Cælanthium, limited to two Cape species, differs from *Pharnaceum* as *Thylacospermum* from *Arenaria*, by the union of the sepals at the base into a campanulate tube, round the edge of which are inserted the stamens, being thus much more decidedly perigynous than in the rest of the group.

The genera *Psammotrophe*, Eckl. & Zeyh., and *Polpoda*, Presl, with uniovulate cells to the ovary, enumerated by Fenzl among Molluginеæ, appear to have nothing to distinguish them from true Phytolaccaceæ. *Adenogramma*, Presl, is also a Phytolaccaceous plant allied to *Giesekia*, where the ovary and fruit are reduced to a single one-seeded carpel, not compounded of 2 or 3 carpels although one-seeded as in Paronychiaceæ. *Acrossanthes*, on the other hand, both in habit and character, belongs to the apetalous Ficoideæ.

IV. Paronychiaceæ.

Without having sufficiently examined all the genera of this Order to ascertain their limits with respect to each other, or the order of their arrangement, we have, however, verified the ordinal characters in all the following (except *Cardionema*):—

1. *Corrigiola*, Linn. (an exceptional genus in its prominent petals and alternate leaves); 2. *Herniaria*, Linn.; 3. *Illecebrum*, Linn.; 4. *Cardionema*, DC.; 5. *Pentacæna*, Bartl.; 6. *Paronychia*, Juss. (including *Siphonychia*, Torr. et Gray, and *Anychia*, Rich., and perhaps altogether, with *Cardionema* and *Pentacæna*, artificial sections of *Illecebrum*); 7. *Habrosia*, Fenzl; 8. *Sclerocephalus*, Boiss.; 9. *Gymnocarpos*, Forsk.; 10. *Pteranthus*, Forsk.; 11. *Cometes*, Burm.; 12. *Dicheranthus*, Webb; 13. *Pollichia*, Soland.; 14. *Guilleminea*, H. B. et K.; 15. *Mniarum*, Forst.; 16. *Scleranthus*, Linn.; and 17. *Lastarriea*, A. Gay.

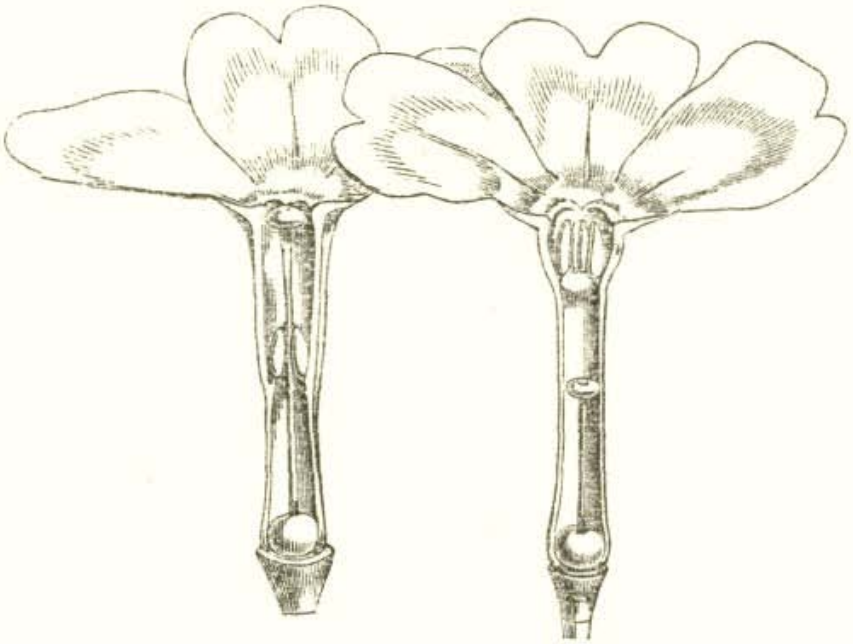
On the Two Forms, or Dimorphic Condition, in the Species of *Primula*, and on their remarkable Sexual Relations. By Charles Darwin, M.A., F.R.S., F.L.S., &c.

[Read Nov. 21, 1861.]

If a large number of Primroses or Cowslips (*P. vulgaris* and *veris*) be gathered, they will be found to consist, in about equal numbers, of two forms, obviously differing in the length of their pistils and stamens. Florists who cultivate the Polyanthus and Auricula are well aware of this difference, and call those which display the globular stigma at the mouth of the corolla "pin-headed" or "pin-eyed," and those which display the stamens "thumb-eyed." I

will designate the two forms as long-styled and short-styled. Those botanists with whom I have spoken on the subject have looked at the case as one of mere variability, which is far from the truth.

