast Province, but apparently extinct at the type locality, Mazeras, which has grown into a large town. Collections referred to as var. *humbertiana* by Mbugua (2007) are *S. ballyi*.

**S. gracillima** Chahinian (Sansevieria 12: 3–4, ills., 2005). **Type:** Somalia, Bay Prov. (Lavranos & Bauer 27839 in Chahinian 336 [MO, NY]). — **Distr:** S Somalia; dense semi-deciduous forest on granite inselberg, 600 m.

≡ *Dracaena gracillima* (Chahinian) Byng & Christenhusz (2018); **incl.** *Sansevieria gracilis* var. *somaliensis* Chahinian (2005) (*nom. inval.*, Art. 36.1, 37.1).

[3a] Acaulescent, with runners; runners 7–10 cm; **L** 8–10, densely spiralled, slightly spreading, cylindrical with shallow groove on the upper surface to  $\frac{1}{2}$  the leaf length, 6–22 × 0.9 cm, base 9 mm thick, with spine-like tip, dark green with conspicuous bands of lighter green, edge of the groove reddish, surface smooth; **Inf** to 17 cm, simple, elongated, peduncle dark green, with 3 sterile bracts, fertile portion lax, 1–3 **Fl** per cluster; **Bra** triangular, 2 × 2 mm; **Ped** 2 mm; **Fl** brownish, tube 6–7 mm, lobes 14–15 × 2 mm.

Described as similar to *S. gracilis*, but with shorter leaves and shorter flowers, which are a different colour.

**S. grandicuspis** Haworth (Synops. Pl. Succ., 67, 1812). **Type:** not typified. — **Distr:** Unknown.

**Incl.** *Sansevieria ensifolia* Haworth (1812); **incl.** *Sansevieria pumila* Haworth (1812).

[3c] Acaulescent, rhizomatous; **L** 5–15, erect or ascending-spreading, linear-lanceolate, 18–50 × 1.25–3.8 cm, sometimes narrowed to a channelled petiole to 15 cm, with alternating transverse bands of dull dark and lighter green, with 5–7 longitudinal dark green impressed lines, shortly narrowed above to a 17–50 mm green flexible subulate tip, margin green, surface smooth; **Inf** and **Fl** not known.

Originally described with flowers not seen, with no illustration or herbarium specimen, and still little-known. Possibly better treated as a name of unresolved application. Included in *S. zeylanica* by Chahinian (2005a) and Govaerts (2014+), and in *S. aethiopica* by Mansfeld (2015a). A more likely candidate is *S. roxburghiana*, which has long subulate leaf tips. The specimen referred to this species by Mbugua (2007) is *S. dooneri* (Newton & Webb 2011).

**S. hallii** Chahinian (Sansevieria J. 5: 7–10, ills., 1996). **Type:** Zimbabwe, East Region (Hall 67/799 [MO, UPS]). — **Lit:** Rulkens & Baptista (2009b); Jaarsveld & Condy (2015). **Distr:** Moçambique, Zimbabwe, RSA (N Limpopo); rocky outcrops, 300–360 m. **I:** Jaarsveld (2016).

≡ *Dracaena hallii* (Chahinian) Byng & Christenhusz (2018).

[2] Acaulescent, rhizomatous; rhizome 1.8–3 cm Ø, grey-orange; **L** 1–3, erect, cylindrical with a deep groove on the upper surface, to 60 × 5 cm, dark greyish-green with numerous longitudinal lines, with inconspicuous transverse bands when young, narrowed to a 6 mm obtuse or rounded tip, margin chestnut-brown edged white, surface rough; **Inf** to 18 cm, capitate, fertile portion to 16 cm Ø, dense; **Bra** triangular, 18 × 6 mm; **Fl** white tinged purple, tube 45–78 mm, lobes 25–29 mm.

**S. hargeisana** Chahinian (Sansevieria J. 3(3): 53–55, ills., 1994). **Type:** Somalia, North-Central Region (Lavranos 7382 [MO, UPS]). — **Distr:** Somalia; limestone plateau with sparse vegetation, 1200 m.

≡ *Dracaena hargeisana* (Chahinian) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; **L** 4–8, rosulate, spreading, cylindrical with a basal adaxial groove for  $\frac{1}{8}$ – $\frac{1}{3}$  of the length, with a white membranous margin, 8–20 cm, base 10–14 mm thick, tip cuspidate with brown band at the base, dark green with lighter green transverse bands and 5–7 dark green longitudinal lines, surface rough; **Inf** 14–18 cm, simple, peduncle with 3 sterile bracts, fertile portion 4.5–6 cm, semidense, 2–4 **Fl** per cluster; **Ped** <1 mm; **Fl** tube 8 × 1.5 mm, lobes 8–9 × 1.5–2 mm.

Included in *S. phillipsiae* by Thulin (1995), in the first edition of this handbook, and by Lebrun & Stork (2014), but treated as distinct by Jankalski (2007c), with rhizomes instead of runners, and shorter leaves and flowers.

**S. humiflora** D. J. Richards (Sansevieria 10: 3–6, ills., 2004). **Type:** Zimbabwe, Manicaland (Richards R889 [SRGH]). — **Distr:** SE Zimbabwe (Manicaland); dry bushland, c. 530 m.

≡ *Dracaena humiflora* (D. J. Richards) Byng & Christenhusz (2018).

[2] Acaulescent, rhizomatous, forming tangled clumps; rhizome 2–3 cm Ø, light reddish-brown; **L** 1–3, spreading-reflexed, flat-canalicate, recurved, 25–45 × to 8 cm, base 10–15 mm thick, dark green, lower surface sometimes with faint lighter bands or patches, both surfaces with

longitudinal grooves, margin slightly wavy, brown, surface rough, tip blunt; **Inf** 6–7 cm, simple, peduncle mostly subterranean, fertile portion dense, capitate, 4 **Fl** per cluster; **Bra** 12.5–15 × 10 mm; **Ped** 3–4 mm; **Fl** purplish at the base, becoming lighter above, to 150 mm.

The protologue describes the flower tube as up to 15 cm long, but as corolla lobes are not mentioned this probably refers to the whole flower. This species and *S. scimitariformis* are close to *S. hallii*. Further field work to determine distribution and variation could lead to a reassessment of their distinction as species.

**S. hyacinthoides** (Linné) Druce (Rep. Bot. Exch. Club Soc. Brit. Isles 1913(3): 423, 1914). **Type:** [lecto — icono] Commelin, Praeludia Bot., 84, t. 33, 1703. — **Lit:** Wijnands (1973: 112, with ill.); Obermeyer & al. (1992). **Distr:** Widespread in E parts of S Africa into tropical E Africa, RSA (Eastern Cape, KwaZulu-Natal, Mpumalanga); forming dense stands usually in the shade of trees or shrubs; introduced as neophyte elsewhere.

≡ *Aloe hyacinthoides* Linné (1753) ≡ *Aletris hyacinthoides* (Linné) Linné (1762) ≡ *Dracaena hyacinthoides* (Linné) Mabberley (2017); **incl.** *Aloe hyacinthoides* var. *guineensis* Linné (1753) ≡ *Aletris hyacinthoides* var. *guineensis* (Linné) Linné (1762) ≡ *Aloe guineensis* (Linné) Jacquin (1762) (*nom. illeg.*, Art. 52.1) ≡ *Aletris guineensis* (Linné) Jacquin (1770) (*nom. illeg.*, Art. 52.1) ≡ *Sansevieria guineensis* (Linné) Willdenow (1799) (*nom. illeg.*, Art. 52.1); **incl.** *Sanseverinia thyrsoiflora* Petagna (1787) (*nom. illeg.*, Art. 52.1) ≡ *Sansevieria thyrsoiflora* Thunberg (1794) (*nom. illeg.*, Art. 52.1); **incl.** *Salmia spicata* Cavanilles (1795) ≡ *Sansevieria spicata* (Cavanilles) Haworth (1812); **incl.** *Pleomele aloifolia* Salisbury (1796); **incl.** *Sansevieria latifolia* Bojer (1837); **incl.** *Sansevieria guineensis* var. *β* Kunth (1850) (*incorrect name*, Art. 11.4); **incl.** *Sansevieria nobilis* Godefroy-Lebeuf (1861) (*nom. inval.*, Art. 32.1c); **incl.** *Sansevieria angustiflora* Lindberg (1871); **incl.** *Sansevieria rufocincta* Baker (1875); **incl.** *Sansevieria angustifolia* Baker (1875) (*nom. inval.*, Art. 61.1); **incl.** *Sansevieria grandis* Hooker fil. (1903); **incl.** *Sansevieria grandis* var. *zuluensis*

N. E. Brown (1915); **incl.** *Sansevieria guineensis* var. *latifolia* Bojer ex Morgenstern (1979) (*nom. inval.*, Art. 36.1, 37.1); **incl.** *Sansevieria lancifolia* Morgenstern (1979) (*nom. inval.*, Art. 36.1, 37.1); **incl.** *Sansevieria macrophylla* Sastrapradja ex Morgenstern (1979) (*nom. inval.*, Art. 36.1, 37.1).

[3c] Acaulescent, rhizomatous; rhizome stout, tan-coloured; **L** 2–8, rosulate, erect, lanceolate to broadly linear, 15–60 × 2.5–9 cm, narrowed from the middle or below to the channelled petiole, dull green with numerous closely placed transverse pale green bands that fade with age, usually with a white withered acute or obtuse tip to 17 mm, margin brownish-red, surface smooth; **Inf** 45–75 cm, simple, elongated, fertile portion 22–30 cm, dense, 2–6 **Fl** per cluster; **Bra** ovate-lanceolate to narrowly lanceolate, acute, 4–12.5 × 1.4–3.2 mm; **Ped** 3.2–6.3 mm; **Fl** whitish, tube ±19 mm, lobes 19 mm. — **Cytology:** 2n = 100 (Darlington & Wylie 1955: as *S. grandis*).

Mbugua's (2007) report of this southern African species in Kenya (as *S. grandis*) and Tanzania (as *S. grandis* and *S. hyacinthoides*) is unlikely, and probably based on misidentification of the specimens that he cites. Jankalski (2007a) treats *S. angustiflora* Lindberg as a distinct species. Apparently introduced to other countries; reported by Mai (2016) as a neophyte on Hispaniola, and by Brown (2016) as an invasive species in S Florida.

**S. itumei** (Mbugua) Jankalski (*pro hybr.*) (*Sansevieria* 20: 20, 2009). **Type:** Kenya, Tana River Distr. (Bally & Smith B14404A in *Pfennig* 312 [HBG, B]). — **Lit:** Newton (2016). **Distr:** Kenya; thickets in arid area. **I:** Butler (2012b).

≡ *Sansevieria aethiopica* ssp. *itumei* Mbugua (2007) ≡ *Dracaena ×itumei* (Mbugua) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; **L** 2–3, ascending-spreading, linear or linear-lanceolate, 25–31.5 × 0.8–1.2 cm, upper surface concave, base sometimes slightly narrowed, gradually narrowed above the middle to a subulate tip, dark green with paler green transverse bands, surface smooth; **Inf** simple, peduncle with 4 sterile **Bra** 30 × 10 mm, fertile



portion lax, 2–3 **Fl** per cluster; **Fl** white, tube 18–21 mm, lobes 15–20 mm.

The epithet was published as “itumea”, but is corrected according to ICN Art. 60.12, Rec. 60C. Mbugua (2007) associated this taxon with the geographically remote *S. aethiopica*, and did not give a full description. Some characters here are taken from plants collected recently at the type locality and flowering in cultivation in Nairobi. Jankalski treated it as a “suspected hybrid”, “probably a natural hybrid between *S. raffillii* and *S. gracilis*”, though he gave no evidence for this status, and the putative parents that he suggested are not seen in the vicinity of the type locality. Butler (2012b) also considers hybrid status for the taxon unlikely. Christenhusz & al. (2018) also treat it as a hybrid. Mansfeld (2015a) includes it in *S. aethiopica*. It is here treated as a species (ICN Art. 50, Art. H3.2 + Note 1).

**S. kirkii** Baker (Bull. Misc. Inform. Kew 1887 (5): 8, Fig. 3, 1887). **Type:** Tanzania, Pangani Distr. (*Kirk* s.n. [K]). — **Distr:** Malawi, Tanzania, Zanzibar, Pemba, Moçambique, Zambia.

≡ *Dracaena pethera* Byng & Christenhusz (2018).

**S. kirkii** var. **kirkii** — **Distr:** Malawi, Zimbabwe, Tanzania, Zanzibar, Pemba; coral cliffs and limestone outcrops near sea level. **I:** Brown (1915: 255).

**Incl.** *Sansevieria aubryana* De Wildeman (1905) (*nom. inval.*, Art. 61.1); **incl.** *Sansevieria aubrytiana* Gérôme & Labroy ex N. E. Brown (1915) (*nom. illeg.*, Art. 53.1).

