

On the Character and Hybrid-like Nature of the Offspring from the Illegitimate Unions of Dimorphic and Trimorphic Plants.
By CHARLES DARWIN, M.A., F.R.S., F.L.S., &c.

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VARIOUS plants, which I have called dimorphic and trimorphic, have been described by me in papers read before this Society *. But it may be convenient to recall as briefly as possible the meaning of these terms. Dimorphic species consist of two forms, which naturally exist in about equal numbers: in the long-styled form the pistil is always longer, and the stamens (excepting in the case of *Linum grandiflorum*) are shorter than in the other form. Conversely, in the short-styled form the pistil is shorter and the stamens longer than in the long-styled form. In the latter the pollen-grains are almost always of larger size than in the short-styled form. The sexual union of the two distinct forms is necessary for full fertility: such unions I formerly called heteromorphic; but, for reasons which will immediately appear, it is more convenient to speak of them as legitimate, and the offspring thus produced, as ordinarily occurs in nature, as legitimate. When long-styled or short-styled plants are impregnated with their own-form pollen, the union is not fully fertile, or is even absolutely barren. Such unions, and the offspring raised from them, may be called illegitimate. Thus two legitimate and two illegitimate unions can be effected.

With trimorphic species, the case is more complex. There are three forms, which differ greatly in the length of the pistil; and in each form two sets of stamens exist, differing in length, in the

* "On the two Forms, or Dimorphic Condition, in the species of *Primula*," *Journal of Proceedings, Bot.* vol. vi. (1862) p. 77. "On *Linum*," *ibid.* vol. vii. (1864) p. 69. "On *Lythrum salicaria*," *ibid.* vol. viii. 1864, p. 169.

size of the pollen-grains, and often in colour. The stamens are graduated in length, so that one of the two sets in two of the forms is equal in length to the pistil in the third form. For instance, in the long-styled form the pistil equals in length the longer set of stamens in the mid-styled and short-styled forms. In all three forms the union is fully fertile and legitimate only when the pistil is impregnated with pollen from the stamens which equal it in length. Thus the long-styled form can be legitimately fertilized only by the longer stamens of the mid-styled or short-styled form; it can be illegitimately fertilized by its own two sets of stamens, and by the shorter stamens of both the mid-styled and short-styled forms; so that the long-styled form can be fertilized legitimately in two ways and illegitimately in four ways. The same holds good with the mid-styled and short-styled forms; hence with trimorphic species eighteen unions are possible, of which six are legitimate, and produce legitimate offspring, and twelve are illegitimate and produce illegitimate offspring.

I will give the results of my experiments on the illegitimate offspring of various dimorphic and trimorphic plants in full detail, partly because the observations are extremely troublesome, and will not probably soon be repeated (thus I have been compelled to count under the microscope above 20,000 seeds of *Lythrum Salicaria*), but chiefly because much light is thus indirectly thrown on the important subject of hybridism.

LYTHRUM SALICARIA.

I will commence with this trimorphic species. Of the twelve illegitimate unions, two were completely barren; and I succeeded in raising seedlings from only six, or doubtfully from seven, of the remaining ten illegitimate unions. The experiments are arranged in classes according to the parentage of the plants. In each case I give the average number of seeds per capsule, generally taken from ten capsules, which, according to my experience, is a nearly sufficient number. I give also in each case the maximum number of seeds in any one capsule; and this is a useful point of comparison with the normal standard—that is, with the number of seeds produced by legitimate plants when legitimately fertilized. I give likewise in each case the minimum number. When the maximum and minimum differ greatly, and no remark is made on the subject, it may be understood that the extremes are so closely connected by intermediate figures that the average is fair. Large

capsules were always selected for counting, in order to avoid over-estimating the infertility of the several illegitimate plants. The plants were generally allowed to be freely and legitimately fertilized, through the agency of bees, by illegitimate plants belonging to the two other forms growing close by. This is the fairest plan, and was generally followed; but in several cases (which will always be stated) illegitimate plants were fertilized by pollen taken from legitimate plants belonging to the other two forms; and this, as might have been expected, increased their fertility. Unfortunately *Lythrum Salicaria* is much affected in its fertility by the nature of the season; and to avoid, as far as possible, error from this source, my observations were extended over several years. Some few experiments were tried in 1863. The summer of 1864 was too hot and dry, and, though the plants were copiously watered, some few apparently suffered in their fertility, whilst others were not in the least affected. The years 1865 and, especially, 1866, were highly favourable. Only a few observations were made during 1867.

In order to judge of the degree of infertility of the various illegitimate plants, the following statement of the average and maximum number of seeds produced by ordinary or legitimate plants, when legitimately fertilized, some artificially and some naturally, will serve as a standard of comparison, and may in each case be referred to. But in order to save trouble, I have given under each experiment the percentage of seeds to the nearest whole number, as calculated in comparison with the standard number of the same form.

Standards.

Long-styled form; average number of seeds in each capsule 93; maximum number observed in twenty-three capsules, 159.

Mid-styled form; average number of seeds, 130; maximum number observed in thirty-one capsules, 151.

Short-styled form; average number of seeds, 83.5; but we may, for the sake of brevity, say 83; maximum number observed in twenty-five capsules, 112.

CLASS I. *Illegitimate plants from the long-styled form, fertilized by pollen from the longer or shorter stamens of the same form.*

From this union I raised at different times three lots of seedlings, amounting altogether to 56 plants. I must premise that, from not foreseeing the result, I did not keep a memorandum whether the eight plants of the first lot were the product of the

longer or shorter stamens of the same form ; but I have reason to suspect that they were the product of the latter. These eight plants were much more dwarfed, and much more sterile than those in the other two lots. The latter were raised from a long-styled plant growing quite isolated and fertilized by the agency of bees with its own pollen ; and it is almost certain, from the relative position of the organs of fructification, that the stigma under these circumstances would be fertilized by pollen from the longer stamens.

All the fifty-six plants in these three lots proved long-styled ; now, if the parent plants had been legitimately fertilized by pollen from the longer stamens of the mid-styled or short-styled forms, about one-third alone of the seedlings would have been long-styled, and the other two-thirds would have been mid-styled and short-styled. In some other trimorphic and dimorphic genera we shall find the same curious and inexplicable fact, namely that the long-styled form, fertilized by its own-form pollen, produces almost exclusively long-styled seedlings*.

The eight plants of the first lot were of low stature : three which I measured attained, when fully grown, the heights of only 28, 29, and 47 inches ; whilst a legitimate plant growing close by reached the height of 77 inches. They all betrayed in their general appearance a weak constitution ; they flowered rather later in the season, and at a later age than ordinary plants. Some did not flower every year ; and one plant, in an unprecedented manner, did not flower until three years old. In the two other lots none of the plants grew quite to their full and proper height, as could at once be seen by comparing them with the adjoining rows of legitimate plants. In several plants in all three lots, many of the anthers were either shrivelled or contained brown and tough, or pulpy matter, without any good pollen-grains, and they never shed their contents ; they were in the state designated by Gärtner† as contabescent, which term I will for the future use. In one flower all the anthers were contabescent excepting two, which appeared to the naked eye sound ; but under the microscope about two-thirds of the pollen-grains were seen to be small and shrivelled. In another plant, in which all the anthers appeared sound, many of the pollen-grains were shrivelled

* Dr. Hildebrand first called attention (*Bot. Zeitung*, Jan. 1, 1864, S. 5) to this subject in the case of *Primula sinensis* ; but his results were not nearly so uniform or striking as mine.

† Beiträge zur Kenntniss der Befruchtung, 1844, S. 116.

and of unequal sizes. I observed, under the circumstances immediately to be stated, the number of seeds produced by six plants (*Exp. I to VI.*) in the first lot of eight plants, and by three plants in each of the other two lots belonging to the present class.

Experiment I. This long-styled plant was allowed during 1863 to be freely and legitimately fertilized by an adjoining illegitimate mid-styled plant, but it did not yield a single seed-capsule. It was then removed and planted in a remote place close to a brother long-styled plant No. II., so that it must have been freely though illegitimately fertilized; under these circumstances it did not yield during 1864 and 1865 a single capsule. I should here state that a *legitimate* or ordinary long-styled plant, when growing isolated and freely, though illegitimately fertilized by insects with its own pollen, yielded an immense number of capsules, which contained on an average 21.5 seeds.

Exp. II. This long-styled plant, after flowering during 1863 close to an illegitimate mid-styled plant, produced less than twenty capsules, which contained on an average between four and five seeds. When subsequently growing in company with No. I., by which it will have been illegitimately fertilized, it yielded in 1866 not a single capsule, but in 1865 it yielded twenty-two capsules: the best of these, fifteen in number, were examined; eight contained no seed, and the remaining seven contained on an average only three seeds, and these seeds were so small and shrivelled that I doubt whether they would have germinated.

Exp. III. & IV. These two long-styled plants, after being freely and legitimately fertilized by the same illegitimate mid-styled plant during 1863 were as miserably sterile as No. II.

Exp. V. This long-styled plant, after flowering in 1863 close to the illegitimate mid-styled plant, yielded only four capsules, which altogether included only five seeds. During 1864, 1865, and 1866, it was surrounded either by illegitimate or legitimate plants of the other two forms; but it did not yield a single capsule. It was a superfluous experiment, but I likewise artificially fertilized in a legitimate manner twelve flowers; but not one produced a capsule; so that this plant is almost absolutely barren.

Exp. VI. This long-styled plant, after flowering during the favourable year of 1866, surrounded by illegitimate plants of the other two forms, did not produce a single capsule.

Exp. VII. This long-styled plant was the most fertile of the eight plants of the first lot. During 1865 it was surrounded by illegitimate plants of various parentage, many of which were highly fertile,

and must thus have been legitimately fertilized. It produced a good many capsules, ten of which yielded an average of 36.1 seeds, with a maximum of 47 and a minimum of 22; so that this plant produced 39 per cent. of the full number of seeds. During 1864 it was surrounded by legitimate and illegitimate plants of the other two forms; and nine capsules (one poor one being rejected) yielded an average of 41.9 seeds, with a maximum of 56, and a minimum of 28; so that, under these favourable circumstances, this plant, the most fertile of the first lot, did not yield, when legitimately fertilized, quite 45 per cent. of the full complement of seeds.

In the second lot of plants in the present class, descended from the long-styled form fertilized by its own pollen, and almost certainly from the longer stamens, the plants, as already stated, were not nearly so dwarfed or so sterile as in the first lot. All produced plenty of capsules. I counted the number of seeds in only three plants, viz. Nos. VIII., IX., & X.

Exp. VIII. This plant was allowed to be freely fertilized in 1864 by legitimate and illegitimate plants of the other two forms, and yielded from ten capsules an average of 41.1 seeds, with a maximum of 73 and a minimum of 11. Hence this plant produced only 44 per cent. of the full complement of seeds.