In the Cowslip, in the long-styled form, the stigma projects just above the tube of the corolla, and is externally visible; it stands high above the anthers, which are situated halfway down the tube,



Long-styled. Short-styled.

and cannot be easily seen. In the short-styled form the anthers are attached at the mouth of the tube, and therefore stand high above the stigma; for the pistil is short, not rising above halfway up the tubular corolla. The corolla itself is of a different shape in the two forms, the throat or expanded portion above the attachment of the anthers being much longer in the long-styled than in the short-styled form. Village children notice this difference, as they can best make necklaces by threading and slipping the corollas of the long-styled flowers into each other. But there are much more important differences. The stigma in the long-styled plants is globular, in the short-styled it is depressed on the summit, so that the longitudinal axis of the former is sometimes nearly double that of the latter. The shape, however, is in some degree variable; but one difference is persistent, namely, that the stigma of the long-styled is much rougher: in some specimens carefully compared, the papillæ which render the stigmas rough were in the long-styled form from twice to thrice as long as in the short-styled. There is another and more remarkable difference, namely, in the size of the pollen-grains. I measured with the micrometer many

specimens, dry and wet, taken from plants growing in different situations, and always found a palpable difference. The measurement is best made with grains distended with water, in which case, the usual size of the grains from short-styled flowers is seen to be $\frac{10-11}{7000}$ of an inch in diameter, and those from the long-styled about $\frac{7}{7000}$ of an inch, which is in the proportion of three to two; so that the pollen-grains from the short stamens are plainly smaller than those from the long stamens which accompany the short pistil. When examined dry, the smaller grains from the long-styled plants are seen under a low power to be more transparent than the larger grains, and apparently in a greater degree than can be accounted for by their less diameter. There is also a difference in shape, the grains from the short-styled plants being nearly spherical, those from the long-styled being oblong with the angles rounded; this difference in shape disappears when the grains are distended with water. Lastly, as we shall presently see, the short-styled plants produce more seed than the long-styled.

To sum up the differences:—The long-styled plants have a much longer pistil, with a globular and much rougher stigma, standing high above the anthers. The stamens are short; the grains of pollen smaller and oblong in shape. The upper half of the tube of the corolla is more expanded. The number of seeds produced is smaller.

The short-styled plants have a short pistil, half the length of the tube of the corolla, with a smooth depressed stigma standing beneath the anthers. The stamens are long; the grains of pollen are spherical and larger. The tube of the corolla is of the same diameter till close to its upper end. The number of seeds produced is larger.

I have examined a large number of flowers; and though the shape of the stigma and the length of the pistil vary, especially in the short-styled form, I have never seen any transitional grades between the two forms. There is never the slightest doubt under which form to class a plant. I have never seen the two forms on the same plant. I marked many Cowslips and Primroses, and found, the following year, that all retained the same character, as did some in my garden which flowered out of their proper season in the autumn. Mr. W. Wooler, of Darlington, however, informs us that he has seen the early blossoms on Polyanthuses which were not long-styled, but which later in the season produced flowers of this form. Possibly the pistils may not in these cases have become fully developed during the early spring. An excellent

proof of the permanence of the two forms is seen in nursery gardens, where choice varieties of the Polyanthus are propagated by division; and I found whole beds of several varieties, each consisting exclusively of the one or the other form. The two forms exist in the wild state in about equal numbers: I collected from several different stations, taking every plant which grew on each spot, 522 umbels; 241 were long-styled, and 281 short-styled. No difference in tint or size could be perceived in the two great masses of flowers.

I examined many cultivated Cowslips (*P. veris*) or Polyanthuses, and Oxlips; and the two forms always presented the same differences, including the same relative difference in the size of the pollen-grains.

Primula Auricula presents the two forms; but amongst the improved fancy kinds the long-styled are rare, as these are less valued by florists, and seldomer distributed. There is a much greater relative inequality in the length of the pistils and stamens than in the Cowslip, the pistil in the long-styled form being nearly four times as long as in the short-styled, in which it is barely longer than the ovarium; the stigma is nearly of the same shape in both forms, but it is rougher in the long-styled, though the difference is not so great as in the two forms of the Cowslip. In the long-styled plants the stamens are very short, rising but little above the ovarium. The pollen-grains of these short stamens from the long-styled plants, when distended with water, were barely $\frac{5}{6000}$ of an inch in diameter, whereas those from the long stamens of the short-styled plants were barely $\frac{7}{6000}$, showing a relative difference of five to seven. The smaller grains of the long-styled plants were much more transparent, and before distention with water more triangular in outline than those of the other form. In one anomalous specimen with a long pistil, the stamens almost surrounded the stigma, so that they occupied the position proper to the stamens of the short-styled form; but the small size of the pollen-grains showed that these stamens had been abnormally developed in length, and that the anthers ought to have stood at the base of the corolla.

In the two forms of *Primula Sinensis*, the pistil is about twice as long in the one as in the other. The stigma of the long-styled varies much in shape, but is considerably more elongated and rougher than that of the short-styled, the latter being nearly smooth and spherical, but depressed on the summit. The shape of the throat of the corolla in the two forms differs as in the Cow-

slip, as does the length of the stamens. But it is remarkable that the pollen-grains of both forms, wet and dry, presented no difference in diameter; they vary somewhat in size, as do the pollen-grains of all the species, but in both forms the average diameter was rather above $\frac{10}{6000}$ of an inch. There is one remarkable difference in the two forms of this species, namely (as we shall presently more fully see), that the short-styled plants, if insects be excluded and there be no artificial fertilization, are quite sterile, whereas the long-styled produce a moderate quantity of seed. But when both forms are properly fertilized, the short-styled flowers (as with Cowslips) yield more seed than the long-styled. In a lot of seedlings which I raised, there were thirteen long-styled and seven short-styled plants.