[2] Acaulescent, rhizomatous; rhizome stout; **L** 1–3, erect or ascending-spreading, sometimes the terminal part recurved, elongate-lanceolate or broadly lorate, 75–275 × 6–9 cm, narrowed gradually from about the middle to the stout channelled petiole, whitish-brown, greyish-green, mottled or transversely banded light green, with 3–9 dark green longitudinal lines, with a 8.5–12.7 mm pale whitish-brown firm acute tip, margin wavy, reddish-brown, surface smooth; **Inf** to 60 cm, simple, capitate, peduncle dull purplish-brown, speckled pale green or dull whitish, fertile portion 3.8–10 cm, dense; **Bra** ovate or oblong-ovate,

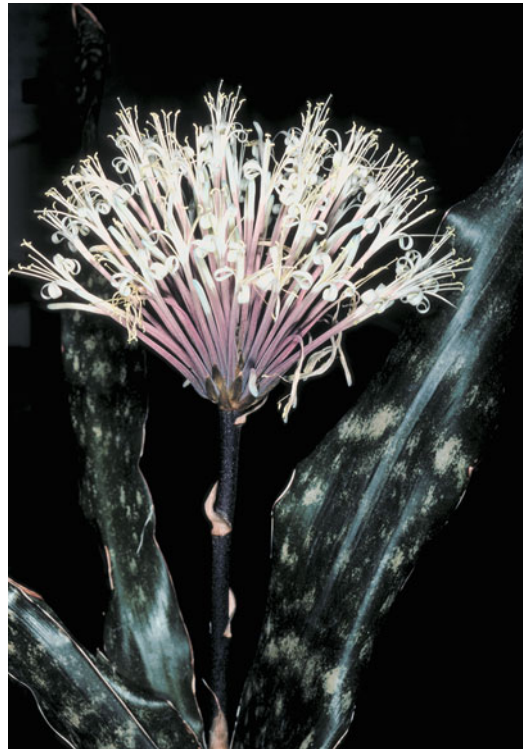
acute or subobtuse, 25–38 × 8.5–19 mm; **Ped** 6.4–10.5 mm; **Fl** tube 114–127 mm, pale purplish or dull pink, lobes 32–45 mm, white.

**S. kirkii** var. **pulchra** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 256, 1915). **Type:** Zanzibar (*Last* s.n. [K]). — **Distr:** Zanzibar, Pemba, Misali. **I:** Pfennig (1977b: 552). — Fig. 4.

≡ *Dracaena pethera* var. *pulchra* (N. E. Brown) Byng & Christenhusz (2018); **incl.** *Sansevieria longiflora* Gérôme & Labroy (1903) (*nom. illeg.*, Art. 53.1).

[2] Differs from var. *kirkii*: **L** more conspicuously marked with whitish-green, buff or almost reddish spots or irregular bands, margin red-brown with white membranous edge; **Bra** lanceolate.

Populations of *S. kirkii* seen on Pemba Island (*Newton* 5611) and Misali Island (*Newton* 5616) have plants varying from strongly marked with spots or bands to almost uniformly green and



**Fig. 4** *Sansevieria kirkii* var. **pulchra**. (Copyright: J. Trager).



unmarked, and so the var. *pulchra* is doubtfully distinct.

**S. laevifolia** R. H. Webb & L. E. Newton (*Sansevieria* 34: 9, ills. (pp. 11–12), 2016). **Type:** Kenya, Rift Valley Prov. (*Webb-Yocum* 1022 [EA]). — **Distr:** Kenya (Rift Valley Prov.); bushland, 1900 m.

[3a] Shortly caulescent, stoloniferous; stem erect, to 20 cm, runners to 37 cm; **L** to 15, distichous, ascending to spreading, cylindrical with deep grooves, 55–85 (–100) × 1.5–2 cm, upper surface with a channel 12–20 × 2 cm, 5–8 mm deep, dark green, with few or no markings or transverse bands, apex conical, pungent, 2–5 mm, white, surface slightly rough to mostly smooth; **Inf** 50–60 (–75) cm, simple, fertile portion ±40 cm, with 3–5 **Fl** per cluster; **Bra** scarious, triangular, 55 × 5 mm; **Fl** tube 40 mm, cream, lobes 15–20 mm, pale yellow.

**S. lavranii** R. H. Webb & Myklebust (*Sansevieria* 37: 10–11, ills., 2018). **Type:** Somalia (*Lavranos* 23295 [MO]). — **Distr:** SE Somalia (Mogadishu); savanna, 90 m.

[1] Caulescent, rhizomatous, forming dense stands, rhizome 5 cm Ø, stem to 10 cm; **L** 6–9, mostly distichous, ascending to spreading, lanceolate, canaliculate, 60–100 cm, tip pungent, orange-white, with a herringbone pattern of red-orange, margin green, surface smooth; **Inf** 75 cm, paniculate with up to 12 branches and 3–5 secondary branches, fertile portion to 55 cm, semidense, with (1–) 4 (–5) flowers per cluster; **Ped** 1 mm; **Fl** yellow-green, 5–10 mm.

**S. liberica** G r me & Labroy (*Bull. Mus. Hist. Nat. (Paris)* 9: 170, 173, Fig. 4, 1903). **Type:** Liberia (*Julien* s.n. [P, K]). — **Distr:** Central African Republic, Ivory Coast, Ghana, Liberia, Nigeria, Sierra Leone, Togo; dry shady places by streams and rock outcrops.

≡ *Dracaena liberica* (G r me & Labroy) Byng & Christenhusz (2018); **incl.** *Sansevieria chinensis* L. Gentil ex N. E. Brown (1915); ≡ *Sansevieria gentilis* Mattei (1918) (*nom. illeg.*, Art. 52.1); **incl.** *Sansevieria wanguiae* Mbugua (1995) (*nom. inval.*, Art. 29.1, 32.1a).

[3c] Acaulescent, rhizomatous; rhizome ±1.9 cm Ø, pale greyish; **L** 1–6, erect or sub-erect, spreading with age, lanceolate, 46–106 × 5–12.5 cm, narrowed downwards from below the middle, dark green, usually with indistinct transverse paler green bands, narrowed upwards from above the middle to a 2–12 mm green flexible subulate acute tip becoming whitish, margin cartilaginous, pale reddish-brown, surface smooth; **Inf** 60–80 cm, simple, elongated, fertile portion lax; **Bra** lanceolate; **Fl** white, ± 50 mm.

Originally described with flowers not seen. The last synonym was proposed in an unpublished thesis and was never formally published, but it was listed by Jankalski (2007c). The epithet was originally “wanguia”, but is corrected in accordance with ICN Art. 60.12, Rec. 60C.

**S. lineata** T. G. Forrest (*Sansevieria* 30: 11, ills. (pp. 10–11), 2013). **Type:** Uganda, Kyegegwa Distr. (*Forrest* 303 [MHU]). — **Distr:** Uganda; shallow soil on granite inselberg. ≡ *Dracaena bugandana* Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome 0.9–1.5 cm Ø, burnt orange; **L** 2–6, erect, oblanceolate, 28–72 × 2–4.8 cm, base a channelled petiole 16–35 cm, with soft green subulate tip 3–6 mm, grass-green with irregular zig-zag transverse bright greenish-white bands, and 14–23 longitudinal dark green lines below, a few incomplete central lines above, margin green, surface smooth; **Inf** 48–73 cm, simple, peduncle dark greenish-purple with dull whitish specks, with 3–4 sterile **Bra** 10–40 mm long, fertile portion lax, 2–6 **Fl** per cluster; **Bra** ovate-acute, 5–12 × 3–5 mm, with 1–5 brown nerves; **Ped** 4–5 mm, dark purple; **Fl** tube 10 mm, purple with 6 darker longitudinal lines, lobes 14–17 × 2 mm, white with median purple stripe.

So far known only from the type locality. The epithet ‘bugandana’, chosen upon transferring the taxon to *Dracaena* because the name *D. lineata* was already occupied, is a misnomer. This species does not occur in Buganda, but in the Toro Kingdom (Forrest in lit.). Inappropriate epithets such as this cannot be replaced (ICN Art. 51).

**S. longiflora** Sims (Curtis's Bot. Mag. 53: t. 2634 + text, 1826). **Type:** Cult. England (*Anonymus* s.n. [[icono]: l.c. t. 2634]). — **Distr:** Angola, Namibia, Democratic Republic of the Congo [Zaire], Equatorial Guinea (Bioko Island).

≡ *Dracaena longiflora* (Sims) Byng & Christenhusz (2018).

**S. longiflora** var. **fernandopoensis** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 257, 1915). **Type** [syn]: Equatorial Guinea, Bioko Island (*Barter* 2060 [K]). — **Distr:** Equatorial Guinea (Bioko Island).

≡ *Dracaena longiflora* var. *fernandopoensis* (N. E. Brown) Byng & Christenhusz (2018).

[3c] Differs from var. *longiflora*: **Ped** 5.3–6.4 mm; **Fl** tube 63.5–76 mm.

The typification is not yet resolved, and *Mann* 1169 (K) represents a second syntype. Not included in Mansfeld (2015a).

**S. longiflora** var. **longiflora** — **Distr:** Angola, Moçambique, Namibia, Democratic Republic of the Congo [Zaire], Zambia, Zimbabwe; sandy soil, usually in shade.

[3c] Acaulescent, rhizomatous; rhizome 2.5 cm Ø; **L** ± 4–6, rosulate, spreading, lanceolate, 30–150 × 4–9 cm, narrowed to a 7.6 cm channelled petiole, dark green with paler green spots scattered or in irregular transverse bands, with a 3.2–6.3 mm brown hard spine-like tip, margin hardened, red-brown or yellowish, surface smooth; **Inf** 33–68 cm, simple, elongated, fertile portion 7.5–38 cm, dense, 2–3 **Fl** per cluster; **Bra** lanceolate, acute, 12.7–25.4 mm; **Ped** 1.6–3.2 mm; **Fl** tube 89–102 mm, greenish-white, lobes 25–38 mm, white.

**S. longistyla** la Croix (Kew Bull. 59(4): 617–618, ills. (p. 620), 2005). **Type:** Malawi (*Brummitt* 10284 [K]). — **Distr:** C Malawi; sand and thicket near lake shore, c. 480 m.

≡ *Dracaena longistyla* (la Croix) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome ±3 cm Ø, orange; **L** lanceolate, apiculate, 33 × 7.3 cm, flat, base folded, dark bluish-green, mottled pale bluish-green, margin red, surface slightly rough

on both surfaces; **Inf** 48–58 cm, simple, peduncle 22–32 cm, with 3–5 ovate bracts 3–3.8 × 1.6–1.8 cm, fertile portion 21–27 × 9–12 cm, dense, 1–3 **Fl** per cluster; **Bra** 9–10 × 2–3 mm, papery; **Ped** 3–4 mm; **Fl** greenish-white, tube 50–65 mm, lobes 15–20 mm; **Sti** and **Sty** 100–110 mm, exerted 38–40 mm.

Close to *S. longiflora* (Jankalski 2007c), but also to *S. braunii* and possibly conspecific with this according to Butler (2009).

**S. lunatifolia** L. E. Newton (Cact. Succ. J. (US) 87(3): 116–118, ills., 2015). **Type:** Kenya, Rift Valley Prov. (*Newton* 5683 [EA, K]). — **Distr:** S Kenya (Rift Valley Prov.: Kajiado Distr.); grazed scrub, 1445 m; known only from the type collection.

≡ *Dracaena lunatifolia* (L. E. Newton) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; rhizome 3 cm Ø, whitish; **L** 2–3, sessile, spreading obliquely, 85–130 × 4–6.5 cm, 2–2.7 cm thick, with a 12 mm deep and 8 mm wide channel along the upper surface, dark green with irregular transverse bands or blotches of very pale green, margins red-brown with very narrow fraying whitish edge, apex soft, blunt, whitish, surface rough; **Inf** erect, to 110 cm, simple, peduncle with 6 triangular-attenuate sterile **Bra** to 13 cm, fertile portion 75 cm, lax, with up to 7 **Fl** per cluster; **Bra** triangular-attenuate, 18 × 5 mm, whitish with prominent green midrib; **Ped** 5–6 mm; **Fl** white with green midstripe on the lobes, tube 18–23 mm, lobes 25 mm.

Jankalski stated online that this is probably a hybrid, even a spontaneous polyploid, but no evidence was given and I am not aware of any chromosome count (Newton 2016).

**S. masoniana** Chahinian (Cact. Succ. J. (US) 72(1): 31, ill., 2000). **Type:** Democratic Republic of the Congo [Zaire] (*Mason* s.n. in *Chahinian* 258 [MO, NY]). — **Distr:** Democratic Republic of the Congo [Zaire].

≡ *Dracaena masoniana* (Chahinian) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome ±4 cm Ø; **L** 1–2 per shoot, erect, leathery,

oblanceolate, to 100 × 18 cm, tip acute, dull greyish-green with lighter mottling, margins fibrous, chestnut-brown, surface rough, basal sheath with purplish transverse bands; **Inf** to 53 cm, simple, elongated, peduncle light green with purple lines, fertile portion subdense, 1–2 **Fl** per cluster; **Fl** greenish-white, tube 26–30 mm, 3 mm Ø at the base, widening to 4 mm at the mouth, lobes 24–28 × 3 mm.

Original locality not known. Cultivated for many years under the cultivar name ‘Mason Congo’.

**S. metallica** Gérôme & Labroy (Bull. Mus. Hist. Nat. (Paris) 9: 170, 172, Fig. 3, 1903). **Type:** Cult. Paris (*Anonymus* s.n. [P, K]). — **Distr:** Tropical Africa, RSA.