Exp. IX. This long-styled plant was allowed in 1865 to be freely fertilized by illegitimate plants of the other two forms, most of which were moderately fertile. Fifteen capsules yielded an average of 57.1 seeds, with a maximum of 86 and a minimum of 23. Hence the plant yielded 61 per cent. of the full complement of seeds.

Exp. X. This long-styled plant was freely fertilized at the same time and in the same manner as the last. Ten capsules yielded an average of 44.2 seeds, with a maximum of 69 and a minimum of 25; hence this plant yielded 47 per cent. of the full complement of seeds.

The nineteen long-styled plants of the third lot, of the same parentage as the last lot, were treated differently; for they flowered during 1867 by themselves, so that they must have been illegitimately fertilized by each other. It has already been stated that a legitimate long-styled plant, growing by itself and visited by insects, yielded an average of 21.5 seeds per capsule, with a maximum of 35; but, to judge fairly of its fertility, this plant, as well as others, ought to have been observed during successive seasons. We may infer from analogy that, if several legitimate long-styled plants were to fertilize each other, the average number

of seeds would be increased; but how much increased I do not know; hence I have no perfectly fair standard of comparison by which to judge of the fertility of the three following plants of the present lot, the seeds of which I counted.

Exp. XI. This long-styled plant produced a large crop of capsules, and seemed to be one of the most fertile of the whole lot of nineteen plants. The average from ten capsules was 35.9 seeds, with a maximum of 60 and a minimum of 8.

Exp. XII. This and the following long-styled plant produced very few capsules; ten yielded an average of only 15.4 seeds, with a maximum of 30 and a minimum of 4.

Exp. XIII. This plant offers an anomalous case; for it flowered profusely, but produced very few capsules; yet these capsules contained numerous seeds. Ten capsules yielded an average of 71.9 seeds, with a maximum of 95 and a minimum of 29. Considering that this plant was illegitimate, and illegitimately fertilized by its brother long-styled seedlings, the average and the maximum are so remarkably high that I cannot at all understand the case.

CLASS II. Illegitimate plants from the short-styled form, fertilized by pollen from the shorter stamens of the same form.

I raised from this union nine plants, of which eight were short-styled and one long-styled; so that there seems to be a strong tendency with this form to reproduce, when self-fertilized, the parent form; but the tendency is not so strong as with the long-styled. These nine plants never attained the full height of legitimate plants growing close to them. The anthers in many of the flowers on several plants were contabescent.

Exp. XIV. This short-styled plant was allowed during 1865 to be freely and legitimately fertilized by illegitimate plants descended from self-fertilized mid-, long- and short-styled plants. Fifteen capsules yielded an average of 28.3 seeds, with a maximum of 51 and a minimum of 11. The seeds themselves were small and irregular in shape; hence this plant produced only 33 per cent. of the proper number of seeds. Although so sterile on the female side, none of its anthers were contabescent.

Exp. XV. This short-styled plant, treated like the last during the same year, yielded an average, from fifteen capsules, of 27 seeds with a maximum of 49 and a minimum of 7. But two poor capsules may be rejected, and then the average rises to 32.6, with the same maximum of 49 and a minimum of 20; so that this plant attained 38 per cent. of the normal standard of fertility

and was rather more fertile than the last, yet many of the anthers were contabescent.

Exp. XVI. This short-styled plant, treated like the two last, yielded from ten capsules an average of 77·8 seeds, with a maximum of 97 and a minimum of 60; so that this plant produced 94 per cent. of the full number of seeds.

Exp. XVII. This, the one long-styled plant of the same parentage as the last three plants, when freely and legitimately fertilized in the same manner as the last, yielded an average from ten capsules of 76·3 rather poor seeds, with a maximum of 88 and a minimum of 57. Hence this plant produced 82 per cent. of the proper number of seeds. Twelve flowers under a net were artificially and legitimately fertilized by pollen from a legitimate short-styled plant; and nine capsules yielded an average of 82·5 seeds, with a maximum of 98 seeds and a minimum of 51; so that its fertility was increased by the action of pollen from a legitimate plant, but still did not reach the normal standard.

CLASS III. *Illegitimate plants from the mid-styled form fertilized by pollen from the longer stamens of the same form.*

After two trials, I succeeded in raising only four plants from this illegitimate union. These proved to be three mid-styled and one long-styled; but from so small a number we can hardly judge of the tendency in mid-styled plants when self-fertilized to reproduce the same form. These four plants never attained their full and normal height; the long-styled plant had several of its anthers contabescent.

Exp. XVIII. This mid-styled plant, when freely and legitimately fertilized during 1865 by illegitimate plants descended from self-fertilized long-, short-, and mid-styled plants, yielded an average from ten capsules of 102·6 seeds, with a maximum of 131 and a minimum of 63: hence this plant did not produce quite 80 per cent. of the normal number of seeds. Twelve flowers were artificially and legitimately fertilized by pollen from a legitimate long-styled plant, and yielded from nine capsules an average of 116·1 seeds, which were finer than in the previous case, with a maximum of 135 and a minimum of 75; so that, as in *Exp. XVII.*, pollen from a legitimate plant increased the fertility, but did not bring it up to the full standard.

Exp. XIX. This mid-styled plant, fertilized in the same manner and at the same period with the last, yielded an average from ten capsules of 73·4 seeds, with a maximum of 87 and a minimum of 64; hence this plant produced only 56 per cent. of the full number

of seeds. Thirteen flowers were artificially and legitimately fertilized by pollen from a legitimate long-styled plant, and yielded ten capsules with an average of 95.6 seeds; so that the application of pollen from a legitimate plant added, as in the two previous cases, to the fertility, but did not bring it up to the proper standard.

Exp. XX. This long-styled plant, of the same parentage with the last two mid-styled plants, and freely fertilized in the same manner, yielded an average from ten capsules of 69.6 seeds, with a maximum of 83 and a minimum of 52; hence the plant produced 75 per cent. of the full number of seeds.

CLASS IV. *Illegitimate plants from the short-styled form fertilized by pollen from the longer stamens of the long-styled form.*

In the three previous classes, plants raised from the three forms fertilized by pollen from either the longer or shorter stamens of the same form, but not of the same individual plant, have been described. Six other illegitimate unions are possible, namely between the three forms and the stamens in the other two forms which do not correspond in height with the pistil. But I succeeded in raising plants from only three of these six unions. From one of them, forming the present Class, twelve plants were raised; these consisted of eight short-styled, and four long-styled plants, with not one mid-styled. These twelve plants never attained quite their full and proper height, but by no means deserved to be called dwarfs. The anthers in some of the flowers were contabescent. One plant was remarkable from all the longer stamens in every flower and from many of the shorter stamens having their anthers in this condition. The pollen of four other plants, in which none of the anthers were contabescent, was examined; in one a moderate number of grains were minute and shrivelled, but in the other three they appeared perfectly sound. With respect to the power of producing seed, five plants (*Exps. XXI. to XXV.*) were observed: one yielded scarcely more than half the normal number; a second was slightly infertile; but the three others actually produced a larger average number, with a higher maximum, than the standard. In my concluding remarks on *Lythrum* I shall recur to this fact, which at first appears inexplicable.

Exp. XXI. This short-styled plant, freely and legitimately fertilized during 1865 by illegitimate plants, descended from self-fertilized long-, mid- and short-styled parents, yielded an average from ten capsules of 43 seeds, with a maximum of 63 and a minimum of 26; hence this plant, which was the one with all its

longer and many of its shorter stamens contabescent, produced only 52 per cent. of the proper number of seeds.

Exp. XXII.—This short-styled plant produced perfectly sound pollen, as viewed under the microscope. During 1866 it was freely and legitimately fertilized by other illegitimate plants belonging to the present and the following class, both of which include many highly fertile plants. Under these circumstances it yielded from eight capsules an average of 100·5 seeds, with a maximum of 123 and a minimum of 86; so that it produced 121 per cent. of seeds in comparison with the normal standard. During 1864 it was allowed to be freely and legitimately fertilized by *legitimate* and illegitimate plants, and yielded an average, from eight capsules, of 104·2 seeds, with a maximum of 125 and a minimum of 90; consequently it produced 125 per cent. of the normal standard. In this case, as in some previous cases, pollen from legitimate plants added in a small degree to the fertility of the plant; and the fertility would, perhaps, have been still greater had not the summer of 1864 been very hot, and certainly unfavourable to some of the plants of *Lythrum*.

Exp. XXIII.—This short-styled plant produced perfectly sound pollen. During 1866 it was freely and legitimately fertilized by the other illegitimate plants specified under the last experiment, and yielded an average, from eight capsules, of 113·5 seeds, with a maximum of 123 and a minimum of 93. Hence this plant produced no less than 136 per cent. of the normal standard.

Exp. XXIV.—This long-styled plant produced pollen which seemed under the microscope sound; but some of the grains did not swell when placed in water. During 1864 it was legitimately fertilized by *legitimate* and illegitimate plants in the manner described under *Exp. XXII.*, but yielded an average, from ten capsules, of only 55 seeds, with a maximum of 88 and a minimum of 24, thus attaining 59 per cent. of the normal fertility. This low degree of fertility, I presume, was owing to the unfavourable season; for during 1866, when legitimately fertilized by *illegitimate* plants in the manner described under *Exp. XXII.*, it yielded an average, from eight capsules, of 82 seeds, with a maximum of 120 and a minimum of 67, thus producing 88 per cent. of the normal number of seeds.

Exp. XXV.—The pollen of this long-styled plant contained a moderate number of poor and shrivelled grains; and this is a surprising circumstance, as it yielded an extraordinary number of seeds. During 1866 it was freely and legitimately fertilized by

illegitimate plants, as described under Exp. XXII., and yielded an average, from eight capsules, of 122.5 seeds, with a maximum of 149 and a minimum of 84. Hence this plant produced no less than 131 per cent. of the normal standard.

CLASS V.—Illegitimate plants from the mid-styled form, fertilized by pollen from the shorter stamens of the long-styled form.

I raised from this union twenty-five plants, which proved to be seventeen long-styled and eight mid-styled, but not one short-styled. None of these plants were in the least dwarfed. I examined, during the highly favourable season of 1866, the pollen of four plants: in one mid-styled plant, some of the anthers of the longer stamens were contabescent, but in the other anthers the pollen-grains were mostly sound, as they were in all the anthers of the shorter stamens; in two other mid-styled and in one long-styled plant many of the pollen grains were small and shrivelled; and in the latter plant as many as a fifth or sixth appeared to be in this state. I counted the seeds in five plants (Exp. XXVI. to XXX.), of which two were moderately sterile and three fully fertile.