Of *Primula ciliata* a long-styled specimen, and of *P. ciliata*, var. *purpurata*, a short-styled specimen, were sent me from Kew by Prof. Oliver. This case, however, is hardly worth giving, as the variety *purpurata* is said* to be a hybrid between this species and *P. auricula*; and the height of the stamens in the one form does not correspond with the height of the stigma in the other, as they would have done had they been the same species. There was, however, the usual difference in the roughness of the stigmas in the two forms, and the pollen-grains, distended in water, measured $\frac{6}{6000}$ and $\frac{4-5}{6000}$ of an inch in diameter. Single trusses were sent me of *P. denticulata* and *P. Piedmontana* which were long-styled, and of *P. marginata* and *nivalis* which were short-styled; and the general character of the organs leaves hardly any doubt on my mind that these species are dimorphic. In a single flower of *P. Sibirica*, however, which was sent me from Kew, the stigma reached up to the base of the anthers; so that this species is not dimorphic, or not dimorphic as far as the length of the pistil and stamens are concerned, unless indeed this single specimen was anomalous, like that mentioned of *P. auricula*.

We thus see that the existence of two forms is very general, if not universal, in the genus *Primula*. The simple fact of the pollen-grains differing in size and outline, and the stigma, in shape and roughness, in two sets of individuals of the same species, is curious. But what, it may be asked, is the meaning of these several differences? The question seems worthy of careful investigation, for, as far as I know, the use or meaning of dimorphism in plants has never been explained; hence, I will give my obser-

* Sweet's 'Flower Garden,' vol. v. tab. 123.

vations in detail, though I am far from supposing that all cases of dimorphism are alike. The first idea which naturally occurred was, that the species were tending towards a dioicous condition; that the long-styled plants, with their rougher stigmas, were more feminine in nature, and would produce more seed; that the short-styled plants, with their long stamens and larger pollen-grains, were more masculine in nature. Accordingly, in 1860, I marked some Cowslips of both forms growing in my garden, and others growing in an open field, and others in a shady wood, and gathered and weighed the seed. In each of these little lots the short-styled plants yielded, contrary to my expectation, most seed. Taking the lots together, the following is the result:—

	No. of Plants.	No. of Umbels produced.	No. of Capsules produced.	Weight of seed in grains.
Short-styled Cowslips	9	33	199	83
Long-styled Cowslips	13	51	261	91

If we reduce these elements for comparison to similar terms, we have—

	No. of Plants.	Weight of seed in grains.	No. of Umbels.	Weight of seed.	No. of Capsules.	Weight of seed in grains.
Short-styled Cowslips	10	92	100	251	100	41
Long-styled Cowslips	10	70	100	178	100	34

So that, by all the standards of comparison, the short-styled are the most fertile; if we take the number of umbels (which is the fairest standard, for large and small plants are thus equalized), the short-styled plants produce more seed than the long-styled, in the proportion of four to three.

In 1861 I tried the result in a fuller and fairer manner. I transplanted in the previous autumn a number of wild plants into a large bed in my garden, treating them all alike; the result was—

	No. of Plants.	No. of Umbels.	Weight of seed in grains.
Short-styled Cowslips ...	47	173	745
Long-styled Cowslips ...	58	208	692

These figures, reduced as before, give the following proportions:—

	Number of Plants.	Weight of seed in grains.	Number of Umbels.	Weight of seed in grains.
Short-styled Cowslips ...	100	1585	100	430
Long-styled Cowslips ...	100	1093	100	332

The season was much better this year than the last, and the plants grew in good soil, instead of in a shady wood or struggling with other plants in the open field; consequently the actual produce of seed was considerably greater. Nevertheless we have the same relative result; for the short-styled plants produced more seed than the long-styled in the proportion of three to two; but if we take the fairest standard of comparison, namely, the number of umbels, the excess is, as in the former case, as four to three.

I marked also some Primroses, all growing together under the same conditions; and we here see the product:—

	No. of Plants.	Total No. of Capsules.	Good Capsules.	Weight of seed in grains.	Or by Calculation:	Good Capsules.	Weight of seed.
Short-styled Primroses	8	49	40	16		100	40
Long-styled Primroses	9	68	50	10		100	20

The number of Primrose plants tried was hardly sufficient, and the season was bad; but we here again see (excluding the capsules which contained no seed) the same result in a still more marked manner, for the short-styled plants were twice as productive of seed as the long-styled plants.

I had, of course, no means of ascertaining the relative fertility of the two forms of the Chinese Primrose in a natural condition, and the result of artificial fertilization can hardly be trusted; but sixteen capsules from long-styled flowers, properly fertilized, produce 9·3 grains' weight of seed, whereas eight capsules of short-styled flowers produced 6·1 grains; so that if the same number, namely, 16 of the latter, had been fertilized, the weight of seed would have been 12·2, which would have been nearly in the proportion of four to three, as in Cowslips.

Looking to the trials made during two successive years on the large number of Cowslips, and on these facts with regard to common Primroses and Chinese Primroses, we may safely conclude that the short-styled forms in these species are more productive

than the long-styled forms; consequently the anticipation that the plants having largely developed pistils with rougher stigmas, and having shorter stamens with smaller pollen-grains, would prove to be more feminine in their nature is exactly the reverse of the truth. If the species of *Primula* are tending to become dioicous, which possibly may be the case, the future hypothetical females would have short pistils, and the males would have short stamens; but this tendency is accompanied, as we shall presently see, by other conditions of the generative system of a much more singular nature. Anyhow, the possibility of a plant thus becoming dioicous by slow degrees is worthy of notice, as the fact would so easily escape observation.