≡ *Dracaena zebra* Byng & Christenhusz (2018).

**S. metallica** var. **longituba** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 247, 1915). **Type:** K. — **Distr:** Tropical Africa; exact provenance unknown.

[3c] Differs from var. *metallica*: **Inf** peduncle brownish-green or dull purplish; **Fl** tube ±30 mm, lobes 30 mm.

Possibly occurring in Moçambique (Jankalski 2007a).

**S. metallica** var. **metallica** — **Distr:** Tropical Africa, RSA; details of the geographical range unknown.

**Incl.** *Sansevieria guineensis* var. *β* Schultes (1829) (*incorrect name*, Art. 11.4); **incl.** *Sansevieria guineensis* Baker (1875) (*nom. illeg.*, Art. 53.1).

[3c] Acaulescent, rhizomatous; rhizome 1.9–2.5 cm Ø, bright red, becoming pale brown in light; **L** 1–4, erect or upper part spreading or recurved, lanceolate, 45–152 × 5–12.7 cm, narrowed from about the middle to a 10–60 cm channelled petiole, dull dark green, upper surface with obscure irregular transverse bands, lower surface more distinctly marked, with a 3.2–6.4 mm green soft subulate tip, margin soft, green, becoming whitish or pale reddish-brown, surface smooth; **Inf** 45–122 cm, simple, elongated, peduncle light green, fertile portion lax,

2–4 **Fl** per cluster; **Bra** lanceolate, acuminate, 6.4–12.7 mm; **Ped** 4.2–7.4 mm; **Fl** white, tube 12.7–17 mm, lobes 17–23.3 mm. — **Cytology:** 2n = 40 (Darlington & Wylie 1955).

**S. metallica** var. **nyasica** N. E. Brown (Bull. Misc. Inform. Kew 1915 (5): 247, Fig. 20, 1915). **Type:** Malawi (*Buchanan* s.n. [K]). — **Distr:** Malawi.

≡ *Dracaena zebra* var. *nyasica* (N. E. Brown) Byng & Christenhusz (2018).

[3c] Differs from var. *metallica*: **Ped** 4.2–6.4 mm; **Fl** tube 14.8–16.9 mm, greenish-white or tinged red, lobes 19 mm, white.

Not recognized as distinct by Croix (2010).

**S. newtoniana** T. G. Forrest (Cact. Succ. J. (US) 86(2): 76–78, ill., 2014). **Type:** Uganda, Mubende Distr. (*Forrest* 266 [MHU]). — **Distr:** C Uganda (Mubende & Kiboga Distr.); thickets on grassland, 1130–1180 m.

≡ *Dracaena newtoniana* (T. G. Forrest) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous, rhizome 4–5 cm Ø, light brownish-yellow; **L** 2–6 (–9), erect, slightly curved outwards, elongate-lanceolate, 86–170 × 8–11 cm, base narrowed, sometimes to a channelled petiole to 65 cm, tip attenuate, mid-green, lower surface lighter with faint cross-banding or blotches when young, margin reddish-brown, upper surface smooth, lower surface slightly rough; **Inf** to 86 (–124) cm, simple, peduncle light green, with 6–7 **Bra** 6.5–11 × 2.5–3.8 cm, fertile portion dense, with 3–6 flowers per cluster; **Bra** oblong, acute, 12–35 × 3–10 mm, green edged white; **Ped** 7–9 mm; **Fl** white, sometimes tinged pink and mauve near the apex, tube 45–48 mm, lobes 25–27 mm; **Fr** 8–10 mm Ø.

**S. nilotica** Baker (J. Linn. Soc., Bot. 14: 548, 1875). **Type:** Sudan, White Nile Prov. (*Murie* s.n. [K]). — **Distr:** Central African Republic, Ethiopia, Sudan, Uganda.

≡ *Dracaena nilotica* (Baker) Byng & Christenhusz (2018); **incl.** *Acyntha massae* Chiovenda (1940) ≡ *Sansevieria massae* (Chiovenda) Cufodontis (1971).

**S. nilotica** var. **nilotica** — **Distr:** Central African Republic, SW Ethiopia, Sudan, Uganda; riverine woodland, 900–1450 m.

[3c] Acaulescent, rhizomatous; rhizome  $\pm 1.9$  cm  $\varnothing$ ; **L** 2–3, lorate, 91–122  $\times$  2.5–5.7 cm, narrowed gradually to a 30.5–61 cm channelled petiole, conspicuously marked with numerous closely placed irregular zigzag transverse narrow bands of dark green and paler green, with a 4.2–16.9 mm green soft subulate tip, margin green, surface smooth; **Inf** 53–76 cm, simple, elongated, fertile portion 30–46 cm, lax, 4–10 **Fl** per cluster in the lower part, 2–3 in the upper part; **Bra** lanceolate, acute, 4.2–10.6 mm; **Ped** 7.4–12.7 mm; **Fl** white, tube 9.5–10.6 mm, lobes 11.6–12.7 mm. — **Cytology:**  $2n = 36, 40$  (Roy 1956).

**S. nilotica** var. **obscura** N. E. Brown (Bull. Misc. Inform. Kew 1915 (5): 238–239, 1915). **Type:** Uganda (Dawe s.n. [K]). — **Distr:** Uganda.

[3c] Differs from var. *nilotica*: **L** 4–5, lanceolate or lorate, 60–84  $\times$  3.8–7 cm, narrowed to a 15.2–30.4 cm channelled petiole, grass-green, sometimes with a few inconspicuous transverse bands of slightly paler green 25.4–38 mm apart, with a 12.7–32 mm green soft subulate tip; **Inf** 61–91 cm, peduncle dull mottled green, fertile portion with 3–6 **Fl** per cluster; **Bra** ovate-lanceolate, acute or acuminate, 4.2–8.5 mm; **Ped** 5.8–7.4 mm; **Fl** tube 8.5 mm, dull greenish-white with 6 longitudinal dull purplish lines, lobes 14.8 mm, whitish.

Brown (1915) suggested that this variety might be specifically distinct from var. *nilotica*. Mbugua (2007) does not recognise this as a distinct variety and lists it as a synonym of *S. nilotica*.

**S. nitida** Chahinian (Cact. Succ. J. (US) 73(3): 120–121, ill., 2001). **Type:** Kenya, Coast Prov. (Chahinian 301 [MO, NY]). — **Distr:** S Kenya (Coast Prov.: Kilifi Distr.); open savanna woodland,  $\pm 160$  m.

$\equiv$  *Dracaena nitida* (Chahinian) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous, rhizome to  $\pm 20$  mm  $\varnothing$ , orange; **L** (1–) 2 (–5) per shoot, erect-spreading, lanceolate, to 40  $\times$  6 cm, base narrowing into a petiole, tip acute, dark green,

with greying green blotches in transverse bands, with longitudinal lines, margin fibrous, chestnut-brown, upper surface smooth, shiny, lower surface rough, dull; **Inf** 15–24 cm, simple, elongated, peduncle light green, fertile portion 11–18 cm, dense, 1–2 **Fl** per cluster; **Ped**  $\pm 2$  mm; **Fl** greenish-white, tube 18–24 mm, lobes 20–26 mm.

Close to, and possibly conspecific with, *S. elliptica*.

**S. parva** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 233, Fig. 13C–F, 1915). **Type:** Kenya, Rift Valley Prov. (Powell 15 [K]). — **Lit:** Newton (2003a). **Distr:** Kenya, Uganda; shade in forest, 1660–2135 m. **I:** Pfennig (1977b: 552).

$\equiv$  *Dracaena parva* (N. E. Brown) Byng & Christenhusz (2018); **incl.** *Sansevieria bequaertii* De Wildeman (1921); **incl.** *Sansevieria dambilonensis* hort. ex Heitz & Zeller (1990) (*nom. inval.*, Art. 36.1, 37.1).

[3c] Acaulescent or shortly caulescent, rhizomatous; rhizome 0.85 cm  $\varnothing$ , brownish-orange; stem to 12.7 cm, sometimes concealed by the leaf bases; **L** 6–14, rosulate, ascending, becoming spreading, linear to lanceolate, 20–45  $\times$  0.85–3 cm, narrowed to a channelled petiole to 5 cm, with distinct irregular bands of dark green and paler green, becoming nearly uniform green or obscurely marked with age, narrowed to a 38–76 mm green soft stout subulate tip, margin green, surface smooth; **Inf**  $\pm 30$  cm, simple, elongated, peduncle light green, fertile portion with 1–2 **Fl** per cluster; **Bra** lanceolate, acute, 3.2–4.2 mm; **Ped** 4.2–5.3 mm; **Fl** tube 10.6–11.6 mm, pale pinkish-white, lobes 8.5–9.5 mm, mauve-tinted.

See comment for *S. dooneri*. Mansfeld & Budweg (2015) report that the species can be crossed with *S. ballyi* (female), and that the reciprocal cross is not possible.

**S. patens** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 210–211, Figs. 5A–B, 1915). **Type:** K [ex cult.]. — **Distr:** Origin unknown, probably Kenya. **I:** Newton (2005b); Jankalski (2007a).

$\equiv$  *Dracaena patens* (N. E. Brown) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; rhizome 1.9–2.54 cm Ø; **L** 5–10, distichous, spreading and recurved, cylindrical, laterally compressed with a channel along the upper surface, 45–91 cm, 1.7–4.2 cm thick, narrowed to an abrupt 6.4–12.7 mm whitish hard acute tip, indistinctly marked with dark green and paler green transverse bands, becoming bluish-green with age, with numerous longitudinal blackish-green lines, margin acute, green, sometimes whitish along the basal 2.54–15 cm, surface slightly rough; **Inf** 38 (–76?) cm, simple, elongated, peduncle pale green, fertile portion  $\geq$  25 cm, lax, 2–3 **Fl** per cluster; **Bra** lanceolate, acute, 3.2–6.4 mm; **Ped** 5.3–6.4 mm; **Fl** white, tube 9.5–10.6 mm, lobes 12.7 mm.

Plants matching this description are unknown today. Material in cultivation with this name is regarded by Jankalski (2007a) as probably a garden hybrid, to which he gave the cultivar name ‘Ed Eby’ (though the plant breeds true from seed after self-pollination). Mansfeld (2015a) follows Jankalski in treating this as a hybrid.

**S. pearsonii** N. E. Brown (Bull. Misc. Inform. Kew 1911: 97, 1911). **Type:** Angola, Cunene Prov. (Pearson 2073 [K]). — **Distr:** Angola, Botswana, Namibia, Zimbabwe, RSA (Gauteng, KwaZulu-Natal, North-West Prov., Northern Cape); dry sandy or rocky soil in savanna or open forest. **I:** Brown (1915: 216).

≡ *Dracaena pearsonii* (N. E. Brown) Byng & Christenhusz (2018); **incl.** *Sansevieria deserti* N. E. Brown (1915); **incl.** *Sansevieria rhodesiana* N. E. Brown (1915).

[3b] Acaulescent, rhizomatous; rhizome stout; **L** 3–7, distichous, erect but gradually diverging towards the tips, cylindrical, slightly compressed laterally, with a groove on the upper surface, 50–100 cm,  $\pm$  3.4–3.8 cm thick, narrowed gradually to a 8.5–25 mm whitish rigid terete-subulate acute tip, slightly glaucous-green or bluish-green, when young with faint paler green bands, margin greenish-white, becoming red-brown edged whitish, surface smooth; **Inf**  $\pm$  1 m, simple, elongated, fertile portion with 6–10 **Fl** per cluster; **Ped**

8.5 mm; **Fl** tube 12–25 mm, white, greyish- or bluish-mauve, red-streaked above, lobes 6–10 mm, white or cream with pale pink or mauve.

Originally described with flowers unknown. Waidhofer (1996) and Mbugua (2007) treated *S. deserti* as a separate species, but the Tanzanian specimen cited by Mbugua is probably a misidentification.

**S. pedicellata** la Croix (Kew Bull. 59(4): 620, Fig. 2, 2005). **Type:** Moçambique, Manica Distr. (*Wild* 5638 [K, MO]). — **Distr:** C Moçambique; among rocks in moist evergreen forest on mountains, 700–1000 m. **I:** Rulken & Baptista (2009a).

≡ *Dracaena pedicellata* (la Croix) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome to  $>$  5 cm Ø, light straw-coloured, darker grey when older; **L** 4–6 (–15), linear, flat, 60–140  $\times$  6–13 cm, uniformly green, margin red with white outer edge, tip narrowing for 5 cm to a sharp point, with the margin inrolled; **Inf** 70–130 cm, simple, peduncle 30 cm, with 4–5 broadly lanceolate acute bracts 4–6  $\times$  1.4 cm, green, fertile portion 28–55 cm, 4–6 **Fl** per cluster, clusters  $\pm$  1 cm apart; **Bra** acute, 12–19  $\times$  4–7 mm, papery; **Ped** 9–18 mm; **Fl** whitish, tube 64–95 mm, lobes 17–20 mm.

Described from a single incomplete herbarium specimen, but more information, including comments on variation in the field, is provided by Rulken & Baptista (2009a). Close to *S. conspicua*.