Exp. XXVI.—This mid-styled plant was freely and legitimately fertilized, during the rather unfavourable year 1864, by numerous surrounding legitimate and illegitimate plants. It yielded an average, from ten capsules, of 83.5 seeds, with a maximum of 110 and a minimum of 64, thus attaining 64 per cent. of the normal fertility. During the highly favourable year 1866, it was freely and legitimately fertilized by illegitimate plants belonging to the present Class and to Class IV., and yielded an average, from eight capsules, of 86 seeds, with a maximum of 109 and a minimum of 61, and thus attained 66 per cent. of the normal fertility. This was the plant with some of the anthers of the longer stamens contabescent as above mentioned.

Exp. XXVII.—This mid-styled plant, fertilized during 1864 in the same manner as the last, yielded an average, from ten capsules, of 99.4 seeds, with a maximum of 122 and a minimum of 53, thus attaining to 76 per cent. of the normal fertility. If the season had been more favourable, its fertility would probably have been somewhat greater, but, judging from the last experiment, only in a slight degree.

Exp. XXVIII.—This mid-styled plant, when legitimately fertilized during the favourable season of 1866, in the manner described under Exp. XXVI., yielded an average, from eight capsules, of 89 seeds, with a maximum of 119 and a minimum of 69, thus

producing 68 per cent. of the full number of seeds. In the pollen of both sets of anthers, nearly as many grains were small and shrivelled as sound.

Exp. XXIX.—This long-styled plant was legitimately fertilized during the unfavourable season of 1864, in the manner described under *Exp. XXVI.*, and yielded an average, from ten capsules, of 84.6 seeds, with a maximum of 132 and a minimum of 47, thus attaining to 91 per cent. of the normal fertility. During the highly favourable season of 1866, when fertilized in the manner likewise described under *Exp. XXVI.*, it yielded an average, from nine capsules (one poor capsule having been excluded), of 100 seeds, with a maximum of 121 and a minimum of 77. This plant thus exceeded the normal standard, and produced 107 per cent. of seeds. In both sets of anthers there were a good many bad and shrivelled pollen-grains, but not so many as in the last-described plant.

Exp. XXX.—This long-styled plant was legitimately fertilized during 1866 in the manner described under *Exp. XXVI.*, and yielded an average, from eight capsules, of 94 seeds, with a maximum of 106 and a minimum of 66; so that it attained 101 per cent. of the normal fertility.

Exp. XXXI.—Some flowers on this long-styled plant were artificially and legitimately fertilized by one of its brother mid-styled plants; and five capsules yielded an average of 90.6 seeds, with a maximum of 97 and a minimum of 79. Hence, as far as can be judged from so few capsules, this plant attained, under these favourable circumstances, 98 per cent. of the normal standard.

CLASS VI.—*Illegitimate plants from the mid-styled form fertilized by pollen from the longer stamens of the short-styled form.*

I have shown, in my former paper on *Lythrum Salicaria*, that the union from which these illegitimate plants were derived is far more fertile than any other illegitimate union; for the mid-styled parent, when thus fertilized, yielded an average (all very poor capsules being excluded) of 102.8 seeds, with a maximum of 130; and the plants in the present class accord in character with the but slightly lessened fertility of the parent-union. I raised forty plants; and these attained their full height and were covered with seed-capsules. Nor did I observe any contabescent anthers. It deserves, also, particular notice that these plants, differently from what occurs in any previous class, consisted of all three forms, namely eighteen short-styled, fourteen long-styled, and eight mid-styled plants. From these circumstances, I counted the seed in

only two plants (Exp. XXXII. & XXXIII.), which proved fully fertile.

Exp. XXXII.—This mid-styled plant was freely and legitimately fertilized, during the rather unfavourable year of 1864, by numerous surrounding legitimate and illegitimate plants. Eight capsules yielded an average of 127.2 seeds, with a maximum of 144 and a minimum of 96; so that this plant attained 98 per cent. of the normal standard.

Exp. XXXIII.—This short-styled plant was fertilized in the same manner and at the same time with the last; and ten capsules yielded an average of 113.9, with a maximum of 137, and a minimum of 90. Hence this plant produced no less than 137 per cent. of seeds in comparison with the standard.

Concluding remarks on the illegitimate offspring of the three forms of Lythrum salicaria.

From the three forms occurring in approximately equal numbers in a state of nature, and from the results of sowing seed naturally produced, there is reason to believe that each form when legitimately fertilized, reproduces all three forms in about equal numbers. Now we have seen (and the fact is a very singular one) that the fifty-six plants produced from the long-styled form, when illegitimately fertilized by pollen from the same form (Class I.), were all long-styled. The short-styled form, when self-fertilized (Class II.), produced eight short-styled and one long-styled plant; and the mid-styled form, similarly treated (Class III.), produced three mid-styled and one long-styled offspring; so that these two forms, when illegitimately fertilized by pollen from the same form, evince a strong, but not exclusive, tendency to reproduce the parent-form. When the short-styled form was illegitimately fertilized by the long-styled form (Class IV.), and again when the mid-styled was illegitimately fertilized by the long-styled (Class V.), in each case the two parent-forms alone were reproduced. As thirty-seven plants were raised from these two unions, we may, with much confidence, believe that it is the rule that plants thus produced yield both parent-forms but not the third form. When, however, the mid-styled form was illegitimately fertilized by the short-styled (Class VI.), the same rule did not hold good; for the seedlings consisted of all three forms, but in unequal numbers. Nor is this exception surprising; for the illegitimate union from which these seedlings were derived is, as previously stated,

singularly fertile, and the seedlings themselves exhibit no signs of sterility, and grow to their full height.

Tabulated results of the fertility of the foregoing illegitimate plants, when legitimately fertilized, generally by illegitimate plants, as described under each experiment. Experiments XI., XII., & XIII. are excluded; for these plants were illegitimately fertilized.

Number of Experiment and Standard.	Form.	Average number of seeds produced.	Maximum number in any one capsule.	Minimum number in any one capsule.	Calculated average of seeds relatively to the normal standard, this being taken in each case as 100.
Standard.....	Long-styled	93	150	No record was kept; but all excessively poor capsules were rejected.	
Do.	Mid-styled...	130	151		
Do.	Short-styled	83.5	112		

CLASS I.—Illegitimate plants from the long-styled form, fertilized by pollen from the longer or shorter stamens of the same form.

Experiment I.	Long-styled	0	0	0	0
II.	Do.	4.5	5
III.	Do.	4.5	5
IV.	Do.	4.5	5
V.	Do.	0 or 1	0 or 1
VI.	Do.	0	0
VII.	Do.	36.1	47	22	39
VIII.	Do.	41.1	73	11	44
IX.	Do.	57.1	86	23	61
X.	Do.	44.2	69	25	47

CLASS II.—Illegitimate plants from the short-styled form, fertilized by pollen from the shorter stamens of the same form.

Exp. XIV.	Short-styled	28.3	51	11	33
XV.	Do.	32.6	49	20	38
XVI.	Do.	77.8	97	60	94
XVII.	Long-styled	76.3	88	57	82

CLASS III.—Illegitimate plants from the mid-styled form, fertilized by pollen from the longer stamens of the same form.

Exp. XVIII.	Mid-styled...	102.6	131	63	80
XIX.	Do.	73.4	87	64	56
XX.	Long-styled	69.6	83	52	75

TABLE (continued).

CLASS IV.—*Illegitimate plants from the short-styled form, fertilized by pollen from the longer stamens of the long-styled form.*

Number of Experiment.	Form.	Average number of seeds produced.	Maximum number in any one capsule.	Minimum number in any one capsule.	Calculated average of seeds relatively to the normal standard, this being taken in each case as 100.
Exp. XXI.	Short-styled	43.0	63	26	52
XXII.	Do.	100.5	123	86	121
XXIII.	Do.	113.5	123	93	136
XXIV.	Long-styled	82.0	120	67	88
XXV.	Do.	122.5	149	84	131

CLASS V.—*Illegitimate plants from the mid-styled form, fertilized by pollen from the shorter stamens of the long-styled form.*

Exp. XXVI.	Mid-styled...	86.0	109	61	66
XXVII.	Do.	99.4	122	53	76
XXVIII.	Do.	89.0	119	69	68
XXIX.	Long-styled	100.0	121	77	107
XXX.	Do.	94.0	106	66	101
XXXI.	Do.	90.6	97	79	98

CLASS VI.—*Illegitimate plants from the mid-styled form, fertilized by pollen from the longer stamens of the short-styled form.*

Exp. XXXII.	Mid-styled...	127.2	144	96	98
XXXIII.	Short-styled	113.9	137	90	137

The lessened fertility of most of these illegitimate plants is in many respects a highly remarkable phenomenon. Thirty-three plants in the six classes were subjected to various trials, and the seeds carefully counted. Some were artificially fertilized, but the far greater number were freely fertilized (and this is the better and natural plan) through the agency of insects, by other illegitimate plants. In the right-hand or percentage column in the accompanying Table, a wide difference in fertility between the plants in the first three and the last three classes may be perceived. In the first three classes the plants are descended from the three forms illegitimately fertilized by pollen taken from the same form, but not from the same individual plant. It is necessary to observe this latter circumstance; for, as I shall at some future time show*, most plants, independently of dimor-

* I have given a brief abstract of some of these observations in my work on 'The Variation of Animals and Plants under Domestication,' 1867, vol. ii. p. 128.

phism or trimorphism, when fertilized with their own pollen, are in some degree dwarfed, and sometimes rendered sterile. None of the nineteen plants in the first three classes attained complete fertility; one, however, made a near approach, yielding 96 per cent. of the proper number of seeds. From this high degree of fertility we have many descending gradations, till we reach an absolute zero, when the plants, though bearing many flowers, did not produce, during successive years, a single seed or even seed-capsule. Some of the most sterile plants did not yield a single seed, even when legitimately fertilized by pollen from legitimate plants. The first seven plants in Class I., which are by far the most sterile, probably ought to form a distinct class from the three following plants; for there is reason to suspect that the former are the product of the shorter stamens of the long-styled form, whilst it is almost certain that the latter are descended from the longer stamens of the same form; but, owing to this doubt, they are all arranged under the same class. The several classes differ in their average degree of fertility; and in the same class there is a wide difference in the fertility of the several plants, though descended from the same parents, sown at the same time, and grown in the same soil. None of the plants in the first three classes attained their full and proper stature; the first seven plants, which, as already stated, probably ought to form a distinct class, are by far the most dwarfed, several of them never reaching to half their proper height. These same plants did not flower at so early an age, or so early in the season, as they ought to have done. The anthers in many of their flowers, and in the flowers of some other plants in the first five classes, were either contabescent or included numerous small and shrivelled pollen-grains. As the suspicion at one time occurred to me that the lessened fertility of all the illegitimate plants might be due to the pollen alone being affected, I may remark that this is certainly not the case; for several of them, when fertilized by sound pollen from legitimate plants, did not yield the full complement of seeds; hence it is certain that both the female and male reproductive organs are affected.