In 1860 I found that a few umbels of both long-styled and short-styled Cowslips, which were covered by a net, did not produce seed, though other umbels on the same plants, artificially fertilized, produced an abundance of seed; and this fact shows that the mere covering in itself was not injurious. Accordingly, in 1861 I covered up under a similar net several plants just before they opened their flowers; these turned out as follows:—

	No. of Plants.	No. of Umbels produced.	Product of Seed.
Short-styled	6	24	1·3 grains, or 50 seeds.
Long-styled	18	74	Not one seed.

Judging from the exposed plants which grew all round in the same bed, and had been treated in every way exactly the same, except that they were exposed to the visits of insects, the six short-styled plants ought to have produced 92 grains' weight of seed instead of only 1·3; and the eighteen long-styled plants, which produced not one seed, ought to have produced above 200 grains' weight. The production of the 1·3 grain of seed in the smaller lot was probably due to the action of Thrips or some minute insect. This evidence is sufficient, but I may add that ten pots of Polyanthuses and Cowslips of both forms, protected from insects in my greenhouse, did not set one pod, though artificially fertilized flowers in other pots produced an abundance. So we see that the visits of insects are absolutely necessary to the fertilization of Cowslips. As the exposed plants produced an abundance of seed, the tendency to a dioicous condition, previously remarked on, might have been safely carried on, as we see that there is an effect-

ive agency already at work which would have carried pollen from one sex to the other.

What insects habitually visit Cowslips, as is absolutely necessary for their regular fertility, I do not know. I have often watched them, but perhaps not long enough; and only four times I have seen Humble-bees visiting them. One of these bees was gathering pollen from short-styled flowers alone, another had bitten holes through the corolla; and neither of these would have been effective in the act of fertilization: two others were sucking long-styled plants. I have watched Primroses more attentively during several years, and have never seen an insect visit them; yet from their close similarity in all essential respects to Cowslips, there can hardly be a doubt that they require the visits of insects. Hence I am led to suppose that both Primroses and Cowslips are visited by moths. All the species which I have examined secrete plenty of nectar.

In *Primula Sinensis*, when protected from insects and not artificially fertilized, the case is somewhat, but not materially, different. Five short-styled plants produced up to a given period 116 flowers, which set only seven capsules, whereas twelve other flowers on the same plants artificially fertilized set ten capsules. Five long-styled plants produced 147 flowers, and set sixty-two capsules; so that this form, relatively to the other, sets a far greater number of capsules: yet the long-styled protected flowers do not set nearly so well as when artificially fertilized; for out of forty-four flowers thus treated, thirty-eight set. These remarks apply only to the early setting of the capsules, many of which did not continue swelling. With respect to the product of seed, seven protected short-styled plants, which bore about 160 flowers, produced only half a grain of seed; they ought to have produced 120 grains: so that the short-styled plants, when protected from insects, are nearly as sterile as Cowslips. Thirteen long-styled plants, which bore about 380 flowers, and which as we have seen set many more capsules, produced 25·9 grains of seed; they ought to have produced about 220 grains in weight: so that although far less fertile than the artificially fertilized flowers, yet the long-styled *P. Sinensis*, when protected from insects, is nearly twenty-four times as fertile as the short-styled when protected from insects. The cause of this difference is, that when the corolla of the long-styled plants falls off, the short stamens near the bottom of the tube are necessarily dragged over the stigma and leave pollen on it, as I saw by hastening the fall of nearly withered flowers; whereas in the short-styled flowers, the stamens are seated at the mouth of the corolla,

and in falling off do not brush over the lowly seated stigma. In the Cowslip the corolla does not fall off; and both long-styled and short-styled plants are equally sterile when protected from insects. It is a rather curious case, that the falling of the corolla, or its remaining attached when withered, might have a considerable influence on the numbers of a plant, during a year unfavourable to the visits of the proper insects.

In three short-styled plants of *Primula auricula*, protected from insects, the flowers which I fertilized produced seed, but those which were not touched produced none.

In all the species of *Primula* the pollen readily coheres to any object. In all that I have observed, though the stamens and pistils differ in length relatively to each other in the different species, yet, in the two forms of the same species, the stigma of the one form stands at exactly the same height with respect to the corolla as the anthers of the other form. If the proboscis of a dead Humble-bee, or thick bristle, or rough needle be pushed down the corolla, first of one form, and then of the other, as an insect would do in visiting the two mingled forms, it will be found that pollen from the long-stamened form will adhere round the base of the proboscis, and will be left with certainty on the stigma of the long-styled form; pollen from the short stamens of the long-styled form will also adhere a little above the tip of the proboscis, and some will generally be left on the stigma of the other form. Thus pollen will be carried reciprocally from one form to the other. In withdrawing the proboscis from the long-styled form, with pollen adhering near the tip, there will be a good chance of some being left on the flower's own stigma, in which case there will be self-fertilization; but this by no means always occurs. In the short-styled form, on the other hand (and it is important to remember this), in inserting the proboscis between the anthers situated at the mouth of the corolla, pollen, as I repeatedly found, is almost invariably carried down and left on the flower's own stigma. Moreover minute insects, such as Thrips, numbers of which I have observed in Primrose flowers thickly dusted with pollen, could not fail often to cause self-fertilization. We positively know that the visits of large insects are necessary to the fertilization of the species of *Primula*; and we may infer from the facts just given that these visits would carry pollen reciprocally from one form to the other, and would likewise *tend* to cause self-fertilization, more especially in the short-styled (*i. e.* long-stamened) form.