**S. perrotii** Warburg (Tropenpflanzer 5: 190, ill. (p. 191), 1901). **Type:** Tanzania, Lindi Prov. (*Perrot* s.n. [not located]). — **Lit:** Newton (2014). **Distr:** Tanzania; among bushes on coral.

≡ *Dracaena perrotii* (Warburg) Byng & Christenhusz (2018).

[1] Caulescent; stem erect, to 20  $\times$  2.5 cm, covered by leaf bases; **L** 8–12, distichous, ascending or spreading, cylindrical, laterally slightly compressed, with a deep and wide groove on the upper surface, 91–152 cm, 1.1–1.5 cm thick, narrowed gradually to a whitish hard acute tip, margin reddish-brown, edged white; **Inf**  $\geq$  1.2 m, paniculate, fertile portion lax, 2–4 **Fl** per cluster;



**Fl** tube  $\pm 1.27$  mm, pale greenish, lobes  $\pm 9.5$  mm, whitish inside, purplish outside.

Leaves described by Jankalski (2007a) as pale bluish-glaucous. Included in *S. robusta* by Mbugua (2007), though *S. perrotii* is an earlier name and would have priority if the two were considered to be conspecific (Newton 2014). A plant collected at the Kenya coast by Mr. Tony Dyer is possibly this species.

**S. pfisteri** D. J. Richards (*Sansevieria* 19: 4–7, ill., 2009). **Type:** Angola (*Downs & Pfister* s.n. [SRGH]). — **Distr:** SW Angola; hot stony desert, below limestone ridges.

$\equiv$  *Dracaena pfisteri* (D. J. Richards) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; rhizome 1.5–3 cm  $\varnothing$ , light brown; **L** 8–10 (–15), distichous, erect when young, spreading when displaced by new growth, to 64 cm, cylindrical with adaxial groove 2 cm wide  $\times$  1.5 cm deep from the base to nearly  $\frac{3}{4}$  of the leaf length, dull dark green with faint transverse paler green bands, adaxial groove with brownish margin, with 7 or more very shallow longitudinal grooves with broken dark lines, surface smooth; **Inf** 64 cm, simple, elongated, peduncle pale green with minute whitish linear marks, fertile portion semidense, 6–10 **Fl** per cluster; **Fl** dull yellow, purplish brown at the tip, tube 20–25  $\times$  3 mm, lobes 10 mm.

**S. phillipsiae** N. E. Brown (Hooker's Icon. Pl. 30: t. 3000 + text, 1913). **Type:** Somalia (*Lort Phillips* s.n. [K]). — **Distr:** S & E Ethiopia, Somalia; in the shade of trees, 1250–1450 m.

$\equiv$  *Dracaena phillipsiae* (N. E. Brown) Byng & Christenhusz (2018).

[3a] Caulescent, in clumps to 38 cm tall, with runners; stem erect, branching at or above the base; runners to 20  $\times$  1.3 cm; **L** 5–10, rosulate, ascending, becoming spreading, cylindrical with a deep groove on the upper surface for 5–8.9 cm at the base, 10.2–46 cm, 1.3–1.9 cm thick, narrowed gradually to a 2.1–3.2 mm brown hard acute or obtuse tip, dark and slightly bluish-green, with faint transverse paler green bands when young, margin white, surface smooth; **Inf** 35–46 cm, simple, elongated, fertile portion 23–30 cm, 3–6 **Fl** per

cluster; **Bra** ovate-lanceolate, acute, 3.2–6.4 mm; **Ped** 2.65–3.18 mm; **Fl** white, tube 10 mm, lobes 11.6–12.7 mm.

**S. pinguicula** P. R. O. Bally (*Candollea* 19: 145–147, ill., 1964). **Type:** Kenya, Coast Prov. (*Bally* 4275 [K]). — **Lit:** Newton & Thiede (2015). **Distr:** Kenya.

$\equiv$  *Dracaena pinguicula* (P. R. O. Bally) Byng & Christenhusz (2018).

**S. pinguicula** fa. **disticha** (Pfennig ex Butler) L. E. Newton & Thiede (*Cact. Succ. J. (US)* 87(1): 31, ill. (pp. 30–31), 2015). **Type:** Kenya, Coast Prov. (*Bally* 14976 [EA]). — **Distr:** Kenya (Coast Prov.); sandy plains with open bushland, 120–230 m.

$\equiv$  *Sansevieria pinguicula* ssp. *disticha* Pfennig ex Butler (2012)  $\equiv$  *Dracaena pinguicula* ssp. *disticha* (Pfennig ex A. Butler) Byng & Christenhusz (2018).

[1] Differs from ssp. *pinguicula*: **L** 10–15 cm, distichous, curving upwards.

The type locality is not far from that of ssp. *pinguicula*, and the two variants have been found growing together, so the rank of subspecies, chosen upon transfer of the species to *Dracaena* by Christenhusz & al. (2018), is inappropriate as the rank of subspecies is usually used for geographically separated populations. A specimen in ZSS, cited in the protologue as an isotype, has a different date from that of the holotype and cannot be regarded as a duplicate (ICN Art. 8.2, 9.4). Hence it is regarded as a paratype. As the holotype does not show the distichous leaf arrangement, an epitype was designated (Newton & Thiede 2015).

**S. pinguicula** ssp. **nana** (Chahinian) L. E. Newton & Thiede (*Cact. Succ. J. (US)* 87(1): 32, ill. (p. 31), 2015). **Type:** Kenya, Coast Prov. (*Schwartz & LaFon* s.n. in *Chahinian* 397 [MO, NY]). — **Distr:** Kenya (Coast Prov.); open bushland, 150 m.

$\equiv$  *Sansevieria pinguicula* var. *nana* Chahinian (2013)  $\equiv$  *Dracaena pinguicula* ssp. *nana* (Chahinian) Byng & Christenhusz (2018).

[1] Differs from ssp. *pinguicula*: **L** shorter, darker green; **Fl** white.

**Fig. 5** *Sansevieria pinguicula* ssp. *pinguicula*. (Copyright: U. Eggli)



A compact, dwarf-growing variant of *S. pinguicula*, growing some distance away from the type locality of the species.

***S. pinguicula* ssp. *pinguicula*** — **Distr:** Kenya; sandy plains with open bushland, 120–230 m. **I:** Pfennig (1977a: 510). – Fig. 5.

[1] Shortly caulescent, with runners; stem erect; runners to 8 cm; **L** 5–7, rosulate, cylindrical with a deep groove on the upper surface and 2–7 narrow grooves on the lower surface, 12–30 cm, 2.8–3.5 cm thick, narrowing to a horny acute tip, green, margin brown, surface slightly rough; **Inf** 15–32 cm, paniculate, fertile portion dense, 4–6 **Fl** per cluster; **Ped** 1.5–2 mm; **Per** tube 4–5 mm, lobes 3–4 mm, white with brown mid-stripe.

Chahinian (2005a) states that plants have rosulate leaves in juvenile stages, and distichous leaves when mature. Plants growing and spreading in my garden for over 20 years still have rosulate leaves, but see fa. *disticha* above.

***S. powellii*** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 198, Fig. 1, 1915). **Type:** Kenya, Coast Prov. (*Powell* 5 [K]). — **Distr:** Kenya, Somalia; shade in thickets. **I:** *Sansevieria* J. 3(1): 12–13, 1994. – Fig. 6.

≡ *Acyntha powellii* (N. E. Brown) Chiovenda (1932) ≡ *Dracaena powellii* (N. E. Brown) Byng & Christenhusz (2018).

[1] Caulescent, rhizomatous; stem erect, to  $\geq 1.2$  m  $\times$  2.5 cm; **L** distichous, the ranks becoming twisted around the stem, spreading,



**Fig. 6** *Sansevieria powellii*. (Copyright: L. E. Newton)

semicylindrical, 30–69  $\times$  2.2–2.9 cm,  $\pm$  1.3 cm thick, narrowed gradually to a pale brown hard spine-like acute tip, faintly glaucous grass-green becoming dark bluish-green, margin red-brown edged white, surface slightly rough; **Inf**  $\pm$  46 cm, paniculate, fertile portion subdense, 4–6 **Fl** per cluster; **Bra** convex, fleshy, 1.1–2.1 mm;

**Ped**  $\pm$  3.2 mm; **Fl** dull greenish-white, with dull brownish-purple slender lines outside, tube 6.4 mm, lobes 9.5 mm.

Pfennig (1977a) has suggested that this might be a natural hybrid *S. arborescens*  $\times$  *S. robusta*, but this has yet to be confirmed (Newton 2012a; Butler 2012a).

**S. powysii** L. E. Newton (Bradleya 28: 23–25, ills., 2010). **Type:** Kenya, Coast Prov. (*Powys* 1250 [K, EA]). — **Distr:** S Kenya (Coast Prov.); in dense coastal bushland.

$\equiv$  *Dracaena powysii* (L. E. Newton) Byng & Christenhusz (2018).

[1] Caulescent, rhizomatous; rhizome 2.6–3 cm  $\varnothing$ , pale yellow; stem erect, to 2 m; **L** spiral, spreading, becoming deflexed, triangular, to 43  $\times$  2 cm, 1.7–2 cm thick, canaliculate above, narrowed to pungent 5 mm brownish spine-like tip, upper surface dull green, smooth, lower surface mid-green with  $\pm$ 15 darker longitudinal lines in the lower  $\frac{1}{2}$ , very slightly rough, margin 1 mm, red-brown with whitish fraying edge; **Inf** to 85  $\times$  45 cm, paniculate with up to 20 spreading-ascending branches, lower ones to 35 cm with secondary branching, fertile portion subdense, 4–6 **Fl** per cluster; **Bra** rounded with acute apex, 1  $\times$  1.5 mm, with brownish base and white apex; **Ped** 2 mm, pale green; **Fl** yellowish with brown mid-stripe on the lobes, tube 5–6  $\times$  2.5 mm, lobes to 7  $\times$  1.5–2 mm.

Jankalski (2009c) suggested that this might be the plant in Somalia described as *S. powellii* by Thulin (1995), but Thulin described the leaves as “in 2 ranks”, which fits *S. powellii* but not *S. powysii*, and he did not mention the very thick leaves as in *S. powysii*.

**S. raffillii** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 252, Fig. 22, 1915). **Type:** Kenya, Coast Prov. (*Powell* 7 [K]). — **Distr:** Kenya, Tanzania, Uganda.

$\equiv$  *Dracaena raffillii* (N. E. Brown) Byng & Christenhusz (2018).

**S. raffillii** var. **glauca** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 252–254, Fig. 22, 1915). **Type:** Kenya, Coast Prov. (*Powell* 8 [K]). — **Distr:** Kenya.

[3c] Differs from var. *raffillii*: **L** very dark bluish-green with distinct, but not very conspicuous, irregular spots or wavy transverse bands of lighter green 2.5–5 cm apart, distinctly bluish-glaucous; **Inf** peduncle bluish-glaucous below, lighter green speckled with pale green above; **Bra** linear-lanceolate, acute, 8.5–25.4 mm; **Ped** slightly glaucous, 5.3–6.4 mm.

Apparently collected only once, and possibly only a minor variant of the species.

**S. raffillii** var. **raffillii** — **Distr:** Kenya, Tanzania, Uganda; *Acacia* bushland, 900–1700 m. **I:** *Sansevieria* J. 2(2): 36–37, 1993.

[3c] Acaulescent, rhizomatous; rhizome 2–5 cm  $\varnothing$ , whitish; **L** 1–2, erect, lanceolate or lorate, 68–152  $\times$  5.5–12.5 cm, narrowed below the middle to a sessile base or short petiole, with a short reddish-brown hard tip, with yellowish-green closely placed blotches or irregular transverse bands on darker background, sometimes paler on the lower surface, slightly glaucous, with age with less conspicuous markings, margin hard, reddish-brown, surface smooth; **Inf** 90–115 cm, simple, elongated, fertile portion 61–76 cm, dense, 2–5 **Fl** per cluster; **Bra** ovate-lanceolate, acuminate, 5.3–17 mm; **Ped** 4.2–6.4 mm; **Fl** tube 25–28.6 mm, greenish-white, lobes 28.6–29.6 mm, white.

**S. robusta** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 207, 1915). **Type** [lecto]: Kenya, Taita Distr. (*Grenfell* 13 [K]). — **Lit:** Chahinian (2005b); Newton (2014). **Distr:** Kenya; dry bushland, 600–1500 m. **I:** Mbugua (1994); Newton (1994).

[1] Caulescent, rhizomatous; rhizome to 2 cm  $\varnothing$ , yellowish-white; stem erect, to 60  $\times$   $\geq$ 2.5 cm; **L** 6–14, distichous, erect or slightly spreading, laterally compressed with a wide groove along the upper face, to 2.13 m  $\times$  3.4 cm, to 4.5 cm thick, narrowed gradually to a 6.4–12.7 mm brown hard spine-like tip, dark green, faintly glaucous, with 14–30 longitudinal darker green lines, margin narrowly bordered red-brown, edged white, surface smooth; **Inf** 80–140 cm, paniculate, peduncle greenish-grey, fertile portion 12–20 cm, lax, 4–6 **Fl** per cluster; **Ped**

11–19 mm; **Fl** white or greenish, tube 10–25 mm, lobes 5–10 mm.