Turning now to the fourth, fifth, and sixth classes, and looking to the right-hand column of the Table, we find nearly as many plants with a percentage of seeds above the standard as beneath it. Hence, at first sight, it appears probable that the number of seeds ordinarily produced is much more variable than I have supposed, and, consequently, that the plants in these three classes do not really differ

in their power of yielding seed, but have merely varied temporarily in fertility. Nevertheless we may reject this conclusion as far as the less fertile plants are concerned,—first, because none of the plants in Class IV. attained their proper height, which shows that they were in some manner affected; and, secondly, because many of the plants in Classes IV. & V. produced anthers which were either contabescent or included small and shrivelled pollen-grains. And as in these cases the male organs were manifestly deteriorated, it is by far the most probable conclusion that the female organs were likewise affected, and that this was the cause of the reduced number of seeds.

With respect to the three short-styled and three long-styled plants in the three latter classes, which yield too high a percentage of seeds, the explanation is much more doubtful. The normal standard for the long-styled form was deduced by counting the seeds in twenty-three capsules, and for the short-styled form from twenty-five capsules. I do not pretend that this is a sufficient number of capsules for absolute accuracy; but my experience leads me to believe that a very fair result would thus be gained. As, however, the maximum number observed in the twenty-five capsules of the short-styled form is low, the standard in this case may possibly be not quite high enough. In the case of the illegitimate plants, in order to avoid overestimating their infertility, ten very fine capsules were always selected; and the years 1865 and 1866, during which the plants in the three latter classes were observed, were highly favourable for seed-production. Now, if this plan of selecting very fine capsules during favourable seasons had been followed for obtaining the normal standards, instead of taking, during various seasons, the first capsules which came to hand, the standards would undoubtedly have been considerably higher; and thus the fact of the six foregoing plants appearing to yield an unnaturally high percentage of seeds may, perhaps, be accounted for. On this view, these plants are, in fact, merely fully fertile, and not fertile to an abnormal degree. Nevertheless, as characters of all kinds are liable to variation, especially with organisms unnaturally treated, and as in the three first and more sterile classes, the plants derived from the same parents, and treated in the same manner, certainly did vary much in sterility, it is possible that certain plants, in the latter and more fertile classes, may have varied so as to have acquired an abnormal degree of fertility. But it should be especially observed that, if my standards err in being too low, the sterility of all the many sterile

plants in the several classes, will have to be estimated higher in the same proportion. Finally, we see that the illegitimate plants in the three first classes are all more or less sterile, some being absolutely barren, with one alone almost completely fertile; in the three latter classes, some of the plants are moderately sterile, whilst others are fully fertile or possibly fertile in excess.

The last point which need here be noticed is that, as far as my means of comparison serve, a certain degree of relation exists between the infertility of the illegitimate first unions between the several forms and that of their illegitimate offspring. Thus the two illegitimate unions, from which the seedlings in Classes V. & VI. were derived, yielded a fair amount of seed, and only a few of these plants are in any degree sterile. On the other hand, the illegitimate unions between plants of the same form always yield very few seeds, and their seedlings are the most sterile. But the relation is not strict; for the first six or seven plants in the Table were extremely sterile, out of all proportion to the union from which they were derived. There is also a tolerably close parallelism in each class between the degree of sterility and the dwarfed stature of the plants. As previously stated, an illegitimate plant fertilized by pollen from a legitimate plant has its fertility slightly increased. The importance of the several foregoing conclusions will be apparent at the close of this paper, when the illegitimate unions between the forms of the same species, and their illegitimate offspring, are compared in functional power with the hybrid unions and the hybrid offspring of distinct species.

GENUS OXALIS.

Dr. Hildebrand * has proved that *Oxalis rosea* is a trimorphic species, like *Lythrum Salicaria*. He possessed in the living state the long-styled form alone, and from its seeds, necessarily self-fertilized, he raised seedlings which proved all long-styled; but, unfortunately, he does not state how many plants were raised.

GENUS PRIMULA.

PRIMULA SINENSIS.

I raised during February 1862, from some long-styled plants

* Ueber den Trimorphismus in der Gattung *Oxalis*: Monatsberichte der Akad. der Wissen. zu Berlin, 21st June 1866, p. 373. Also published separately.

illegitimately fertilized by pollen from the same form, twenty-seven seedlings. These were all long-styled. They proved fully fertile or even fertile in excess; for ten flowers, fertilized by pollen from other plants of the same lot, yielded nine capsules, containing on an average 39.75 seeds, with a maximum number in one capsule of sixty-six seeds. Again four of these flowers legitimately crossed by pollen from a legitimate plant, and four flowers on the latter crossed by pollen from the illegitimate seedlings, yielded seven capsules with an average of fifty-three seeds, with a maximum of seventy-two. I must here state that I have found some difficulty in estimating the standard of fertility for the several unions of this species, as the results differed much during successive years*, and the seeds vary so greatly in size that it is hard to decide which ought to be considered good. In order to avoid overestimating the infertility of the several illegitimate unions, I have taken as low standards as possible.

From the foregoing twenty-seven plants, fertilized by their own-form pollen, I raised twenty-five seedling grandchildren; and these were all long-styled; so that from the two illegitimate generations fifty-two plants were raised, and all without exception proved long-styled. These grandchildren grew vigorously and soon exceeded in height two other lots of illegitimate seedlings of different parentage and one lot of equal-styled seedlings presently to be described. Hence I expected that they would turn out highly ornamental plants; but when they flowered, they seemed, as my gardener remarked, to have gone back to the wild state; for the petals were pale-coloured, narrow, sometimes not touching each other, flat, generally deeply notched in the middle, but not flexuous on the margin, and with the yellow eye

* Dr. Hildebrand was much more successful than I was in fertilizing the flowers of *P. sinensis*; yet the number of seeds obtained by him is certainly much too low. Thus he gives (*Bot. Zeitung*, 1864, p. 3) eighteen seeds as the average number produced by the long-styled form, when illegitimately fertilized by the same-form pollen, and forty-one as the number when legitimately fertilized. For the short-styled form, the corresponding numbers are twenty and forty-four. The lowest standards which I can give for the illegitimate and legitimate unions of the long-styled form are thirty-five and at least fifty, and for the short-styled at least twenty-five and sixty-four. It is possible that Dr. Hildebrand's plants were grown in too small pots, or, whilst maturing their seeds, were otherwise treated in an unfavourable manner. This would account for the greater inequality observed by him than that by me between the product of seeds from the legitimate and illegitimate unions, as the latter always suffer most from unfavourable conditions.

or centre conspicuous. Altogether these flowers, in comparison with those of their progenitors, presented a striking difference, which can, I think, be accounted for only on the principle of reversion. One of these grandchildren had most of its anthers contabescent. Seventeen of the flowers were illegitimately fertilized by pollen taken from seedlings of the same lot, and produced fourteen capsules, containing on an average 29.2 seeds; they ought to have contained about thirty-five seeds. Fifteen flowers legitimately fertilized by pollen from an illegitimate short-styled plant (belonging to the lot next to be described) produced fourteen capsules, containing an average of forty-six seeds; they ought to have contained at least fifty seeds. Hence these grandchildren of illegitimate descent appear to have lost, though only in a very slight degree, their full fertility.

From a short-styled form of *P. sinensis*, fertilized by its own-form pollen, I raised, during February 1862, eight seedlings, seven of which were short-styled and one long-styled. These plants grew slowly, and never attained to the full stature of ordinary plants; some of them flowered precociously, and others late in the season. Four flowers on the short-styled plants and four on the long-styled plant were illegitimately fertilized with their own-form pollen and produced only three capsules, containing on an average 23.6 seeds, with a maximum of twenty-nine; but we cannot judge of their fertility from so few capsules; and I have greater doubts about the normal standard for this union than about the standard for the three other unions; but I believe that rather above twenty-five seeds would be a fair estimate. Eight flowers on the short-styled and long-styled illegitimate plants were reciprocally and legitimately crossed; they produced five capsules which contained an average of 28.6 seeds, with a maximum of thirty-six. A reciprocal cross between legitimate plants of the two forms would have yielded an average of at least fifty-seven seeds, with a possible maximum of seventy-four seeds; so that these illegitimate plants are sterile when legitimately crossed.

I succeeded in raising from the seven short-styled illegitimate plants, fertilized by their own-form pollen, only six plants—grandchildren of the first union. These, like their parents, were of low stature, and had so poor a constitution that four died before flowering. With ordinary plants it has been a rare event with me to have more than a single plant die out of a large lot. The two grandchildren which lived and flowered were short-styled; and twelve of their flowers were fertilized with their own-form pollen

and produced twelve capsules containing an average of 28.2 seeds; so that these two plants, though belonging to so weakly a set, were rather more fertile than their parents, and perhaps not at all sterile. Four flowers on the same two grandchildren were legitimately fertilized by a long-styled illegitimate plant, and produced four capsules, containing only 32.2 seeds instead of about sixty-four seeds, which is the normal average I have obtained from legitimate short-styled plants legitimately crossed.

By looking back, it will be seen that at first I raised from a short-styled plant fertilized by its own-form pollen seven short-styled plants and one long styled. These illegitimate plants of the two forms were legitimately crossed, and from their seed fifteen plants were raised, grandchildren of the first illegitimate union. According to analogy half of them ought to have been long-styled and half short-styled; but all were short-styled. Altogether, of the twenty-five plants illegitimately descended from the short-styled grandparent, twenty-four proved to be short-styled and one alone long-styled. Twelve short-styled flowers borne by the fifteen grandchildren were fertilized by pollen taken from plants of the same form belonging to the same lot, and produced eight capsules which contained an average of 21.8 seeds, with a maximum of thirty-five. These figures are rather below the normal standard for such a union. Six flowers were also legitimately fertilized by an illegitimate long-styled plant and produced only three capsules, containing on an average 23.6 seeds with a maximum of thirty-five. Such a union in the case of a legitimate plant ought to have yielded an average of sixty-four seeds, with a possible maximum of seventy-three seeds.

Summary on the transmission of form, constitution, and fertility of the illegitimate offspring of Primula sinensis.—In regard to the long-styled form, the illegitimate offspring, as far as my experience during two generations of fifty-two plants serves*, appear invariably to be long-styled. These plants grew vigorously; but the flowers in one instance were small, appearing as if they had reverted to the wild state. In the first illegitimate generation they were perfectly fertile, and in the second their fertility was only very slightly impaired. With respect to the short-styled

* Dr. Hildebrand (Bot. Zeitung, 1864, p. 5) raised from a similar illegitimate union seventeen plants, of which fourteen were long-styled and three short-styled. From a short-styled plant illegitimately fertilized by its own pollen he raised fourteen plants, of which eleven were short-styled and three long-styled.

form, twenty-four out of twenty-five of their illegitimate offspring were short-styled. They were dwarfed in stature, and one lot of grandchildren had so poor a constitution that four out of six plants perished before flowering. The two survivors, when illegitimately fertilized by their own-form pollen, were rather less fertile than they ought to have been; but their loss of fertility was clearly shown in a special and unexpected manner, namely when legitimately fertilized by other illegitimate plants: thus altogether eighteen flowers fertilized in this manner yielded twelve capsules, which included on an average only 28.5 seeds, with a maximum of forty-five. Now a legitimate short-styled plant would have yielded, when legitimately fertilized, an average of sixty-four seeds, with a possible maximum of seventy-four. This particular kind of infertility will perhaps be best appreciated by a simile: we may assume that six children would on an average be born from each ordinary marriage; but that only three would be born from an incestuous marriage. Now, according to the analogy of *Primula sinensis*, the children of such incestuous marriages, if they continued to marry incestuously, would have their sterility only slightly increased; but their fertility would not be restored by a proper marriage; for if two children, both of incestuous origin, but in no degree related to each other, were to marry, the marriage would of course be strictly legitimate, nevertheless they would not give birth to more than half the full and proper number of children.