These observations led me to test the potency of the two pol-

lens with respect to the two stigmas in *P. veris, Sinensis,* and *auricula.* In each species four crosses can be tried; namely, the stigma of the long-styled by its own-form pollen and by that of the short-styled, and the stigma of the short-styled by its own-form pollen and by that of the other form. It is necessary to use and remember two new terms for these crosses: when the long- and the short-styled stigmas are fertilized by their own-form pollen the union is said to be "homomorphic;" when the long-styled and short-styled stigmas are fertilized by the pollen of the other form, the union is "heteromorphic." I speak of the "own-form pollen," because in the following homomorphic unions, in order to make the experiment perfectly fair, I never placed the pollen of the same flower on its own stigma, but, to avoid the possible ill effects of close interbreeding, I always used the pollen from another plant of the same form. In the following experiments all the plants were treated in exactly the same manner, and were carefully protected from insects as far as that is possible. I performed every manipulation myself, and weighed the seed in a chemical balance. Some of the capsules contained no seed, or only two or three, and these are excluded in the column marked "good pods." First for *P. Sinensis*, as the simplest case.

Primula Sinensis.—TABLE I.

	Number of flowers fertilized.	Total number of pods produced.	Number of good pods.	Weight of seed in grains.	By Calculation. Good Pods. : Weight of seed in grains.
Long-styled by own-form pollen (homomorphic union)	20	18	13	5·9	or as 100 to 45
Long-styled by pollen of short-styled (heteromorphic union)...	24	18	16	9·3	or as 100 to 58
Short-styled by own-form pollen (homomorphic union)	7	5	4	0·9	or as 100 to 22
Short-styled by pollen of long-styled (heteromorphic union)...	8	8	8	6·1	or as 100 to 76
Summary :					
The two homomorphic unions	27	23	17	6·8	
The two heteromorphic unions	32	26	24	15·4	

For the sake of comparison, we may reduce these latter figures as follows :—

	Number of flowers fertilized.	Number of good pods.	Weight of seed in grains.	Number of good pods.	Weight of seed in grains.
The two homomorphic unions	100	63	25	100	40
The two heteromorphic unions	100	75	48	100	64

In the first part of the upper table, the number of flowers fertilized and the simple result is shown; and at the right hand, for the sake of comparison, the calculated product of the weight of seed from 100 good pods of each of the four unions is given; showing that in each case the heteromorphic union is more fertile than the homomorphic union. Beneath we have a simple summary of the two homomorphic and the two heteromorphic unions. And lastly, for the sake of comparison, a calculation has been made from this summary; first, assuming that 100 flowers of both kinds of unions were fertilized; and then to the right hand, assuming that 100 good pods were produced from both unions. If we compare the result, we see that the flowers of the two heteromorphic unions produced a greater number of good pods, and a greater weight of seed, than the flowers of the two homomorphic unions; and again (and this is the fairest element of comparison, for accidents are thus almost eliminated), that the good pods from the two heteromorphic unions yielded more seed, in about the proportion of three to two, than those from the two homomorphic unions. The difference in weight from 100 capsules of the two forms is 24 grains, and this is equal to at least 1200 seeds.

Beneath we have Table II. of *P. veris*, or the Cowslip. The upper part is exactly the same as in the Table of *P. Sinensis*, and we see in each case that the heteromorphic is more fertile than the homomorphic union. The calculated results from the summary of the two homomorphic and the two heteromorphic unions are more complex than with the last species, as I wished to show that, however we proceed, the general result is the same. We see that the assumed hundred flowers, heteromorphically fertilized by the pollen of the other forms, yielded more capsules, more good capsules, and a greater weight of seed; but I rely little on this, as some whole umbels perished after being fertilized. The fairest element of comparison is to take the good capsules alone; and we here see that the 100 from the two heteromorphic unions yielded seed which in weight was as 54 to 35 from the 100 good capsules

of the two homomorphic unions,—that is, nearly as three to two, as in the Chinese Primrose.

Primula veris.—TABLE II.

	Number of flowers fertilized.	Total number of pods produced.	Number of good pods.	Weight of seed in grains.	By Calculation. Good Pods. { Weight of seed in grains.
Long-styled by own-form pollen (homomorphic union)	20	8	5	2·1	or as 100 to 42
Long-styled by pollen of short-styled (heteromorphic union)...	22	15	14	8·8	or as 100 to 62
Short-styled by own-form pollen (homomorphic union)	15	8	6	1·8	or as 100 to 30
Short-styled by pollen of long-styled (heteromorphic union)...	13	12	11	4·9	or as 100 to 44
Summary :					
The two homomorphic unions	35	16	11	3·9	
The two heteromorphic unions	35	27	25	13·7	