Originally described with flowers unknown, and based on 4 syntypes, all from Taita District. A lectotype was chosen by Mbugua (2007). Mbugua (2007) and Mansfeld (2015a) included *S. perrotii* here and this was followed by The Plant List, after correcting Mbugua's failure to recognize its priority over *S. robusta*. The synonymization was disputed by Newton (2014). When growing in thick bush it can grow taller, but in open situations it does not exceed 60 cm. Chahinian (2005b) recorded variation in the species, and further field work is required to investigate this.

**S. rorida** (Lanza) N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 205, 1915). **Type:** Somalia (Macaluso 177 [PAL?]). — **Lit:** Mangani (1996: with ill.). **Distr:** Somalia; sandy places on the coast near sea-level.

≡ *Sanseverinia rorida* Lanza (1910) ≡ *Acyntha rorida* (Lanza) Chiovena (1916).

[1] Caulescent; stem to 23 cm; **L** 11–15, distichous, ascending-spreading, cylindrical with a groove along the upper surface, 30–53 × 2.5–3.4 cm, 1.9–2.5 cm thick, narrowed gradually to a spine-like tip, green, somewhat glaucous, with numerous darker longitudinal lines on the sides and lower surface, margin reddish-brown, edged white; **Inf** ± 1 m, paniculate, fertile portion 7.6–18 cm, lax, 3–6 **Fl** per cluster; **Bra** deltoid, acute; **Ped** ± 2 mm; **Fl** tube ± 6.4 mm, lobes 10.6–12.7 mm, whitish-yellow with reddish mid-stripe.

Included in *S. ehrenbergii* by Thulin (1995) and Mansfeld (2015a), and mentioned under that species by Lebrun & Stork (2014).

**S. rosulata** T. G. Forrest (Cact. Succ. J. (US) 89(6): 289–292, ill., 2017). **Type:** Uganda, Bukedea Distr. (Forrest 1506 [MHU]). — **Distr:** E Uganda; rock outcrops, sometimes on large ant hills, 1160 m.

[3c] Acaulescent, rhizomatous, rhizome 4 cm Ø, light yellow/brown; **L** 4–12 (–16), rosulate, spreading, lanceolate, 60–100 (–104) × 7–8 (–10) cm, base narrowing slightly, rarely petio- late, tip attenuate-subulate, 3–6 cm, green with

irregular whitish-green elongated blotches, margin narrow, white and sometimes detached as a fibre, with thin inner red line, surface slightly rough; **Inf** 74–92 cm, simple, peduncle mid-green; fertile portion 55–69 cm, dense, with (1–) 4–8 (–9) flowers per cluster; **Bra** linear-lanceolate, attenuate, 1.4–2.8 × 0.4–0.8 mm, green with white margin, with 3–5 darker nerves; **Ped** 3–5 mm; **Fl** white, tinged light green at base and apex, tube 30–42 mm, lobes 25–28 mm.

**S. roxburghiana** Schultes fil. (Syst. Veg. 7: 357, 1829). **Type:** [icono]: Roxburgh, Pl. Corom. 2: 43, t. 184, 1805, as *S. zeylanica*. — **Lit:** Budweg & Mansfeld (2014: history); Mansfeld & Ott (2015). **Distr:** India (Coromandel Coast, Goa, Karnataka, Maharashtra, Tamil Nadu).

≡ *Acyntha roxburghiana* (Schultes fil.) Kuntze (1891) ≡ *Cordylina roxburghiana* (Schultes fil.) Merrill (1923) ≡ *Dracaena roxburghiana* (Schultes fil.) Byng & Christenhusz (2018); **incl.** *Sansevieria zeylanica* Roxburgh (1805) (*nom. illeg.*, Art. 53.1).

[3c] Acaulescent, rhizomatous; **L** 6–24, rosulate, ascending, slightly recurved, linear with a deep groove on the upper surface, 20–60 × 1.3–2.5 cm, narrowed gradually to a 6.4–50 mm green soft tip, green with darker green irregular transverse bands and dark green longitudinal lines, margin green, becoming whitish with age, upper surface smooth, lower surface slightly rough; **Inf** 30–78 cm, simple, elongated, fertile portion 25–38 cm, ± 4 **Fl** per cluster; **Bra** lanceolate, attenuate, 3.2–4.2 mm; **Ped** 5.3–8.5 mm; **Fl** whitish-green, tube 6–8 mm, lobes 8.5–9.5 mm. **Cytology:** 2n = 40 (Darlington & Wylie 1955).

**S. sambiranensis** H. Perrier (Notul. Syst. (Paris) 5(2): 154–156, 1935). **Type** [syn]: Madagascar, Sambirano Distr. (Perrier 8379/8380 [P]). — **Distr:** Madagascar; shaded rocks in humid forest. **I:** Perrier (1938: 5); Vrskovy (2006); Rzepecky (2013).

≡ *Dracaena sambiranensis* (H. Perrier) Byng & Christenhusz (2018).

[2] Acaulescent, rhizomatous; rhizome to 30 × 1–2 cm; **L** 15–20, laxly rosulate,



oblanceolate, 120 × 2.5–9 cm, narrowed below the middle to a 10–20 cm channelled petiole, narrowed to an acute tip, green; **Inf** 2–8 cm, capitate, fertile portion 4–5 cm Ø, dense; **Bra** lanceolate, acute, 6–7 mm; **Ped** 7–20 mm; **Fl** carmine-red, tube ±10 mm, lobes 20–22 mm.

The species was long lost, but 2 collections from 1987 and 1998 have recently been reported (Rzepecky 2013). A preliminary DNA study suggests that this taxon does not belong in *Sansevieria* or *Dracaena* (Mansfeld 2014a).

**S. scimitariformis** D. J. Richards (Sansevieria 5: 8–9, ills., 2003). **Type:** Zimbabwe (*Richards* 2259 [SRGH]). — **Distr:** NE Zimbabwe; amongst rocks on granite hill, c. 890 m.

≡ *Dracaena scimitariformis* (D. J. Richards) Byng & Christenhusz (2018).

[2] Acaulescent, rhizomatous; rhizome 3–4 cm Ø; **L** 4–6, rosulate, spreading, flat-canalicate, 50–70 × 6–10 cm, base 3 cm thick, tip blunt, overall dark green, sometimes with lighter transverse bands, margin slightly wavy, brown; **Inf** 15 cm, simple, peduncle with 4 sterile **Bra**, fertile portion 10 cm, dense, almost capitate, 4–6 **Fl** per cluster; **Bra** 20 mm; **Fl** purplish at the base, becoming lighter and yellowish-green above, 100–120 mm.

The protologue describes the “floral tube” as 10–12 cm long, but as corolla lobes are not mentioned this probably refers to the whole flower. Croix (2010) suggests a possible occurrence in Zambia. This species and *S. humiflora* are close to *S. hallii*. Further field work to determine distribution and variation could lead to a reassessment of their distinction as species.

**S. senegambica** Baker (J. Linn. Soc., Bot. 14: 548, 1875). **Type** [syn]: Senegal (*Perrottet* 782 [K]). — **Distr:** Gambia, Guinea, Guinea-Bissau, Ivory Coast, Senegal, Sierra Leone; shady places. **I:** Brown (1915: 236).

≡ *Dracaena senegambica* (Baker) Byng & Christenhusz (2018); **incl.** *Sansevieria cornui* Gérôme & Labroy (1903); **incl.** *Sansevieria liberiensis* Cornu ex A. Chevalier (1920) (*nom. inval.*, Art. 32.1d?).

[3c] Acaulescent, rhizomatous; rhizome 1.3–1.9 cm Ø, bright red, turning pale brownish in light; **L** 2–4, rosulate, suberect, recurved to spreading nearer the tip, linear-lanceolate to lanceolate, 30–69 × 3–6.4 cm, narrowed at the base to a 2.5–7.6 cm channelled petiole, narrowed gradually from the middle to a 4.2–12.7 mm green soft subulate tip, upper surface dark green sometimes with indistinct paler green transverse bands, lower surface slightly paler with more distinct transverse bands, margin green, surface smooth; **Inf** 30–50 cm, simple, elongated, peduncle light or dark green or mottled purplish, fertile portion lax, 3–6 **Fl** per cluster; **Bra** ovate-lanceolate or oblong-lanceolate, acute, 6.4–8.5 × 2.1–3.2 mm; **Ped** 5.3–8.5 mm; **Fl** white, tinged purple in sun, tube 6.4–12.7 mm, lobes 10.6–19 mm. — **Cytology:** 2n = 40 (Sharma & Chaudhuri 1964).

Based on 2 syntypes, the other being *Richard* 72 (K).

**S. sinus-simiorum** Chahinian (*Sansevieria* 3: 24–26, ills.; 4: 9 [erratum], 2002). **Type:** Malawi (*Burdett* s.n. in *Chahinian* 316 p.p. [MO, NY]). — **Lit:** Thiede & al. (2017). **Distr:** S Malawi; in shade on rocky slopes.

≡ *Dracaena sinus-simiorum* (Chahinian) Byng & Christenhusz (2018); **incl.** *Sansevieria malawiana* hort. (s.a.) (*nom. inval.*, Art. 29.1).

[2] Acaulescent, rhizomatous, rhizome ±5 cm Ø, grey; **L** 8–10, crowded, straight or slightly curved backwards or sideways, occasionally twisting, with a round channel ±½ the width of the leaf at the bottom and widening to sometimes almost the full width of the leaf at the top, to 100–150 cm long, to 6 cm thick, 6 cm wide at the base, slowly tapering to the tip, overall with inconspicuous cross-banding when young, more obscure later, with numerous continuous and interrupted lines, most reaching the apex, margin (edge of channel) acute, chestnut-brown bordered by withered fibres, tip obtuse, surface smooth, waxy; **Inf** simple, capitate, peduncle 29 cm, 16 mm wide at the base, 13 mm at mid-height, with 6 sterile triangular **Bra**, withered, 32–35 × 11.13 mm; fertile portion ±19 cm Ø, dense; **Bra** membranous, 4–8 × 2–4 mm; **Ped** 6–16 mm; **Fl** white tinged with green, when



closed 30–32 mm, 2 mm wide at the tip, 1 mm wide at the bottom, when open tube cylindrical, 82–97 mm, 2 mm wide at the top, 3 mm wide at mid-length, inflated to 4 mm at the bottom, lobes 19–21 × 3 mm.

The hyphen in the epithet was omitted by Christenhusz & al. (2018), contrary to ICN Art. 60.9.

**S. sordida** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 214–215, Fig. 8, 1915). **Type:** K [ex cult.]. — **Distr:** Unknown.

≡ *Dracaena sordida* (N. E. Brown) Byng & Christenhusz (2018).

[3b] Acaulescent or shortly caulescent, rhizomatous; **L** 4–12, distichous, slightly spreading, cylindrical, slightly compressed laterally with a channel down the upper surface, 69–107 × 0.9–1.3 cm, 1.3–1.9 cm thick, becoming flattened towards the base, narrowed to a 0.7–1.1 mm whitish or grey brown-based acute spine-like tip, dull bluish-green with numerous darker longitudinal lines, margin hardened, dark brown edged white, surface very rough; **Inf** 30–60 cm, simple, elongated, peduncle dull light green, with minute white dots, fertile portion 20–45 cm, lax, 7–14 **Fl** per cluster; **Bra** subulate, 3.2–6.4 mm; **Ped** 8.5–12.7 mm; **Fl** tube 7.4–10.6 mm, white or greenish, lobes 14.8–16.9 mm, white inside, green with minute dull purplish dots outside.

I am not aware of any recent field gatherings matching this description, but Mbugua (2007)

claims a disjunct distribution in Kenya, Zambia and RSA.

**S. specksii** R. H. Webb & Myklebust (Sansevieria 37: 7–10, ills., 2018). **Type:** Benin, Atakora (*Specks* 21430 [MO]). — **Distr:** W Benin; savanna, 720 m.

[3c] Acaulescent, rhizomatous, forming dense clumps, rhizome 5 cm Ø; **L** (2–) 3 (–5), ascending to spreading, oblanceolate, canaliculate, (70–) 90 (–110) × 6–7 cm, medium-green with light grey-green irregular transverse bands, with pronounced U-shaped central channel bearing longitudinal lines that are more prominent towards the base, with thin red-brown entire margin, upper surface smooth, lower surface moderately rough, tip 5 mm, white, chartaceous; **Inf** 90 cm, simple, fertile portion to 45 cm, dense, with (4–) 6 (–8) **Fl** per cluster; **Bra** triangular, scarious, 5 × 2 mm; **Ped** 1–2 mm; **Fl** cream, 80–100 mm.

**S. stuckyi** Godefroy-Lebeuf (Sansev. Gigant. Afr. Orient., 13, 17, 33, ills., 1903). **Type:** Moçambique (*Godefroy-Lebeuf* s.n. [K]). — **Distr:** Moçambique, Zimbabwe. **I:** Brown (1915: 220). – Fig. 7.

≡ *Dracaena stuckyi* (Godefroy-Lebeuf) Byng & Christenhusz (2018); **incl.** *Sansevieria andradae* Godefroy-Lebeuf (1903).