Equal-styled variety of Primula sinensis.—As any variation in the structure of the reproductive organs, combined with changed function, is a rare event, the following cases are worth giving in detail. Mr. Scott, in his excellent paper on the reproductive functions in the Primulaceæ*, has recorded some analogous facts. My attention was first called to the subject by observing, in 1862, a long-styled plant, descended from a self-fertilized long-styled parent, with some of its flowers in an anomalous state, namely, with the stamens placed low down in the corolla as in the ordinary long-styled form, but with the pistils so short that the stigmas stood on a level with the anthers. These stigmas were nearly as globular and as smooth as in the short-styled form, instead of being elongated and rough as in the long-styled form. Here, then, we have stamens of the long-styled form and a pistil closely resembling that of the short-styled form combined in the same flower. But

* Journal of Proc. Linn. Soc. Bot. vol. viii. (1864) p. 78.

the structure varied much on the same umbel: for in two flowers the pistil was intermediate in length between that of the long- and that of the short-styled form, with the stigma elongated as in the former, and smooth as in the latter; and in three other flowers the structure was in all respects like that of the long-styled form. These modifications appeared to me so remarkable that I fertilized eight of the flowers with their own pollen, and obtained five capsules, which contained on an average forty-three seeds; and this number shows that the flowers had become abnormally fertile in comparison with those of ordinary long-styled plants when self-fertilized. These facts led me to examine the plants in several small collections, with the following result, showing that the equal-styled variety is not rare.

Name of Owner or Place.	Long-styled Form.	Short-styled Form.	Equal-styled Variety.
Mr. Horwood	0	0	17
Mr. Duck	20	0	9
Baston	30	18	15
Chichester	12	9	2
Holwood	42	12	0
High Elms	16	0	0
Westerham	1	5	0
My own plants from purchased seeds...	13	7	0
Total	134	51	43

In a state of nature the long- and short-styled forms would no doubt occur in equal numbers, as I infer from the analogy of other dimorphic species of *Primula*, and from having raised the two forms of the present species in exactly the same number from flowers which had been *legitimately* crossed. The preponderance in the above Table of the long-styled form over the short-styled (in the proportion of 134 to 51) results from gardeners generally collecting seed from self-fertilized flowers; and I have shown in my previous paper that the long-styled form spontaneously produces much more seed than the short-styled, owing to the anthers in the long-styled form being placed low down in the corolla, so that, when the flowers fall off, the anthers are dragged over the stigma; and we now also know that long-styled plants, when self-fertilized, almost invariably reproduce long-styled offspring.

To return to the equal-styled variety. Mr. Horwood raised from purchased seed four plants, which certainly were not long-

styled, but were either short- or equal-styled, probably the latter. These four plants were kept separate and allowed to fertilize themselves; from their seed the seventeen plants in the Table were raised, which proved all equal-styled. The stamens stood low down in the corolla as in the long-styled form; and the stigmas, which were globular and smooth, were either completely surrounded by the anthers or stood close above them. My son, Mr. W. E. Darwin, made magnified drawings for me, by the aid of the camera lucida, of the pollen of one of the above equal-styled plants; and, in accordance with the position of the stamens, the pollen resembled in the small size of the grains that of the long-styled form. My son also examined pollen from two equal-styled plants which he procured at Southampton; and in both of these the grains differed extremely in size, a large number being small and shrivelled, whilst many were fully as large as those of the short-styled form and rather more globular. It is possible, or even probable, that the increased size of the grains in these plants was due, not to their having assumed the character of the short-styled form, but to monstrosity; for Max Wichura observed pollen-grains of monstrous size in certain hybrids. The vast number of the small and shrivelled grains in the above two cases explains the fact that though equal-styled plants are generally fertile in a high degree, yet some yield few seeds. From the mutual position of the stigma and anthers in the above seventeen plants they could hardly fail to fertilize themselves; and accordingly four of them spontaneously yielded no less than 180 capsules; of these the gardener selected eight fine capsules for sowing; and they included on an average 54.8 seeds, with a maximum of seventy-two. He gave me thirty other capsules, not selected, of which twenty-seven contained good seeds, averaging 35.5 seeds, with a maximum of seventy; but if six poor capsules, each with less than thirteen seeds, be excluded, the average rises to 42.5. These are higher numbers than could be expected from either ordinary form when self-fertilized, and accord with the view that the male organs belong to one form, and the female organs partially to the other form; so that a self-union with the equal-styled variety is in fact a legitimate union.

Seed was saved from the above seventeen self-fertilized equal-styled plants, and produced sixteen plants, which all proved equal-styled, and resembled their parents in all the before-specified respects. The stamens, however, in one plant were seated higher up in the tube of the corolla than in the true long-styled form;

in another plant almost all the anthers were contabescent. These sixteen plants were the grandchildren of the four original plants, which probably were equal-styled; so that this abnormal condition has been faithfully transmitted, probably, through three, and certainly through two generations. The fertility of one of these grandchildren was carefully observed: six flowers were fertilized with pollen from the same flower, and produced six capsules, containing on an average sixty-eight seeds, with a maximum of eighty-two and a minimum of forty. Thirteen capsules spontaneously self-fertilized yielded an average of 53.2 seeds, with the astonishing maximum in one capsule of ninety-seven seeds, and a minimum of fourteen, which latter capsule might fairly have been excluded, and then the average would have been higher. In no legitimate union has so high an average as sixty-eight seeds been observed by me, or nearly such high maxima as eighty-two and ninety-seven. Hence these plants not only have lost their proper dimorphic structure and peculiar functional powers, but have acquired an abnormal grade of fertility—unless, indeed, their high fertility may be accounted for by the stigmas receiving pollen from the circumjacent anthers at exactly the most favourable period.

With respect to Mr. Duck's lot in the Table, seed was saved from a single plant, of which the form was not observed, and this produced nine equal-styled and twenty long-styled plants. The equal-styled resembled in all respects those previously described; and eight of their capsules spontaneously self-fertilized contained on an average 44.4 seeds, with a maximum of sixty-one and a minimum of twenty-three. In regard to the twenty long-styled plants, the pistil in some of the flowers did not project quite so high as in the ordinary long-styled form; and the stigmas, though properly elongated, were smooth; so that we have a slight approach in structure to the pistil of the short-styled form. So it also is in function; for one of these plants produced no less than fifteen spontaneously self-fertilized capsules, and eight of these contained on an average 31.7 seeds, with a maximum of sixty-one. This average would be rather low for a long-styled plant artificially fertilized with its own pollen, but is high for one spontaneously self-fertilized. For instance, thirty-four capsules produced by the illegitimate grandchildren of a long-styled plant, spontaneously self-fertilized, contained on an average only 9.1 seeds, with a maximum of forty-six. Some seeds indiscriminately saved by the gardener from the foregoing equal-styled and long-styled plants produced sixteen seedlings (grandchildren of the original single

plant belonging to Mr. Duck), which consisted of fourteen equal-styled and two long-styled plants; and I mention this fact as an additional instance of the transmission of the equal-styled variety.

The third lot in the Table, namely the Baston plants, are the last which need be mentioned. The long- and short-styled plants were descended from a distinct stock from the fifteen equal-styled plants. The latter were derived from a single plant, which the gardener is positive was not long-styled; hence, probably, it was equal-styled. In all these fifteen plants the anthers, occupying the same position as in the long-styled form, closely surrounded the stigma, which in one instance alone was slightly elongated. Notwithstanding this position of the stigma, the flowers, as the gardener assured me, did not yield many seeds; and this difference from the foregoing cases may perhaps have been caused by the pollen being bad, as in some of the Southampton equal-styled plants.

Conclusions with respect to the equal-styled variety of P. sinensis.—That this is a variation, and not a third or distinct form, as in the trimorphic genera *Lythrum* and *Oxalis*, is clear; for we have seen in an illegitimate long-styled plant its first appearance; and in the case of Mr. Duck's seedlings, long-styled plants, only slightly deviating from the normal state, and equal-styled plants were produced from the same self-fertilized parent. The position of the stamens in their proper place low down in the tube of the corolla, together with the small size of the pollen-grains, show, first that the equal-styled variety is a modification of the long-styled form, and secondly that the pistil is the part which varies, as indeed was obvious in many of the plants. This variation is of frequent occurrence, and when it has once appeared is strongly inherited. It would have possessed little interest if it had consisted of a mere change of structure; but this is accompanied by modified fertility. Its occurrence apparently stands in close relation with the illegitimate birth of the affected plant, and is probably due to reversion; but to this point I shall recur at the close of this paper.

PRIMULA AURICULA.

Although I made no experiments on the illegitimate offspring of this species, I refer to it for two reasons:—First, because I have observed two equal-styled plants in which the pistil resembled in all respects that of the long-styled form,

whilst the stamens had become elongated as in the short-styled form, so that the stigma was almost surrounded by the anthers. The pollen-grains, however, of the elongated stamens resembled in their small size those of the shorter stamens of the long-styled form. Hence these plants have been rendered equal-styled by the increased length of the stamens, instead of, as with *P. sinensis*, by the diminished length of the pistil. Mr. J. Scott observed five other plants in the same state, and he shows* that one of them, when self-fertilized, yielded more seed than an ordinary long- or short-styled form would have done when similarly fertilized, but that it was far inferior in fertility to either form when legitimately crossed. Hence it appears that the male and female organs in this equal-styled variety were in a deteriorated condition, but had been modified in some special manner so as mutually to act on each other more efficiently than in the case of either of the ordinary forms.

The second point which deserves notice is that florists always throw away the long-styled plants, and save seed exclusively from the short-styled form. Nevertheless, as Mr. Scott was informed by a man who raises this species extensively in Scotland, about one-fourth of the seedlings appear long-styled; so that the short-styled form of the Auricula, when fertilized by its own pollen, does not reproduce the same form in so large a proportion as in the case of *P. sinensis*. We may further infer that the short-styled form is not rendered quite sterile by a long course of fertilization with pollen of the same form; but as there would always be some liability to an occasional cross with the other form, we cannot tell how long self-fertilization has been continued. It is possible that our cultivated plants may be much more sterile than those in a state of nature; for Gallesio† speaks with surprise of the exuberant fertility in Italy of the Auricula when it is crossed.