For the sake of comparison, we may reduce these figures as follows :—

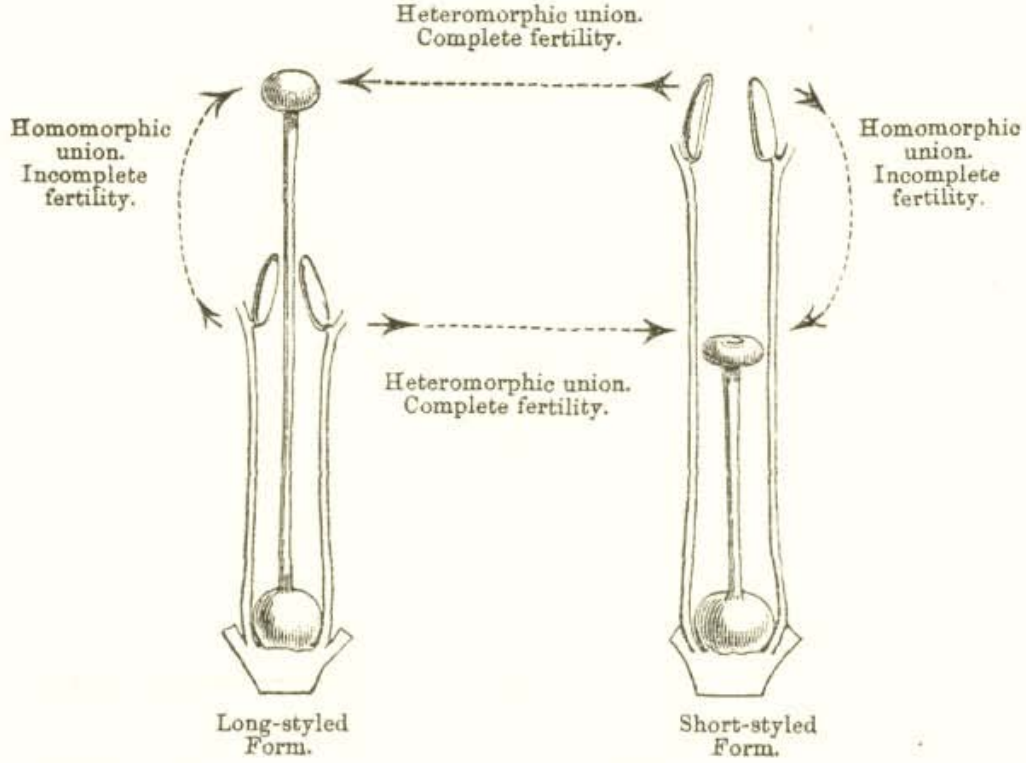
	Number of flowers fertilized.	Total number of pods produced.	Number of good pods.	Weight of seed in grains.	Total number of pods produced.	Weight of seed in grains.	Number of good pods.	Weight of seed in grains.
The two homomorphic unions	100	45	31	11	100	24	100	35
The two heteromorphic unions	100	77	71	39	100	50	100	54

With *P. auricula* I was unfortunate ; my few seedlings, except one poor plant, all came up short-styled ; and of these plants several died or became sick, owing to the hot weather and the difficulty of excluding insects and ventilating the corner of my greenhouse enclosed with net. I finally got only two pods from one union, and three from the other. The result is given in the following table ; and, though worth little, we here again see that the heteromorphic are far more fertile than the homomorphic unions.

Primula auricula.—TABLE III.

	Total number of pods produced.	Number of good pods.	Weight of seed in grains	Good Pods.) Weight of seed in grains.
Short-styled by own-form pollen (homomorphic union) ..	2	1	0·12	or as 100 to 12
Short-styled by pollen of long-styled (heteromorphic union)	3	3	1·50	or as 100 to 50

Whoever will study these three tables, which give the result of 134 flowers carefully fertilized and protected, will, I think, be convinced that in these three species of *Primula* the so-called heteromorphic unions are more fertile than the homomorphic unions. For the sake of clearness, the general result is given in the following diagram, in which the dotted lines with arrows represent how in the four unions pollen has been applied.



We here have a case new, as far as I know, in the animal and vegetable kingdoms. We see the species of *Primula* divided into two sets or bodies, which cannot be called distinct sexes, for both are hermaphrodites; yet they are to a certain extent sexually distinct, for they require for perfect fertility reciprocal union. They might perhaps be called sub-dioicous hermaphrodites. As quadrupeds are divided into two nearly equal bodies of different sexes, so here we have two bodies, approximately equal in number,

differing in their sexual powers and related to each other like males and females. There are many hermaphrodite animals which cannot fertilize themselves, but must unite with another hermaphrodite: so it is with numerous plants; for the pollen is often mature and shed, or is mechanically protruded, before the flower's own stigma is ready; so that these hermaphrodite flowers absolutely require for their sexual union the presence of another hermaphrodite. But in *Primula* there is this wide difference, that one individual Cowslip, for instance, though it can with mechanical aid imperfectly fertilize itself, for full fertility must unite with another individual; but it cannot unite with any individual in the same manner as an hermaphrodite Snail or Earth-worm can unite with any other one Snail or Earth-worm; but one form of the Cowslip, to be perfectly fertile, must unite with one of the other form, just as a male quadruped must and can unite only with a female.

I have spoken of the heteromorphic union in *Primula* as resulting in full fertility; and I am fully justified, for the Cowslips thus fertilized actually gave rather more seed than the truly wild plants —a result which may be attributed to their good treatment and having grown separately. With respect to the lessened fertility of the homomorphic unions, we shall appreciate its degree best by the following facts. Gärtner has estimated the degree of sterility of the union of several distinct species*, in a manner which allows of the strictest comparison with the result of the heteromorphic and homomorphic unions of *Primula*. With *P. veris*, for every hundred seeds yielded by the heteromorphic unions, only sixty-four seeds were yielded by an equal number of good capsules from the homomorphic unions. With *P. Sinensis* the proportion was nearly the same—namely, as 100 to 62. Now Gärtner has shown that, on the calculation of *Verbascum lychnitis* yielding with its own pollen 100 seeds, it yields when fertilized by the pollen of *V. Phœniceum* ninety seeds; by the pollen of *V. nigrum*, sixty-three seeds; by that of *V. blattaria*, sixty-two seeds. So again, *Dianthus barbatus* fertilized by the pollen of *D. superbus* yielded eighty-one seeds, and by the pollen of *D. Japonicus* sixty-six seeds, relatively to the 100 seeds produced by its own pollen. Thus we see—and the fact is highly remarkable—that the homomorphic unions relatively to the heteromorphic unions in *Primula* are more sterile than the crosses between several distinct species relatively to the pure union of those species.