[2] Acaulescent, rhizomatous; rhizome to 5 cm Ø; **L** 1–2 (rarely 3), erect, cylindrical with a groove along the upper surface, 122–275 ×

**Fig. 7** *Sansevieria stuckyi*. (Copyright: U. Eggli)



3.8–6.4 cm, narrowing gradually to a pale brown hard acute subulate tip, dull green, slightly glaucous, with transverse paler green bands and 6–20 longitudinal lines, margin green, surface slightly rough; **Inf** 21–32 cm, simple, capitate, peduncle purple, speckled green, fertile portion  $7 \times 34$  cm at anthesis, dense; **Bra** ovate-lanceolate,  $8\text{--}20 \times 4\text{--}10$  mm; **Fl** tube 90–100 mm, lobes 40 mm. — **Cytology**:  $2n = 116$  (Sharma & Chaudhuri 1964).

Originally described with flowers unknown. See comment for *S. fischeri*. Reported by Takawira-Nyanya (2006) to be extinct in Zimbabwe.

**S. subspicata** Baker (Gard. Chron., ser. 3, 6: 436, 1889). **Type**: Moçambique, Gaza Prov. (Monteiro s.n. [K]). — **Distr**: Moçambique; coastal thickets.

≡ *Dracaena subspicata* (Baker) Byng & Christenhusz (2018); **incl.** *Sansevieria splendens* A. B. Graf (1978) (*nom. inval.*, Art. 36.1, 37.1); **incl.** *Sansevieria patersonii* hort. ex Morgenstern (1979) (*nom. inval.*, Art. 36.1, 37.1).

[3c] Acaulescent, rhizomatous; rhizome 1.3–2.5 cm Ø, pale yellowish-brown; **L** 4–10, erect or recurved-spreading, lanceolate,  $23\text{--}60 \times 2.5\text{--}5.7$  cm, narrowed from the middle or above to a  $3.8\text{--}23 \times 0.4\text{--}0.6$  cm channelled petiole, with a 4.2–6.4 mm green soft subulate tip, deep green, sometimes faintly glaucous, margin green becoming whitish, surface smooth; **Inf** 30–40 cm, simple, elongated, fertile portion lax, 1–2 **Fl** per cluster; **Bra** lanceolate, acute, 2.1–6.4 mm; **Ped** 1.1–2.1 mm; **Fl** tube 23–30 mm, greenish-white, lobes 17–19 mm, white.

**S. subtilis** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 237–238, Fig. 17, 1915). **Type**: Uganda (Dawe s.n. [K]). — **Distr**: Uganda.

≡ *Dracaena subtilis* (N. E. Brown) Byng & Christenhusz (2018).

[3c] Acaulescent, rhizomatous; rhizome 0.85–1.1 cm Ø; **L** 2–4, erect or slightly recurved, linear-lanceolate,  $53\text{--}69 \times 2.5\text{--}4.5$  cm, narrowed to a 5–30 cm channelled petiole, narrowed gradually from the middle or above to a 12.7–25.4 mm green soft subulate tip, green, lower surface sometimes with faint transverse bands, margin green,

surface smooth; **Inf** 38–53 cm, simple, elongated, fertile portion lax, 2–3 **Fl** per cluster; **Bra** lanceolate, acuminate, 3.2–4.2 mm; **Ped** 4.2–7.4 mm; **Fl** tube 6.4–8.5 mm, lobes 10.6–12.7 mm, white.

**S. suffruticosa** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 202, Fig. 3, 1915). **Type**: Kenya (Evans s.n. [K]). — **Lit**: Jankalski (2007b); Webb & Newton (2016). **Distr**: Kenya. ≡ *Dracaena suffruticosa* (N. E. Brown) Byng & Christenhusz (2018).

**S. suffruticosa** var. **longituba** Pfennig (Bot. Jahrb. Syst. 102 (1–4): 178, 1981). **Type**: Kenya, Nairobi Distr. (Pfennig 1336 [EA]). — **Distr**: Kenya; edges of thickets and on sandy cliffs, 1450 m. **I**: Chahinian (1992).

≡ *Dracaena suffruticosa* var. *longituba* (Pfennig) Byng & Christenhusz (2018).

[3a] Differs from var. *suffruticosa*: **L** surface very smooth; **Fl** tube 20 mm.

**S. suffruticosa** var. **suffruticosa** — **Distr**: Kenya; edges of thickets, 1700–1900 m.

[3a] Caulescent, with runners; stem erect, to 30 cm, branching freely 0.8–7.6 cm above ground; runners spreading or ascending, to  $25 \times 1.9$  cm; **L** 7–18, ± distichous or irregular, ascending or spreading, cylindrical with a groove on the upper surface from the base to  $\frac{1}{4}\text{--}\frac{1}{2}$  of the leaf length, 15–60 cm, 1.3–1.9 cm thick, narrowed gradually to a 3.2–4.2 mm brown hard acute spine-like tip, dark green with faint paler green transverse bands when young, with darker green longitudinal lines, surface rough, sometimes smooth near the base; **Inf** 30–38 cm, simple, elongated, peduncle green with numerous whitish minute linear dots, fertile portion 4.5–6.4 cm Ø, dense, 2–5 **Fl** per cluster; **Bra** ovate, acute or acuminate, 1.1–4.2 mm; **Ped** 2.8–4.2 mm; **Fl** whitish or greenish-white, sometimes slightly red-tinged outside, tube ±10 mm, lobes 12.7–14.8 mm.

Pfennig (1981) argued for a type locality near Nakuru.

**S. trifasciata** Prain (Bengal Pl. 2: 1054, 1903). **Type**: Nigeria, Oban Distr. (Talbot s.n. [K]). — **Lit**:

Chahinian (1987: synopsis cultivars); Chahinian (2012: updated synopsis cultivars); Chahinian (2013: updated synopsis cultivars); Chahinian (2014: updated synopsis cultivars); Mangani (2014: history). **Distr:** Nigeria, Democratic Republic of the Congo [Zaire]; naturalized elsewhere (e.g. India).

≡ *Dracaena trifasciata* (Prain) Mabberley (2017).

Widely cultivated in numerous cultivars, see Chahinian (1987) and later updates. A dwarf cultivar (leaves to 50 × 7.5 cm) is ‘Hahnii’ and several derivatives with different leaf sizes, different degrees of variegation, and different shades of green exist.

**S. trifasciata** var. **laurentii** (De Wildeman) N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 240, 1915). **Type:** Democratic Republic of the Congo [Zaire] (*Anonymus* s.n. [K]). — **Distr:** Democratic Republic of the Congo [Zaire]. **I:** Chahinian (1987: 21).

≡ *Sansevieria laurentii* De Wildeman (1904).

[3c] Differs from var. *trifasciata*: **L** with yellow margin to 1 cm wide. — **Cytology:** 2n = 40 (Sharma & Chaudhuri 1964: as *S. laurentii*).

A periclinal chimaera, treated as a cultivar (*S. trifasciata* ‘Laurentii’) by Jankalski (2007a).

**S. trifasciata** var. **trifasciata** — **Distr:** Nigeria. **I:** Chahinian (1987: 20).

**Incl.** *Alettris hyacinthoides* Miller (1768) (*nom. illeg.*, Art. 53.1); **incl.** *Acyntha guineensis* Medikus (1786); **incl.** *Salmia guineensis* Cavanilles (1795); **incl.** *Sansevieria guineensis* Gérôme & Labroy (1903) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria zebrina* L. Gentil (1907) (*nom. inval.*, Art. 32.1c); **incl.** *Sansevieria jacquinii* N. E. Brown (1911).

[3c] Acaulescent, rhizomatous; rhizome 1.3–2.5 cm Ø; **L** 1–2 (–6), erect, linear-lanceolate, 30–122 × 2.5–7 cm, narrowed gradually from ± or above the middle to a channelled petiole, with a 3.2–3.8 mm green subulate tip, with alternating transverse bands of light dull green or clear whitish-green and deep grass-green to almost blackish-green, with slight glaucous bloom, margin green, surface smooth; **Inf** 30–76 cm, simple, elongated, peduncle green with

pale green dots, fertile portion lax, 3–8 **Fl** per cluster; **Bra** ovate or ovate-lanceolate, acuminate, 3.2–12.7 mm; **Ped** 5.3–8.5 mm; **Fl** white, tube 6.4–12.7 mm, lobes 14.8–19 mm. — **Cytology:** 2n = 36 (Sharma & Chaudhuri 1964).

**S. varians** N. E. Brown (Bull. Misc. Inform. Kew 1915(5): 209, 1915). **Type:** K [ex cult.]. — **Distr:** Known from cultivation only, possibly from RSA (see note below).

≡ *Dracaena varians* (N. E. Brown) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; **L** 4–8, distichous, erect or ascending, cylindrical with a groove on the upper surface or semicylindrical with a shallow groove on the upper surface, 38–114 cm, 1.3–2.2 cm thick, narrowed gradually to a 4.2–8.5 mm whitish hard acute tip, dull dark grass-green with numerous dark green longitudinal lines, when young with indistinct lighter green transverse bands, margin green or red-brown often edged white, surface slightly rough; **Inf** 60–76 cm, simple, elongated, peduncle light glaucous-green or greyish-green, fertile portion with 6–10 **Fl** per cluster; **Bra** linear or filiform, acute, 4.2–6.4 mm; **Ped** 4.2–5.3 mm; **Fl** white, speckled with purple at the tips, tube 10.6–12.7 mm, lobes 14.8–16.9 mm.

South African plants described and illustrated by Jaarsveld (1987) and Jaarsveld (1994) as a form of *S. pearsonii* are regarded as this species by Jankalski (2007a). Not included in Lebrun & Stork (2014).

**S. volkensii** Gürke (in Engler, Pfl.-welt Ost-Afr., Teil C, 144, 1895). **Type** [neo]: Tanzania, Pare Distr. (*Wingfield* 1525 [K]). — **Distr:** Kenya, Tanzania; edge of thickets on sandy soil, 500–900 m. **I:** Brown (1915: 212, as *S. intermedia*).

≡ *Dracaena volkensii* (Gürke) Byng & Christenhusz (2018); **incl.** *Sansevieria intermedia* N. E. Brown (1914); **incl.** *Acyntha polyrrhitis* Chiovenda (1932) ≡ *Sansevieria polyrrhitis* (Chiovenda) Chiovenda ex Guidotti (1932); **incl.** *Sansevieria quarrei* De Wildeman (1932); **incl.** *Sansevieria humbertiana* Guillaumin (1940) ≡ *Sansevieria gracilis* var. *humbertiana* (Guillaumin) Mbugua (2007) ≡ *Dracaena serpenta* var.

*humbertiana* (Guillaumin) Byng & Christenhusz (2018).

[3b] Acaulescent, rhizomatous; **L** 2–7, erect or ascending, semicylindrical, 45–122 cm, 1.3–1.9 cm thick, narrowed gradually to a whitish acute spine-like tip, dull deep green, becoming slightly bluish-green, sometimes with faint whitish transverse bands, margin green or whitish, surface slightly rough; **Inf** 20–46 cm, simple, elongated, peduncle light greyish-green, fertile portion  $\pm$ 30–40 cm, dense, 3–6 **Fl** per cluster; **Bra** ovate or ovate-lanceolate, acute, 2.1–4.2 mm; **Ped** 2.1 mm; **Fl** white, tube 14.8–19 mm, pale greenish, lobes 12.7–19 mm, white or greenish-white with minute purplish spots on the outside.

*S. humbertiana*, included here as a synonym, was recombined as *Dracaena serpenta* var. *humbertiana* by Christenhusz & al. (2018).

**S. zanzibarica** Gérôme & Labroy (Bull. Mus. Hist. Nat. (Paris) 9: 170, 172–173, fig. 19, 1903). **Type:** Tanzania / Zanzibar? (*Sacleux* s.n. [P]). — **Distr:** Tanzania or Zanzibar.

**Incl.** *Sansevieria ehrenbergii* Gérôme & Labroy (1903) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria ehrenbergii* De Wildeman (1905) (*nom. illeg.*, Art. 53.1).

[–] Very shortly caulescent; **L** distichous, recurved-spreading, linear-lanceolate, 15–30  $\times$  1.9–2.5 cm, dull dark green with bluish-grey bloom, margin reddish-brown; **Inf** and **Fl** not known.

Originally described with flowers unknown, and still a little-known species. Jankalski (2007a) suggests that it is possibly *S. perrotii*, and he was followed by Lebrun & Stork (2014). Included in *S. arborescens* by Mansfeld (2015a).

**S. zeylanica** (Linné) Willdenow (Spec. Pl. 2: 159, 1799). **Type:** [lecto — icono]: Commelin, Hort. Med. Amstelod. Pl. Rar. 2: 41, t. 21, 1701. — **Lit:** Mansfeld & Ott (2015). **Distr:** Sri Lanka, India (Tamil Nadu); rocky or sandy places in dry regions. **I:** Wijnands (1973: 110).

$\equiv$  *Aloe hyacinthoides* var. *zeylanica* Linné (1753)  $\equiv$  *Aletris hyacinthoides* var. *zeylanica* (Linné) Linné (1762)  $\equiv$  *Aloe zeylanica* (Linné) Jacquin (1762)  $\equiv$  *Aletris zeylanica* (Linné) Miller

(1768)  $\equiv$  *Dracaena zeylanica* (Linné) Mabblerley (2017); **incl.** *Aletris zeylanica* Lamarck (1789) (*nom. illeg.*, Art. 53.1); **incl.** *Sansevieria indica* Herter (1956) (*nom. illeg.*, Art. 52.1).