PRIMULA VULGARIS, Brit. Fl.

Var. *acaulis* of Linn. and *P. acaulis* of Jacq.

Before giving my observations on the illegitimate offspring of the Primrose, it will be convenient to show, under the form of a Table, the degree of fertility in this species of the two illegitimate and two legitimate unions; for this has not hitherto been anywhere recorded:—

* Journal Proc. Linn. Soc. viii. (1864) p. 91.

† Teoria della Riproduzione Veg. 1816, p. 67.

Form and union.	Number of flowers fertilized.	Number of good capsules.	Average number of seeds per capsule.	Maximum number of seeds in any one capsule.	Minimum number of seeds in any one capsule.
Long-styled form, fertilized by own-form pollen. Illegitimate union	21	14	52.2	66	30
Long-styled form, fertilized by pollen from short-styled. Legitimate union	12	11	66.9	77	47
Short-styled form, fertilized by own-form pollen. Illegitimate union	18	7	18.8*	43	5
Short-styled form, fertilized by pollen from long-styled. Legitimate union	8	7	65.0	75	48

* Probably too low an average.

Var. *rubra*.—Mr. Scott states † that this variety, which grew in the Botanic Garden in Edinburgh, was quite sterile when fertilized by pollen from the common Primrose, as well as from a white variety of the same species, but that some of the plants, when artificially fertilized with their own pollen, yielded a moderate supply of seed. He was so kind as to send me some of the self-fertilized seed, from which I raised the plants immediately to be described. I may premise that my experiments on the seedlings, made on a large scale, do not accord in the result with those made by Mr. Scott on the parent plant.

First, in regard to the transmission of form and colour. The parent plant was long-styled, and of a rich purple colour. From the self-fertilized seed 23 plants were raised; of these 18 were purple, of different shades, with 2 of them a little streaked and freckled with yellow, thus showing a tendency to reversion; and 5 were yellow, but generally with a brighter orange centre than in the wild flower. All the plants were profuse flowerers. All were long-styled; but the pistil varied a good deal in length even on the same plant, being rather shorter, or considerably longer, than in the normal long-styled form; and the stigmas likewise varied in shape. Hence it is probable that an equal-styled variety of the primrose would be found by careful search; and I have received two accounts of plants apparently in this condition. The stamens

† Proc. Linn. Soc. viii. (1864) p. 98.

in the seedlings always occupied their proper position low down in the corolla; and the pollen-grains were of the small size proper to the long-styled form, but were mingled with many minute and shrivelled grains. The yellow-flowered and the purple-flowered plants of this first generation were fertilized under a net by their own pollen, and the seed separately sown. From the former, 22 plants were raised, and all were yellow and long-styled. From the latter or the purple-flowered plants, 24 long-styled plants were raised, of which 17 were purple and 7 yellow. In this last case we have an instance of reversion in colour, without the possibility of any cross, to a great-grandparent or to a more distant ancestor if the parent of the Edinburgh plant was not yellow. Altogether, 23 plants in the first generation, and 46 in the second generation, were raised; and the whole of these 69 illegitimate plants were long-styled.

Eight purple-flowered and two yellow-flowered plants of the first illegitimate generation were fertilized in various ways by their own pollen and by that of the common Primrose; and the seeds were separately counted, but I could detect no difference in the fertility of the purple and yellow varieties. Hence, in the Table on the following page, the results are run together.

If we compare the figures in this Table with those previously given, showing the normal fertility of the common Primrose, we shall see that the illegitimate purple- and yellow-flowered varieties are very sterile. For instance, 72 flowers were fertilized with pollen from the same plants and produced only 11 good capsules; but by the standard they ought to have produced 48 capsules; and each of these ought to have contained on an average 52.2 seeds, instead of only 11.5 seeds. When these plants were illegitimately and legitimately fertilized by pollen from the common Primrose, the average numbers were increased, but were far from attaining the normal standards. So it was when both forms of the common Primrose were fertilized by pollen from the illegitimate varieties; and this shows that their male as well as their female organs are in a deteriorated condition. The sterility of these plants was shown in another way, namely, by their not producing any capsules when the access of all insects (except such minute ones as Thrips) was prevented; for under these circumstances the common long-styled Primrose produces a considerable number of capsules. Hence there can be no doubt that the fertility of these plants is greatly impaired. The loss is not correlated with the colour of the flower; and it was to ascertain this point that I made

so many experiments. As the parent plant growing in Edinburgh was found by Mr. Scott to be in a high degree sterile, it may have transmitted the same tendency to its offspring, independently of

Nature of plant experimented on, and kind of union.	Number of flowers fertilized.	Number of good capsules.	Average number of seeds per capsule.	Maximum number of seeds in any one capsule.	Minimum number of seeds in any one capsule.
Purple- and yellow-flowered illegitimate long-styled plants, <i>illegitimately</i> fertilized by pollen from the same plant	72	11	11.5	26	5
Purple- and yellow-flowered illegitimate long-styled plants, <i>illegitimately</i> fertilized by pollen from the common long-styled primrose	72	39	31.4	62	3
Or, if the ten poorest capsules, including less than 15 seeds, be rejected, we get	72	29	40.6	62	18
Purple- and yellow-flowered illegitimate long-styled plants, <i>legitimately</i> fertilized by pollen from the common short-styled Primrose	26	18	36.4	60	9
Or, if the two poorest capsules, including less than 15 seeds, be rejected, we get	26	16	41.2	60	15
The long-styled form of common Primrose, <i>illegitimately</i> fertilized by pollen from the long-styled illegitimate purple- and yellow-flowered plants	20	14	15.4	46	1
Or, if the three poorest capsules be rejected, we get	20	11	18.9	46	8
The short-styled form of common Primrose, <i>legitimately</i> fertilized by pollen from the long-styled illegitimate purple- and yellow-flowered plants	10	6	30.5	61	6

their illegitimate birth. I am, however, inclined to attribute some weight to the illegitimacy of their descent, both from the analogy of other cases, and more especially from the fact that when the plants were *legitimately* fertilized by pollen of the common Primrose they yielded an average, as may be seen in the Table, of only five more seeds than when *illegitimately* fertilized by the same pollen. Now we know that it is eminently characteristic of the

illegitimate offspring of *Primula sinensis* that they yield but few more seeds when legitimately fertilized than when fertilized by their own-form pollen.

PRIMULA VERIS, Brit. Fl.

Var. *officinalis* of Linn., *P. officinalis* of Jacq.

Seeds from the short-styled form of the Cowslip fertilized by the same-form pollen germinate so badly that I raised from three successive sowings only fourteen plants, which consisted of nine short-styled and five long-styled plants. Hence the short-styled form of the cowslip, when self-fertilized, does not transmit the same form nearly so truly as does that of *P. sinensis*. From the long-styled form, fertilized by its own-form pollen, I first raised three long-styled plants, and from their self-fertilized seed 53 long-styled grandchildren, from their seed 4 long-styled great-grandchildren, and again from their seed 20 long-styled great-great-grandchildren. From two other long-styled plants, fertilized by their own-form pollen, 72 plants were raised, which consisted of 68 long-styled and 4 short-styled. As in this latter case the two parent plants, whilst under the net, did not produce a sufficiency of pollen, I committed, through forgetfulness, a capital error, and took some pollen from an adjoining uncovered long-styled plant. Now I have found on the proboscis of humble-bees of two species and of a moth (*Cucullia*), which were caught sucking the flowers of the Cowslip, an abundance of pollen of both forms. Hence, by taking the anthers of the uncovered long-styled plant, which probably had been visited by insects, the flowers under the net might have accidentally received a few grains from the short-styled form. Whether the appearance of the four short-styled plants in this set of seedlings may thus be accounted for I know not; but it is the sole exception which has occurred with me of a long-styled form of any plant, when self-fertilized, failing to produce the same form. Dr. Hildebrand, however, states that, out of 17 plants of *P. sinensis* derived from the self-fertilized long-styled form, three were short-styled. Altogether, in the first lot of seedlings, consisting of four generations, and in the second lot, 152 plants were raised, and all were long-styled with the exception of the just-mentioned four short-styled plants.

From the first seeds sown I raised from a self-fertilized short-styled plant one short-styled and two long-styled plants, and from a self-fertilized long-styled plant three long-styled plants. The fertility of these six illegitimate plants was carefully observed.

But I must here premise that I cannot give any accurate standard of comparison as far as the number of the seeds is concerned; for though I counted the seeds of many legitimate or ordinary plants when fertilized in various ways, the number of seeds varied so greatly during successive seasons that it would obviously have been unfair to take a general average as the standard of comparison for illegitimate unions made during any particular season. Moreover the seeds in the same capsule frequently differ so much in size that it is scarcely possible to decide which ought to be counted as good seed. There remains as a standard of comparison the proportional number of fertilized flowers which produce capsules containing any seed. Some of the above six plants were so excessively sterile during successive seasons, that no doubt could be entertained on the subject.

First, for the one illegitimate short-styled plant. In the course of three seasons 27 flowers were illegitimately fertilized by pollen from the same plant, and they yielded only a single capsule, which contained a rather high number of seeds for a union of this nature, namely, 23 seeds. As a standard of comparison I must add that during the same three seasons 44 flowers borne by legitimate short-styled plants were self-fertilized, and yielded 26 capsules; so that the fact of the 27 flowers on the illegitimate plant having produced only one capsule proves how sterile it was. To show that the conditions of life were favourable, I should here state that numerous plants of this and other species of *Primula* all produced an abundance of capsules whilst growing in the same soil and situation as the present and following plants. The sterility in the above illegitimate short-styled plant depended on both the male and female organs being in a deteriorated condition. This was manifestly the case with the pollen; for many of the anthers were shrivelled or contabescent. Nevertheless some of the anthers contained pollen, with which I succeeded in fertilizing some flowers on the illegitimate long-styled plants immediately to be described. Four flowers on this same short-styled plant were likewise legitimately fertilized with pollen from one of the following long-styled plants; but only one capsule was produced, containing 26 seeds; and this is a very low number for a legitimate union.