The meaning or use of the existence in *Primula* of the two

* Versuche über die Bastarderzeugung, 1849, s. 216.

forms in about equal numbers, with their pollen adapted for reciprocal union, is tolerably plain; namely, to favour the intercrossing of distinct individuals. With plants there are innumerable contrivances for this end; and no one will understand the final cause of the structure of many flowers without attending to this point. I have already shown that the relative heights of the anthers and stigmas in the two forms lead to insects leaving the pollen of the one form on the stigma of the other; but, at the same time, there will be a strong probability of the flower's own pollen being likewise placed on the stigma. It is perfectly well known that if the pollen of several closely allied species be placed on the stigma of a distinct species, and at the same time, or even subsequently, its own pollen be placed on the stigma, this will entirely destroy the simultaneous or previous action of the foreign pollen. So again if the pollen of several varieties, including the plant's own pollen, be placed on the stigma, one or more of the varieties will take the lead and obliterate the effect of the others: but I have not space here to give the facts on which this conclusion is grounded. Hence we may infer as highly probable that, in *Primula*, the heteromorphic pollen which we know to be so much the most effective would obliterate the action of the homomorphic pollen when left on the flower's own stigma by insects; and thus we see how potent the dimorphic condition of the pollen in *Primula* will be in favouring the intercrossing of distinct individuals. The two forms, though both sexes are present in each, are in fact dioicous or unisexual. Whatever advantage there may be in the separation of the sexes, towards which we see so frequent a tendency throughout nature, this advantage has been here so far gained, that the one form is fertilized by the other, and conversely; and this is effected by the pollen of each form having less potency than that of the other on its own stigma.

Bearing on this view of the final cause of the dimorphism of the *Primulas*, there is another curious point. If we look at the right-hand figures of the four first lines in the previous tables of *P. Sinensis* and *veris*, we shall see that one of the homomorphic unions, namely, the short-styled by its own-form pollen, is considerably more sterile than the other; and in *P. auricula*, though here there is no other homomorphic union as a standard of comparison, this union is likewise excessively sterile. That the fertility of this union is really less in a marked degree than in the other three unions, we have an independent proof in the seeds germinating less perfectly and much more slowly than those from the other unions.

This fact is the more remarkable, because we have clearly seen that the short-styled form in the Cowslip in a state of nature is the most productive of seed. This form bears its anthers close together at the mouth of the corolla, and I observed long before I had ascertained the relative fertility of the four unions, in passing the proboscis of a dead Humble-bee or bristle down the the corolla, that in this form the flower's own pollen was almost certain to be left on its own stigma; and, as I wrote down at the time, the chance of self-fertilization is much stronger in this than in the other form. On this view we can at once understand the good of the pollen of the short-styled form, relatively to its own stigma, being the most sterile; for this sterility would be the most requisite to check self-fertilization, or to favour intercrossing. Hence, also, it would appear that there are four grades of fertility from the four possible unions in *Primula*; of the two homomorphic unions, as we have just seen, one is considerably more sterile than the other. In the wild state we know that the short-styled plants are more fertile than the long-styled; and we may infer as almost certain, that in the wild state, when the flowers are visited by insects, as is absolutely necessary for the production of seed, and when pollen is freely carried from one form to the other, that the unions are heteromorphic; if so, there are two degrees of fertility in the heteromorphic unions, making altogether four grades of fertility.

Two or three other points deserve a passing notice. The question whether the Primrose and Cowslip (*P. vulgaris* and *veris*) are distinct species or varieties has been more disputed and experimented on than in any other plant. But as we now know that the visits of insects are indispensable to the fertilization of these plants, and that in all probability the heteromorphic pollen of a Primrose would be prepotent on the stigma of a Cowslip over the homomorphic pollen of a Cowslip, the numerous experiments which have been made, showing that Oxlips appear amongst the seedlings of Cowslips, cannot be trusted, as the parent plants do not appear to have been carefully protected from insects*. I am far from wishing to affirm that pure Cowslips will not produce Ox-

* Mr. Sidebotham (Phytologist, vol. iii. pp. 703–5) states that he protected his plants from crossing; but as he gives in detail all the precautions which he took, and says nothing about artificial fertilization, we may conclude that he did not fertilize his plants. As he raised very numerous seedlings, he would have had to fertilize many flowers, if they had been really well guarded against the visits of insects. Hence I conclude that his results are not worthy of trust.

lips, but further experiments are absolutely necessary. We may also suspect that the fact noticed by florists*, that the varieties of the Polyanthus never come true from seed, may be *in part* due to their habitually crossing with other varieties of the Polyanthus.