[3b] Acaulescent, rhizomatous; rhizome 1.3–1.5 cm  $\varnothing$ ; **L** 5–11, erect below, slightly recurved above, linear to semicylindrical with a groove on the upper surface, 45–76  $\times$  0.9–2.1 cm, 5–8.5 mm thick, narrowed gradually to a 12.7–38 mm long green soft subulate acute tip, dark green with lighter green transverse bands, with 4–7 darker green longitudinal lines, margin green, surface almost smooth; **Inf** 55–65 cm, simple, elongated, lax, up to 6 **Fl** per cluster; **Fl** white, grey-tipped, tube 20–25 mm, lobes to 35 mm. — **Cytology:** 2n = 40, 42 (Darlington & Wylie 1955); 2n = 42 (Janaki-Ammal 1945).

Described with flowers not seen, and still a little-known species. Binojkumar (2002) claims that this species also occurs in India. Mansfeld & Ott (2015) give the leaf size as 30–40  $\times$  1.5–2 cm.

## References

- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- APG (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181(1): 1–20. <https://doi.org/10.1111/boj.12385>
- Binojkumar, M. S. (2002) A study on the genus *Sansevieria* Thunb. (*Dracaenaceae*) in India. J. Econ. Taxon. Bot. 26(2): 455–463, ills., key.
- Bos, J. J. (1984) *Dracaena* in West Africa. Agric. Univ. Wageningen Pap. 84–1–126 pp., ills., maps, key. <http://edepot.wur.nl/283694>
- Bos, J. J. (1998) *Dracaenaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 238–241, ills., key. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_30](https://doi.org/10.1007/978-3-662-03533-7_30)
- Brown, N. E. (1915) *Sansevieria*. A monograph of all known species. Bull. Misc. Inform. Kew 1915(5): 185–261, ills., key, 2 tt. <http://biodiversitylibrary.org/page/11492707>
- Brown, S. H. (2016) Winter-Frühlingsblüher in Süd-Florida. *Sansevieria Online* 4(1): 28–32, ills.
- Budweg, H.-G. (2014) Die rätselhaften Früchte der *Sansevierien*. *Sansevieria Online* 2(1): 4–31, ills.



- Budweg, H.-G. (2016) Die Blütenstände der Sansevierien. *Sansevieria Online* 4(2): 4–24, ills.
- Budweg, H.-G. & Mansfeld, P. A. (2014) *Sansevieria roxburghiana* von der Koromandelküste. *Sansevieria Online* 2(1): 45–51, ills.
- Butler, A. (2009) Is this the real *Sansevieria braunii* Engler & Krause? *Sansevieria* 19: 11–12, ills.
- Butler, A. (2012a) *Sansevieria powellii*, species or hybrid? Dr Horst Pfennig's experiments. *Sansevieria* 26: 7–18, ills.
- Butler, A. (2012b) *Sansevieria ×itumea* (Mbugua) Jankal. history and further thoughts. *Sansevieria* 28: 19–20, ills.
- Carlquist, S. & Schneider, E. L. (2007) Origins and nature of vessels in monocotyledons. 9. *Sansevieria*. *South Afr. J. Bot.* 73(2): 196–203, ills. <https://doi.org/10.1016/j.sajb.2006.11.002>
- Chahinian, B. J. (1987) The *Sansevieria trifasciata* varieties. A presentation of all cultivated varieties. Reseda (US): Trans Terra Publishing.
- Chahinian, B. J. (1992) Editors' notes. *Sansevieria J.* 1(3): 33, 45, ill.
- Chahinian, B. J. (2005a) The splendid *Sansevieria*. Buenos Aires (AR): Published by the author.
- Chahinian, B. J. (2005b) The many faces of *Sansevieria robusta* N. E. Brown. *Sansevieria* 11: 3–6, ills.
- Chahinian, B. J. (2012) The *Sansevieria trifasciata* varieties — a new look — [part I] / part II. *Sansevieria* 27: 2–6, 28: 2–12, ills.
- Chahinian, B. J. (2013) The *Sansevieria trifasciata* varieties — a new look — part III / part IV. *Sansevieria* 29: 2–13, 30: 2–9, ills.
- Chahinian, B. J. (2014) The *Sansevieria trifasciata* varieties — a new look — part V / VI. *Sansevieria* 31: 2–11, 32: 2–10, ills.
- Christenhusz, M. J. M. [& al. 2018], Fay, M. F. & Byng, J. W. (eds.) (2018) The Global Flora. A practical flora to vascular plant species of the world. Special Edition, GLOVAP Nomenclature Part 1, Vol. 4. Bradford (GB): Plant Gateway.
- Croix, I. la (2010) *Dracaenaceae*. In: Timberlake, J. R. & Martins, E. S. (eds.): *Flora Zambesiaca*, vol. 13, part 2, pp. 13–35, ills., key. Richmond (GB): Royal Botanic Gardens, Kew, for the Flora Zambesiaca Managing Committee.
- Darlington, C. D. & Wylie, A. P. (1955) Chromosome atlas of flowering plants. London (GB): Allen & Unwin.
- Friis, I. (1995) *Sansevieria forskaoliana*, a new name for *Sansevieria abyssinica*. *Sansevieria J.* 4(1): 3–8, ills.
- Govaerts, R. H. A. (comp.) (2014+) World checklist of selected plant families [continuously updated]. Richmond (GB): Trustees of the Royal Botanic Gardens, Kew. <http://apps.kew.org/wcsp>
- Hepper, F. N. & Friis, I. (1994) The plants of Pehr Forsskål's *Flora Aegyptiaco-Arabica*. Richmond (GB) etc.: Royal Botanic Gardens Kew in association with the Botanical Museum Copenhagen.
- Jaarsveld, E. J. van (1987) The succulent riches of South Africa and Namibia and their adaptive strategies. *Aloe* 24(3–4): 45–92, ills.
- Jaarsveld, E. J. van (1994) The *Sansevieria* species of South Africa and Namibia. *Aloe* 31(1): 11–15, ills., key.
- Jaarsveld, E. J. van (2016) *Sansevieria hallii* in the Gonarezhou National Park (Eastern Zimbabwe). *Sansevieria* 35: 8–14, ills.
- Jaarsveld, E. J. van & Condy, G. (2015) *Sansevieria hallii*. *Flow. Pl. Afr.* 64: 42–46, ills., map.
- Janaki-Ammal, E. K. (1945) In: Darlington, C. D. & Janaki-Ammal, E. K.: Chromosome atlas of cultivated plants. London (GB): Allen & Unwin.
- Jankalski, S. (2004) *Sansevieria erythraeae*. *Sansevieria* 9: 18–21, ill.
- Jankalski, S. (2007a) Brown's *Sansevieria* monograph — an update. *Sansevieria* 15: 21–29.
- Jankalski, S. (2007b) Notes on the *Sansevieria suffruticosa* group. *Sansevieria* 17: 7–13, ills., key.
- Jankalski, S. (2007c) *Sansevieria* species described since Brown's monograph. *Sansevieria* 17: 19–28.
- Jankalski, S. (2009a) The *Sansevieria* inflorescence and new sections proposed. *Sansevieria* 19: 8–10, ills.
- Jankalski, S. (2009b) *Sansevieria* hybrids. *Sansevieria* 20: 15–21, ills.
- Jankalski, S. (2009c) The typification of *Sansevieria arborescens*. *Sansevieria* 20: 22–26, ills.
- Jankalski, S. (2015) Infrageneric species groups in *Sansevieria*. *Sansevieria* 33: 15–19, ills., key.
- Jankalski, S. (2016) *Sansevieria ballyi* and its cultivars. *Sansevieria* 35: 18–21, ills.
- Joyner, J. F. [& al. 1951], Pate, J. B., Gangstad, E. O. & Seale, C. C. (1951) The potentialities of *Sansevieria* for fiber production in South Florida. *Proc. Soil Sci. Soc. Florida* 11: 138–139.
- Jumelle, H. (1923) *Le Sansevieria canaliculata* et *le Sansevieria stuckyi*. *Bull. Mus. Nation. Hist. Nat.* 29(8): 607–612.
- Khalumba, M. L. [& al. 2008], Mbugua, P. K. & Kungu, J. B. (2008) Ethnobotanical studies on four species of the genus *Sansevieria* Thnb. in Kenya. *East Afr. J. Bot.* 1(2): 161–164.
- Koller, A. L. & Rost, T. L. (1988a) Leaf anatomy in *Sansevieria (Agavaceae)*. *Amer. J. Bot.* 75(5): 615–633, ills. <http://www.jstor.org/stable/2444196>
- Koller, A. L. & Rost, T. L. (1988b) Structural analysis of water-storage tissue in leaves of *Sansevieria (Agavaceae)*. *Bot. Gaz.* 149(3): 260–274, ills. <http://www.jstor.org/stable/2995258>
- Lavranos, J. J. (1994) The discovery of *Sansevieria* sp. "Eyl". *Sansevieria J.* 3(3): 51–52.
- Lebrun, J.-P. & Stork, A. L. (2014) Tropical African flowering plants. Ecology and distribution. Volume 8: Monocotyledons 2 (*Anthericaceae – Palmae*). Genève (CH): Ville de Genève, Éditions des Conservatoire et Jardin Botaniques.
- Lu, P.-L. & Morden, C. W. (2014) Phylogenetic relationships among Dracaenoid genera (*Asparagaceae: Nolinoideae*) inferred from chloroplast DNA loci. *Syst. Bot.* 39(1): 90–104. <https://doi.org/10.1600/036364414X678035>
- Mabberley, D. J. (2017) *Mabberley's Plant-Book. A portable dictionary of plants, their classification and uses*. Ed. 4. Cambridge (GB): Cambridge University Press.