With respect to the five illegitimate long-styled plants, derived from self-fertilized short-styled and long-styled parents, their fertility was observed during the same three years. These five plants, when self-fertilized, differed considerably from each other

in fertility, as in the case of the illegitimate long-styled plants of *Lythrum Salicaria*; and their fertility varied much according to the season. I may premise, as a standard of comparison, that during the same years 56 flowers on legitimate or ordinary long-styled plants of the same age, and grown in the same soil, were fertilized with their own pollen, and yielded 27 capsules. On the first of the five illegitimate long-styled plants, 36 flowers were self-fertilized in the course of the three years, but they did not produce a single capsule. Many of the anthers on this plant were contabescent; but some seemed to contain sound pollen: nor were the female organs quite impotent; for I obtained from a legitimate cross one capsule with good seed. On the second illegitimate long-styled plant, 44 flowers were fertilized during the same years with their own pollen, but they produced only a single capsule. The third and fourth plants were in a very slight degree more productive. The fifth and last plant was decidedly more fertile; for 42 self-fertilized flowers yielded 11 capsules. Altogether, in the course of the three years, no less than 160 flowers produced by the five illegitimate long-styled plants were fertilized with their own pollen, and yielded only 22 capsules. According to the standard above given, they ought to have produced 80 capsules. These 22 capsules contained on an average 15.1 seeds. I believe, subject to the doubts before specified, that with legitimate plants the average from a union of this nature would have been above 20 seeds. Twenty-four flowers on the same five illegitimate plants were legitimately fertilized by pollen from the above-described illegitimate short-styled plants, and produced only 9 capsules, which is an extremely small number for a legitimate union. These 9 capsules, however, contained an average of 38 apparently good seeds, which is as large a number as legitimate plants sometimes yield. But this high average was almost certainly false; and I mention the case for the sake of showing the difficulty of arriving at a fair result; for this average mainly depended on two capsules containing the extraordinary numbers of 75 and 56 seeds; but these seeds, though I felt bound to count them, were so poor that, judging from trials actually made in other cases, I do not suppose that one would have germinated; and therefore they ought not to have been included. Lastly, 20 flowers were legitimately fertilized by pollen from a legitimate plant, and this increased their fertility; for they produced 10 capsules. Yet this is but a very small proportion for a legitimate union.

Hence there can be no doubt that these five long-styled plants

and the one short-styled illegitimate plant were extremely sterile. Their sterility was shown, as in the case of hybrids, in another way, namely, by their flowering profusely, and especially by the long endurance of the flowers. For instance, I fertilized many flowers on these plants, and fifteen days subsequently (viz. on March 22nd) I fertilized numerous long-styled and short-styled flowers on common Cowslips which grew close by. These latter flowers, on April 8th, were withered, whilst most of the illegitimate flowers remained quite fresh for several days subsequently; so that some of these illegitimate plants, after being fertilized, remained in full bloom for above a month.

I must add a few words on the degree of fertility of the 53 illegitimate long-styled grandchildren, descended from the long-styled plant which was first fertilized with its own pollen. The pollen in two of these grandchildren was examined and found to include a multitude of small and shrivelled grains. Nevertheless these plants were not very sterile; for 25 flowers, fertilized with their own pollen, produced 15 capsules, containing an average of 16.3 seeds. As already stated, the probable average with legitimate plants for a union of this nature is rather above 20 seeds. But it should be observed that these plants were remarkably healthy and vigorous, being placed under highly favourable conditions, and grown in pots in the greenhouse; and we shall hereafter have occasion to show that such treatment greatly increases the fertility of the Cowslip. When these same plants were planted during the next year (which, however, was unfavourable) out of doors, in the same place with all the other plants, 20 self-fertilized flowers produced only 5 capsules, containing extremely few and wretched seeds. Four long-styled great-grandchildren were raised, as previously stated, from the self-fertilized grandchildren: they were kept under the same highly favourable conditions in the greenhouse; and 10 self-fertilized flowers yielded the large proportion of 6 capsules, containing on an average 18.7 seeds. Although, under the circumstances just stated, we cannot compare the fertility of these plants with those of the first generation, grown out of doors, yet we may infer that illegitimate descent during three successive generations did not much, or, at all, increase their sterility.

Equal-styled red variety of P. veris.—Mr. Scott has described* a plant of this kind growing in the Botanic Garden of Edinburgh. He states that it was highly self-fertile, although insects were

* Proc. Linn. Soc. vol. viii. (1864) p. 105.

excluded; and he explains this anomalous circumstance by showing, first, that the anthers and stigma are in close apposition, and, secondly, that the stamens with their pollen resemble the stamens of the short-styled form, whilst the pistil resembles that of the long-styled form both in length and in the structure of the stigma. Hence the self-union of this variety is, in fact, a legitimate union, and consequently is highly fertile. Mr. Scott further states that this variety yielded very few seeds when fertilized by either the long- or short-styled common Cowslip, and, again, that both forms of the latter, when fertilized by the equal-styled variety, likewise produced very few seeds. But the experiments with the Cowslip tried by Mr. Scott were few in number; and I suspect that the results were accidental. Anyhow my observations on equal-styled seedlings derived from the Edinburgh plant do not, as we shall see, confirm his results.

I raised 20 plants from self-fertilized seed sent me by Mr. Scott; and they all produced red flowers, varying slightly in tint. Of these, two were strictly long-styled both in structure and in function; for their reproductive powers were tested by crosses with both forms of the common cowslip. Six plants were equal-styled; but on the same plant the pistil varied a good deal in length during different seasons. This was likewise the case, according to Mr. Scott, with the parent plant. Lastly, 12 plants were in appearance short-styled; but they varied much more in the length of their pistils than the ordinary short-styled Cowslip, and they differed widely from the latter in their powers of reproduction. Short-styled Cowslips, when insects are excluded, are extremely barren: for instance, on one occasion six fine plants produced only about 50 seeds (that is, less than the product of two good capsules), and on another occasion not a single capsule. Now, when the above 12 so-called short-styled seedlings were similarly treated, all, except two or three, produced a great abundance of capsules, containing numerous seeds, which germinated remarkably well. Moreover three of these plants, which during the first year were furnished with quite short pistils, on the following year produced pistils of extraordinary length. Hence the greater number of the so-called short-styled plants cannot be distinguished in function from the equal-styled variety, which they likewise partially resemble in structure. The stamens in all these eighteen plants are seated high up in the corolla, as in the true short-styled Cowslip; and the pollen-grains resemble those of the same form in their large size, but are mingled with a few shrivelled grains. In function

this pollen is identical with that of the short-styled Cowslip; for ten long-styled flowers of the common Cowslip were legitimately fertilized by pollen from a true equal-styled variety, and produced six capsules, containing on an average 34.4 seeds; whilst seven capsules on a short-styled Cowslip illegitimately fertilized by the same pollen yielded an average of only 14.5 seeds.

As the eighteen equal-styled and so-called short-styled plants differ from each other in their powers of reproduction, and as this is an important subject, I will give a few details with respect to five of them. First, an equal-styled plant, protected from insects (as in all the following cases, with one stated exception), spontaneously produced numerous capsules, five of which gave an average of 44.8 seeds, with a maximum in one capsule of 57. But six capsules, which had been fertilized by pollen from a short-styled Cowslip (and this is a legitimate union), gave an average of 28.5 seeds, with a maximum of 49; and this is a much lower average than might have been expected. Secondly, nine capsules from an equal-styled plant, which was *not* protected from insects, but probably was self-fertilized, gave an average of 45.2 seeds, with a maximum of 58. Thirdly, a plant which had a very short pistil in 1865, produced spontaneously many capsules, six of which contained an average of 33.9 seeds, with a maximum of 38. In 1866 this same plant had a pistil of wonderful length; for it projected quite above the anthers, and the stigma resembled that of the long-styled form. In this condition it produced spontaneously a vast number of fine capsules, six of which contained almost exactly the same average number as before, viz. 34.3, with a maximum of 38. Four flowers on this plant, legitimately fertilized by pollen from a short-styled cowslip, yielded capsules with an average of 30.2 seeds. Fourthly, a short-styled plant spontaneously produced in 1865 an abundance of capsules, ten of which contained an average of 35.6 seeds, with a maximum of 54. In 1866 it had become in all respects long-styled, and ten capsules gave almost exactly the same average, viz. 35.1 seeds, with a maximum of 47. Eight flowers on this plant, legitimately fertilized by pollen from a short-styled Cowslip, produced six capsules, with the high average of 53 seeds, and the high maximum of 67. Eight flowers were also fertilized by pollen from a long-styled Cowslip (this being an illegitimate union), and produced seven capsules, containing an average of 24.4 seeds, with a maximum of 32. The fifth and last plant remained in the same condition during both years: it had a pistil rather longer than that of the true short-styled form,

with the stigma smooth, as it ought to be in this form, but abnormal in shape, like a much-elongated inverted cone. It produced spontaneously many capsules, five of which, in 1865, gave an average of only 15.6 seeds; and in 1866 ten capsules still gave an average only a little higher, viz. of 22.1, with a maximum of 30. Sixteen flowers were fertilized by pollen from a long-styled Cowslip, and produced 12 capsules, with an average of 24.9 seeds and a maximum of 42. Eight flowers were fertilized by pollen from a short-styled Cowslip, but yielded only two capsules, containing 18 and 23 seeds. Hence this plant, in function and partially in structure, is in an almost exactly intermediate state between the long-styled and short-styled form, but inclining towards the short-styled; and this accounts for the low average of seeds which it produced when spontaneously self-fertilized.

We thus see that the foregoing five plants differ much from each other in fertility. In two individuals a great difference in the length of the pistil during two succeeding years made no difference in the number of seeds produced. As all five plants possessed the male organs of the short-styled form in a perfect state, and the female organs of the long-styled form in a more or less complete state, they spontaneously produced a surprising number of capsules, which generally contained a large average of remarkably good seeds. With ordinary Cowslips, legitimately fertilized, I once obtained from plants cultivated in the greenhouse the high average, from seven capsules, of 58.7 seeds, with a maximum in one capsule of 87 seeds; but from plants grown out of doors I never obtained a higher average than 41 seeds. Now two of the equal-styled plants, grown out of doors and spontaneously self-fertilized, gave averages of 44 and 45 seeds; but this high fertility may perhaps be attributed to the stigma receiving pollen from the surrounding anthers at exactly the right period. Two of these plants, fertilized by pollen from the long-styled cowslip (and this in fact is a legitimate union), gave a lower average than when self-fertilized. On the other hand, one plant, when similarly fertilized by the Cowslip, yielded the unusually high average of 53 seeds, with a maximum of 67. Lastly, as we have just seen, one of these plants was in an almost exactly intermediate condition in its female organs between the long- and short-styled forms, and consequently, when self-fertilized, yielded a low average of seed. If we add together all the experiments which I made on the equal-styled plants, 41 spontaneously self-fertilized capsules (insects having been excluded) gave an average of 34 seeds, which is exactly the same

number as the parent plant yielded in Edinburgh. Thirty-four flowers, fertilized with pollen from the long-styled Cowslip (and this is an analogous union), produced 17 capsules, containing an average of 33.8 seeds. It is a rather singular circumstance, for which I cannot account, that 20 flowers, artificially fertilized with pollen from the same plants, yielded only ten capsules, containing the low average of 26.7 seeds.