The simple fact of two individuals of the same undoubted species, when homomorphically united, being as sterile as are many distinct species when crossed, will surprise those who look at sterility as a special endowment to keep created species distinct. Hybridizers have shown† that individual plants of the same species vary in their sexual powers, so far that one individual will unite more readily than another individual of the same species with a distinct species. Seeing that we thus have a groundwork of variability in sexual power, and seeing that sterility of a peculiar kind has been acquired by the species of *Primula* to favour intercrossing, those who believe in the slow modification of specific forms will naturally ask themselves whether sterility may not have been slowly acquired for a distinct object, namely, to prevent two forms, whilst being fitted for distinct lines of life, becoming blended by marriage, and thus less well adapted for their new habits of life. But many great difficulties would remain, even if this view could be maintained.

Whether or not the dimorphic condition of the *Primulæ* has any bearing on other points in natural history, it is valuable as showing how nature strives, if I may so express myself, to favour the sexual union of distinct individuals of the same species. The resources of nature are illimitable; and we know not why the species of *Primula* should have acquired this novel and curious aid for checking continued self-fertilization through the division of the individuals into two bodies of hermaphrodites with different sexual powers, instead of by the more common method of the separation of the sexes, or by the maturity of the male and female elements at different periods, or by other such contrivances. Nor do we know why nature should thus strive after the intercrossing of distinct individuals. We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis. When we look to the state in which young mammals and birds are born, we can at least see that the object gained is

* Mr. D. Beaton, in 'Journal of Horticulture,' May 28, 1861, pp. 154, 244.

† Gärtner, Bastarderzeugung, s. 165.

not, as has sometimes been maintained, mere dissemination. The whole subject is as yet hidden in darkness.

I will now only add that cases of dimorphism, like that of *Primula*, seem to be far from rare in the vegetable kingdom, though they have been little attended to. A large and important class of analogous facts will probably soon be discovered. Professor Asa Gray* informs me, that he and Dr. Torrey have described several Rubiaceous genera, in which some plants have exserted stamens, and others exserted pistils. "Mitchella offers an interesting instance of this structure from its relationship, through *Nertera*, to *Coprosma*, one of the few dicœcious genera of *Rubiaceæ*, and in which the stamens are elongated in the male flowers and the styles in the females." The long-styled hermaphrodite flowers of Mitchella would probably be found more productive of seed than the short-styled; in the same way, but in a reversed manner, as in *Primula*, the short-styled flowers are more productive than the long-styled; from which fact I inferred that, if *Primula* were to become dicœcious, the females would have short pistils and the males short stamens, these being the corresponding organs necessary for a heteromorphic union with full fertility. In the dicœcious *Coprosma*, on the other hand, the females have long pistils, and the males have long stamens. These facts probably show us the stages by which a dicœcious condition has been acquired by many plants.

Prof. A. Gray also informs me that another Rubiaceous genus (*Knoxia*) in India has been described by Dr. Wight, with a similar structure; and this, I am told, is the case with *Cinchona*. Several species of North American *Plantago* are dimorphic, as is *Rhamnus lanceolatus*, as far as its female organs are concerned. In the *Borragineæ*, Dr. Torrey has observed a strongly marked instance in *Amsinckia spectabilis*: in some dried flowers sent me by Prof. Gray, I find that the pistil in the one form is more than twice as long as in the other, with a corresponding difference in the length of the stamens; in the short-styled flowers the grains of pollen, as in *Primula*, apparently are larger, in the proportion of nine to seven, than in the long-styled flowers, which have the short stamens; but the difference can hardly be determined with safety in dried flowers. In *Mertensia alpina*, another member of

* See also Prof. Asa Gray's 'Manual of the Botany of the N. United States,' 1856, p. 171. For *Plantago*, see p. 269.

the *Borragineæ*, Prof. Gray finds a new and inexplicable case,—namely, some specimens with the stamens and pistil sub-exserted, and other specimens with *both* organs seated low down the tube of the corolla. Dr. Torrey and Prof. Gray have designated all such plants as "dicœciously dimorphous." In the *Labiatæ*, Mr. Bentham informs me that several species of *Ægiphyla*, and some of *Mentha*, are dimorphic like *Primula*. The case of *Thymus* is different, as I know from my own observations; but I will not here enlarge on this genus. Again, as I hear from Mr. Bentham, numerous species of *Oxalis* are similarly dimorphic. I can add the genus *Linum*. So that we already know of species (generally several in the same genus) having distinct dimorphic individuals, as far as structure is concerned, however it may prove in function, in no less than eight natural orders.

With respect to *Linum*, I will not here enter on details, as I intend to try further experiments next summer; but I may state, that I observed many years ago two forms in *Linum flavum*, with both the pistils and stamens differing in length. In *Linum grandiflorum* there are likewise two forms which present no difference in their male organs, but the pistil and stigmatic surfaces are much longer in the one form than in the other. The short-styled form, I have good reason to believe, is highly fertile with its own pollen; whether it be more fertile with the pollen of the long-styled form, I cannot at present say. The long-styled form, on the other hand, is quite sterile with its own pollen: several plants grew in my garden, remote from the short-styled plants; their stigmas were coloured blue with their own pollen; but although they produced a vast number of flowers, they did not produce a single seed-capsule. It seemed a hopeless experiment; but I had so much confidence from my trials on *Primula*, that I put a little pollen from the short-styled plants on the stigmas (already blue with their own pollen) of twelve flowers on two of the long-styled plants. From these twelve flowers I got eight remarkably fine seed-capsules; the other flowers not producing a single capsule. The existence of plants in full health, and capable of bearing seed, on which their own pollen produces no more effect than the pollen of a plant of a different order, or than so much inorganic dust, is one of the most surprising facts which I have ever observed.