- Mai, E. (2016) Die Dominikanische Republik auch für Sansevierienfreunde. *Sansevieria Online* 4(1): 4–11, ill.
- Mangani, R. (1996) *Sansevieria rorida* (Lanza) N. E. Brown. *Sansevieria J.* 5(1): 11–17, ill.
- Mangani, R. (2014) The history of *Sansevieria trifasciata* Prain. *Sansevieria* 32: 11–19, ill.
- Mansfeld, P. A. (2013a) Die Gattung *Sansevieria*. Alle Arten und ihre Pflege. Hamburg (DE): Published by the author / Books on Demand GmbH.
- Mansfeld, P. A. (2013b) Neugliederung der Gattung *Sansevieria* (*Asparagaceae*). *Kakt. and. Sukk.* 64(2): 35–38, ill., key.
- Mansfeld, P. A. (2014a) Madagascar und seine Sansevierien. *Sansevieria Online* 2(1): 32–37, ill.
- Mansfeld, P. A. (2014b) *Sansevieria forskaoliana* — ein neuer Name für *Sansevieria dawei*. *Sansevieria Online* 2(2): 4–13, ill., maps.
- Mansfeld, P. A. (2014c) Die Feldnummern der Sansevierien. *Sansevieria Online* 2014(Sonderheft): 1–23.
- Mansfeld, P. A. (2015a) Die Systematik der Gattung *Sansevieria* (*Asparagaceae*) — ein aktueller Stand. *Sansevieria Online* 3(1): 20–29.
- Mansfeld, P. A. (2015b) Die unverwechselbare *Sansevieria bacularis*. *Sansevieria Online* 3(2): 35–39, ill., map.
- Mansfeld, P. A. (2016a) *Sansevieria ballyi* L. E. Newton (*Asparagaceae*) and newly found field notes. *Bradleya* 34: 225–229, map, ill.
- Mansfeld, P. A. (2016b) Blütenbildung bei *Sansevieria burmanica*. *Sansevieria Online* 4(2): 45–51, ill.
- Mansfeld, P. A. & Budweg, H.-G. (2015) Erstbeschreibung von: *Sansevieria ballyi* × *Sansevieria parva* hybr. nov. *Sansevieria Online* 3(1): 12–19, ill.
- Mansfeld, P. A. & Ott, G. H. F. (2015) The history of *Sansevieria burmanica* N. E. Br. and its rediscovery. *Bradleya* 33: 105–109, map, key, ill.
- Mansfeld, P. A. & Rosigkeit, J. (2016) Pagodenhaft und blühfreudig: *Sansevieria francisii*. *Sansevieria Online* 4(1): 33–39, ill., map.
- Mbugua, P. K. (1994) Three *Sansevieria* species of Kenya. I. *Sansevieria robusta* N. E. Br. *Cact. Succ. J. (US)* 66(2): 87–88, ill., map.
- Mbugua, P. K. (1998) Three *Sansevieria* species of Kenya. II. *Sansevieria braunii*. *Cact. Succ. J. (US)* 70(6): 311–312, ill.
- Mbugua, P. K. (2003) *Sansevieria dawei* Stapf: Its description and distribution in Africa. *Sansevieria* 7: 5–6, ill.
- Mbugua, P. K. (2007) *Sansevieria*. In: Beentje, H. J. & Ghazanfar, S. A. (eds.): *Flora of Tropical East Africa: Dracaenaceae*; pp. 10–41. Richmond (GB): Royal Botanical Gardens, Kew.
- Menale, B. [ & al. 2013], Luca, P. de & Guacchio, E. del (2013) A plea to restore Petagna's authorship for the genus *Sansevieria*, nom. cons. (*Liliaceae*). *Taxon* 62(2): 387–390, ill. <https://doi.org/10.12705/622.7>
- Newton, L. E. (1994) Observations on flowering of *Sansevieria robusta* in Kenya. *EANHS Bull.* 24(1): 8–11.
- Newton, L. E. (2003a) *Sansevieria dooneri* and *S. parva*. *Sansevieria* 7: 10–11, ill.
- Newton, L. E. (2003b) Additional cases of *Sansevieria* being chewed by animals. *Sansevieria* 8: 3.
- Newton, L. E. (2004) Sunbirds feeding on *Sansevieria* flowers. *Nat. East Africa* 34(2): 8, ill.
- Newton, L. E. (2005a) Horst Pfennig (1933–1994). *Sansevieria* 11: 7–8, ill.
- Newton, L. E. (2005b) What is *Sansevieria patens*? *Sansevieria* 13: 3.
- Newton, L. E. (2007) The inflorescence in the genus *Sansevieria*. *Sansevieria* 15: 15–16, ill.
- Newton, L. E. (2009a) The identity of *Sansevieria arborescens* (*Ruscaceae*), with an amplified description, and description of a new species. *Bradleya* 27: 153–158, ill.
- Newton, L. E. (2009b) Elephants like *Sansevierias*. *Sansevieria* 20: 8–10, ill.
- Newton, L. E. (2010) Notes on *Sansevieria ballyi*, with description of a new cultivar. *Sansevieria* 22: 10–12, ill., map.
- Newton, L. E. (2011) Thoughts on the *Sansevieria* inflorescence. *Sansevieria* 24: 7–10, ill.
- Newton, L. E. (2012a) Comments on *Sansevieria powellii*. *Sansevieria* 26: 6.
- Newton, L. E. (2012b) The identity of *Sansevieria bagamoyensis*. *Bradleya* 30: 103–106, ill.
- Newton, L. E. (2014) *Sansevieria robusta* and *Sansevieria perrotii*. *Sansevieria* 32: 24–25, ill.
- Newton, L. E. (2016) Species versus hybrid *Sansevierias*. *Sansevieria* 34: 2–4, ill.
- Newton, L. E. & Mbugua, P. K. (1993) *Sansevieria* leaves: A thirst quencher for baboons. *Sansevieria J.* 2(1): 5–6.
- Newton, L. E. & Thiede, J. (2015) Rank adjustments for the infraspecific taxa of *Sansevieria pinguicula* P. R. O. Bally (*Asparagaceae* / *Dracaenaceae*). *Cact. Succ. J. (US)* 87(1): 28–32, ill. <https://doi.org/10.2985/015.087.0105>
- Newton, L. E. & Webb, R. H. (2011) The Tanzanian “*Sansevieria grandicuspis*” unmasked. *J. East Afr. Nat. Hist.* 100(1–2): 141–144, ill. <https://doi.org/10.2982/028.100.0110>
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>
- Obermeyer, A. A. [ & al. 1992], Immelmann, K. L. & Bos, J. J. (1992) *Dracaenaceae, Asparagaceae, Luzuriagaceae* and *Smilacaceae*. In: Leistner, O. A. (ed.): *Flora of Southern Africa*, Vol. 5, part 3. Pretoria (ZA): National Botanic Institute.
- Perrier, H. (1938) 40e famille. Liliacées (*Liliaceae*). In: Humbert, H. (ed.): *Flore de Madagascar*. Tananarive (MG): Imprimerie Officielle. <http://biodiversitylibrary.org/page/12247520>
- Pfennig, H. (1977a) Rasenbildend bis baumartig: Die *Sansevierien*. *Gartenpraxis* 1977: 506–511, ill.
- Pfennig, H. (1977b) Die Kultur der *Sansevierien*. *Gartenpraxis* 1977: 550–553, ill.
- Pfennig, H. (1981) Zur Systematik und Kultur einiger ostafrikanischer *Sansevieria*-Arten (*Agavaceae*). *Bot. Jahrb. Syst.* 102(1–4): 169–179, map.

- Powys, J. G. L. (1996) Island fairies of the night. *Sansevieria J.* 5(1): 3–6.
- Rauh, W. (1963) Über einige interessante Sukkulente aus Kenia. *Sukkulentekunde* 7/8: 108–127, ills.
- Roy, M. (1956) A cytological investigation of the different species of *Sansevieria* with the aid of the improved technique. *Caryologia* 8: 221–230. <https://doi.org/10.1080/00087114.1956.10797561>
- Rulkens, A. J. H. & Baptista, O. J. (2009a) Field observations and local uses of the poorly known *Sansevieria pedicellata* from Manica Province in Mozambique. *Sansevieria* 20: 2–7, ills.
- Rulkens, A. J. H. & Baptista, O. J. (2009b) Field impressions and ethno-veterinary plant use of *Sansevieria hallii* and related species in central Mozambique. *Sansevieria* 21: 8–14, ills.
- Rulkens, A. J. H. & Baptista, O. J. (2013) Notes on the distribution of *Sansevieria burdettii* Chahinian. *Sansevieria* 29: 14–16, ills.
- Rzepecky, A. (2013) *Sansevieria sambiranensis* H. Perr. *Sansevieria* 29: 18–23, ills.
- Sharma, A. K. & Chaudhuri, M. (1964) Cytological studies as an aid in assessing the status of *Sansevieria*, *Ophiopogon* and *Curculigo*. *Nucleus (Calcutta)* 7(1): 43–58.
- Speirs, D. C. (1984) *Sansevieria* species FKH 432. *Brit. Cact. Succ. J.* 2(3): 81–82, ills.
- Symoens, B. (2014) The origin of the name *Sansevieria* revealed? *Sansevieria* 31: 12–17, ills.
- Takawira-Nyenya, R. (2006) A taxonomic study of the genus *Sansevieria* (*Dracaenaceae*) in Zimbabwe. In: Ghazanfar, S. A. & Beentje, H. J. (eds.): *Taxonomy and ecology of African plants, their conservation and sustainable use*. Proc. 17th. AETFAT Congress, Addis Ababa, Ethiopia; pp. 61–71. Richmond (GB): Royal Botanical Gardens Kew.
- Takawira-Nyenya, R. & Stedje, B. (2011) Ethnobotanical studies in the genus *Sansevieria* Thunb. (*Asparagaceae*) in Zimbabwe. *Ethnobot. Res. Applic.* 9: 421–443, ills., map. <https://doi.org/10.17348/era.9.0.421-443>
- Takawira-Nyenya, R. [ & al. 2014], Newton, L. E., Wabuyele, E. & Stedje, B. (2014) Ethnobotanical studies in the genus *Sansevieria* Thunb. (*Asparagaceae*) in Coast Province of Kenya. *Ethnobot. Res. Applic.* 12: 51–69, ills. <http://www.ethnobotanyjournal.org/vol12/i1547-3465-12-051.pdf>
- Teketay, D. (1995) The genus *Sansevieria* Thunb. in Ethiopia. A contribution to the flora of Ethiopia. *Sansevieria J.* 4(2): 43–58, ills., map, key.
- Thiede, J. (1993) Notes on the *Sansevieria* species of Malawi. *Sansevieria J.* 2(2): 27–34, (3): 51–52, ills., map, key.
- Thiede, J. & Campbell-Barker, T. P. (2015) *Sansevieria burdettii* (*Asparagaceae* / *Dracaenaceae*): Its history, introduction and distribution, with new localities. *Bradleya* 33: 27–33, map, ills.
- Thiede, J. [ & al. 2009], Hargreaves, B. J. & Downs, P. E. (2009) A gorgeous gem. *Sansevieria downsii* at Njakwa Gorge, Malawi. *Cact. Succ. J. (US)* 81(5): 224–229, 255, ills., map. <https://doi.org/10.2985/015.081.0501>
- Thiede, J. [ & al. 2017], Campbell-Barker, T. P. & Hargreaves, B. J. (2017) New records for the flora of Mount Mulanje, Malawi: *Sansevieria sinus-simiorum* Chahin. (*Asparagaceae* / *Dracaenaceae*), *Crassula swaziensis* Schönland and *Crassula setulosa* Harvey (*Crassulaceae*). *Bradleya* 35: 129–138, ills., map. <https://doi.org/10.25223/brad.n35.2017.a12>
- Thulin, M. (ed.) (1995) *Flora of Somalia*. Volume 4. Angiospermae (*Hydrocharitaceae* – *Pandanaceae*). Richmond (GB): Royal Botanic Gardens Kew.
- Vrskovy, B. P. (2006) *Sansevierie z Cerveného ostrova a hyacintovky*. *Cactaceae etc.* 16(4): 132–140, ills.
- Vrskovy, B. P. (2009) A brief account of the *Sansevierias* of Yemen. *Sansevieria* 20: 11–14, ills.
- Waidhofer, A. (1996) *Sansevieria deserti* (*Agavaceae*). *Cact. Succ. J. (US)* 68(1): 9–11, ills.
- Webb, R. H. & Newton, L. E. (2016) *Sansevieria laevifolia* R. H. Webb & L. E. Newton: A new species from the Rift Valley of Kenya, with a discussion of the *Sansevieria suffruticosa* complex. *Sansevieria* 34: 9–13, ills., map.
- Wijnands, D. O. (1973) Typification and nomenclature of two species of *Sansevieria* (*Agavaceae*). *Taxon* 22(1): 109–114. <https://doi.org/10.2307/1218041>
- Wilson, F. D. (1962) Florida H-13, a promising *Sansevieria* hybrid as a source of cordage fiber. Gainesville (US): Everglades Experimental Station.



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**Part XVIII**

**The Family Xanthorrhoeaceae**







## Xanthorrhoeaceae

U. Eggli

Perennial woody pachycaul small trees to stemless herbs with massive underground **R**stock, branched or unbranched, stems with secondary thickening growth; **L** numerous in dense **Ros** at the stem tips, xeromorphic, narrowly oblong to filiform-linear, often wiry, tough, tips often spiny, basally often broadened and resiniferous, persistent when old; **Inf** spike-like, massively cylindrical on a woody leafless scape, dense-flowered; **Fl** bisexual, sessile, actinomorphic, 3-merous, in tight clusters surrounded by **Bra**; **Per** with 6 dry and chaffy persistent **Tep** in 2 series (often called sepals and petals), **Tep** free, **OTep** chartaceous, **ITep** white or yellow; **St** 3 + 3; **Anth** dorsifixed, introrse; **Ov** superior, of 3 united **Ca**, with septal **Nec**, 3-locular with 2 rows of ovules; **Sty** with undivided **Sti**; **Fr** loculicidal capsules with 1–2 **Se** per locule; **Se** with black testa and copious endosperm.

**Order:** Asparagales

**Important Literature:** Bedford & al. (1986), Clifford (1998).

**Distribution:** Tropical and subtropical Australia.

In traditional classifications, *Xanthorrhoeaceae* embraced 10 genera with  $\pm$  100 species, but the family has for long been known to be heterogeneous (Clifford 1998). In its strict sense it is now restricted to the genus *Xanthorrhoea*, and the genera *Baxteria*, *Calectasia*, *Dasypogon* and *Kingia* are placed in the separate family *Dasypogonaceae* (including *Baxteriaceae*, *Calectasiaceae* and *Kingiaceae*). *Dasypogonaceae* were regarded as unplaced at the base of the Commelinids (APG 2009), and were moved to Arecales by APG (2016); they are restricted to W Australia.

On the other hand, APG (2009), following suggestions already made earlier (APG 2003), opted for enlarging *Xanthorrhoeaceae* by including *Asphodelaceae* and *Hemerocallidaceae* (no succulents) as synonyms. Such an amount of lumping of well-established families does not result in a phylogenetically more correct classification (Nyffeler and Eggli 2010), and we and Smith & Figueiredo (this volume for *Asphodelaceae*) prefer to maintain the *Asphodelaceae* as separate family, and accept the *Xanthorrhoeaceae* in their narrow circumscription.

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Species of *Xanthorrhoea* (28–30 species in Australia) are sometimes included in succulent plant collections but are more properly regarded as mere xerophytes with woody stems. There are no indications that any form of water storage exists.

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## References

- APG (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436. <https://doi.org/10.1046/j.1095-8339.2003.t01-1-00158.x>
- APG (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161(2): 105–121. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- APG (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181(1): 1–20. <https://doi.org/10.1111/boj.12385>
- Bedford, D. J. [& al. 1986], Lee, A. T., Macfarlane, T. D., Henderson, R. J. F. & George, A. S. (1986) *Xanthorrhoeaceae*. In: George, A. S. (ed.): Flora of Australia, 46: 88–171, ills., keys. Canberra (AU): Australian Government Publishing Service.
- Clifford, H. T. (1998) *Xanthorrhoeaceae*. In: Kubitzki, K. (ed.): The families and genera of vascular plants; 3: 467–470, ills. Berlin (DE) etc.: Springer Verlag. [https://doi.org/10.1007/978-3-662-03533-7\\_29](https://doi.org/10.1007/978-3-662-03533-7_29)
- Nyffeler, R. & Eggli, U. (2010) An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28: 125–144. <https://doi.org/10.5167/uzh-35243>

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