As bearing on inheritance, it may be added that 72 seedlings were raised from one of the red-flowered strictly equal-styled self-fertilized plants derived from the Edinburgh plant which was similarly characterized. These 72 grandchildren all bore, as in the first generation, red flowers, with the exception of one plant, which reverted in colour to the common Cowslip. In regard to structure, nine plants were truly long-styled, and had their stamens seated low down in the corolla in the proper position; the remaining 63 plants were equal-styled, though the stigma in about a dozen of them stood a little below the anthers. We thus see that the anomalous combination in the same plant, of male and female sexual organs which properly exist in distinct forms or plants, is inherited with much force. Thirty-six seedlings were also raised from long- and short-styled common Cowslips, crossed by pollen of the equal-styled variety. Of these plants one alone was equal-styled, 20 were short-styled but with the pistil in three of them rather too long, and the remaining 15 were long-styled. In this case we have an illustration of the difference between simple inheritance and prepotency of transmission; for the equal-styled variety, when self-fertilized, transmits its character, as we have seen, with much force, but when crossed with the common Cowslip cannot withstand the greater power of transmission of the latter.

Genus PULMONARIA.

I have little to say on this genus. I obtained some seeds of *P. officinalis* from a garden where the long-styled form alone grew, and raised eleven seedlings, which were all long-styled. These plants were named for me by Dr. Hooker; but I have some doubts whether they belong to the same species as that described under the same name by Dr. Hildebrand*; for he found the long-styled form absolutely sterile with its own pollen, whilst my long-styled seedlings and the parent plants when self-fertilized yielded a fair supply of seed. It is, however, possible that these plants may have varied in function, as in the case of the so-called short-

* Bot. Zeitung, 1865, p. 13.

styled individuals belonging to the equal-styled variety of *Primula veris*, and thus have become self-fertile. The long-styled form of *Pulmonaria angustifolia* is, like Dr. Hildebrand's plant, absolutely sterile with its own pollen, so that I could never procure a single seed. On the other hand, the short-styled form, differently from that of *P. officinalis*, is fertile with its own pollen in a quite remarkable degree for a dimorphic plant. From seeds carefully self-fertilized I raised 18 plants, of which 13 proved to be short-styled and 5 long-styled. I did not observe their power of producing seed; but this, from the fertility of the first union, probably would have been nearly perfect.

CONCLUSIONS IN REGARD TO THE ILLEGITIMATE OFFSPRING OF TRIMORPHIC AND DIMORPHIC PLANTS.

It is remarkable in how many points and how closely illegitimate unions between the two or three forms of the same species, together with their illegitimate offspring, resemble hybrid unions between distinct species together with their hybrid offspring. In both cases we meet with every degree of sterility, from very slightly lessened fertility to absolute barrenness, when not even a single seed-capsule is produced. In both cases the facility of effecting the first union is much influenced by the conditions to which the plants are exposed*. Both with hybrids and illegitimate plants the innate degree of sterility is highly variable in plants raised from the same mother plant. In both cases the male organs are more plainly affected than the female; and we often find contabescent anthers enclosing shrivelled and utterly powerless pollen-grains. The more sterile hybrids, as Max Wichura has well shown, are sometimes much dwarfed in stature, and have so weak a constitution that they are liable to premature death; and we have seen exactly parallel cases with the illegitimate seedlings of *Lythrum* and *Primula*. Many hybrids are the most persistent and profuse flowerers, as are some illegitimate plants. When a hybrid is crossed by either pure parent form, it is notoriously much more fertile than when crossed *inter se* or by another hybrid; so when an illegitimate plant is fertilized by a legitimate plant, it is more fertile than when fertilized *inter se* or by another illegitimate plant. When two species are crossed and they produce numerous

* This has been remarked by many experimentalists in effecting crosses between distinct species; and in regard to illegitimate unions I have given a striking illustration in the case of *Primula veris* in a foot-note to my paper on *Lythrum*, in *Proc. Linn. Soc.* vol. viii. (1864) p. 180.

seeds, we expect as a general rule that their hybrid offspring will be moderately fertile; but if the parent plants produce extremely few seeds, we expect that the hybrids will be very sterile. But there are marked exceptions, as shown by Gärtner, to this rule. So it is with illegitimate unions and illegitimate offspring: thus the mid-styled form of *Lythrum Salicaria*, when illegitimately fertilized by pollen from the longer stamens of the short-styled form, produced an unusual number of seeds; and their illegitimate offspring were not at all, or hardly at all, sterile. On the other hand, the illegitimate offspring from the long-styled form, fertilized by pollen from the same form, yielded few seeds, and the illegitimate offspring thus produced were very sterile; but they were more sterile than might have been expected relatively to the difficulty of effecting the union of the parent sexual elements. No point is more remarkable in regard to the crossing of species than their unequal reciprocity. Thus species A will fertilize B with the greatest ease; but B will not fertilize A after hundreds of trials. We have exactly the same case with illegitimate unions; for the mid-styled *Lythrum salicaria* was easily fertilized by illegitimate pollen from the longer stamens of the short-styled form, and yielded many seeds; but the latter form did not yield a single seed when fertilized by the longer stamens of the mid-styled form.

Another important point is prepotency. Gärtner has shown that when two species are fertilized with each other's pollen, if they be afterwards fertilized with their own pollen, or with that of the same species, this is so prepotent over the foreign pollen that the effect of the latter, though placed on the stigma some time previously, is entirely destroyed. Exactly the same thing occurs with illegitimate unions, as I ascertained in the following manner: I fertilized illegitimately a long-styled common Cowslip with pollen from the same form, and exactly twenty-four hours afterwards I fertilized the same stigmas legitimately with pollen from a short-styled dark-red Polyanthus. I should state that I raised many seedlings from crossed Cowslips and the Polyanthus, and know their peculiar appearance. I further know by the test of the fertility of the mongrels, as well *inter se* as with both parent forms, that the Polyanthus is a variety of the Cowslip, and not of the Primrose (*P. vulgaris*) as some authors have supposed. Now from the long-styled Cowslip, fertilized in the manner just described, I raised thirty seedlings, every one of which had flowers coloured more or less red, so that the legitimate Polyanthus-pollen wholly obliterated the influence of the illegitimate Cowslip-pollen

which had been placed on the stigmas twenty-four hours previously, and not a single pure Cowslip was produced. We thus see that there is the closest agreement in all the above-specified and most characteristic points between hybrid unions with their hybrid offspring and illegitimate unions with their illegitimate offspring.

The parallelism in the two following relations is not so clear, but apparently holds good. We know that when dimorphic and trimorphic plants are legitimately fertilized the seedlings consist in about equal numbers of the two or three proper forms. But we have seen that when the long-styled *Lythrum* was illegitimately fertilized by its own-form pollen, all the offspring, fifty-six in number, were long-styled; so it was with the fifty-two illegitimate children and grand-children of the long-styled *Primula sinensis*; with the sixty-nine of *P. vulgaris*, and, with the exception of four short-styled plants, with the 152 illegitimate children, grandchildren, great-grandchildren, and great-great-grandchildren of *P. veris*. The exceptional case of the four short-styled plants may perhaps be accounted for by an error, as previously explained, in the method of fertilization. Lastly, from the self-fertilized long-styled *Pulmonaria officinalis* eleven seedlings were raised, and these were all long-styled. Dr. Hildebrand has recorded an analogous case with the long-styled form of *Oxalis rosea*. With respect to the short-styled form, when plants of this nature are illegitimately fertilized by their own-form pollen, short-styled offspring are generally produced in unnaturally large proportion*. In two instances when one form of the *Lythrum* was illegitimately fertilized, not by its own-form pollen, but by that of another form, the offspring (thirty-seven in number) belonged to the two parent forms, but not one to the third form, as would have occurred with a legitimate union. From a third illegitimate union between the forms of *Lythrum* the offspring (forty in number) consisted of all three forms in rather unequal proportions; but this union was much less sterile than any other illegitimate union. From these various facts it is manifest that an illegitimate union seriously disturbs the natural and proper proportional numbers of the two or three sexual forms. Now if we turn to hybrid unions between species which have their

* Since this paper was read before the Society, I have raised illegitimate seedlings from both the long-styled and short-styled forms of *Polygonum Fagopyrum* or common Buckwheat. As yet only 49 seedlings from the self-fertilized long-styled form have flowered, and of these 45 are long-styled and four short-styled; so that the rule does not here hold quite so strictly as in the cases given in the text. Of the 33 seedlings from the self-fertilized short-styled form, 19 are short-styled and 14 are long-styled.

sexes separated, we find something of the same kind; for Max Wichura* has shown that with hybrid willows the proportion between the male and female plants is very different from what it is with the pure parent species. Naudin † has also observed in the case of hybrid *Lyffæ* that the racemes, which ought to bear male flowers alone, included both sexes, and that some plants had become female by the complete disappearance of the male flowers. With hybrid animals the just proportion of the two sexes is likewise disturbed, the males being in excess ‡. Hence hybridism, like illegitimacy of birth, certainly appears to affect the sex of the offspring.

It is manifest, from the facts previously given, that there is a strong tendency in *Primula sinensis*, *veris*, *Auricula*, and *vulgaris* to produce equal-styled varieties. This singular variation may be compared with those cases of monstrous hermaphroditism which occasionally occur both in the animal and vegetable kingdoms; for as with unisexual organisms the opposite sexes are sometimes combined in the same individual in a more or less perfect manner, so here the opposite or reciprocal sexual forms are combined in the same plant and flower. In *Primula sinensis*, *vulgaris*, and *veris* it is the female organ or pistil which varies; for the pistil in the first two species is properly long-styled, and in the latter species properly short styled; whilst in the long-styled *P. Auricula* it is the male organs or stamens which vary. Illegitimate birth seems to be one chief exciting cause of this variation; for I observed its first appearance and various stages in illegitimate plants of *P. sinensis*; and we know that it frequently occurs in *P. Auricula*, which is generally propagated in an illegitimate manner. Simple cultivation, however, suffices to cause it; for I observed one incipient case in a long-styled *P. veris* which had been removed from the fields and cultivated in good soil; and I have heard of instances in cultivated long-styled plants of *P. vulgaris*. When this variation

* Die Bastardbefruchtung im Pflanzenreich, 1835, p. 43.

† Nouvelles Archives du Muséum, tom. i. p. 113.

‡ This was first observed by Buffon, and has since been confirmed, but perhaps hardly by sufficient facts, by Flourens in his 'Longévitè Humaine,' 1855, p. 154. Dr. O. Staudinger, of Dresden, has recently informed me that he has never seen, in the case of Lepidoptera, a single hybrid of the female sex. He has either bred or obtained above sixty hybrids between *Smerinthus ocellata* ♂ and *populi* ♀; and all these are males except two, which are partially hermaphrodites. This latter circumstance deserves notice in reference to the subject discussed in the following paragraph of the text, namely, on the tendency in illegitimate plants to combine both sexual forms in the same plant; for this may be considered a kind of hermaphroditism.

has once appeared, it is inherited with remarkable force. Plants which have become equal-styled, and have thus lost their dimorphic structure, are perfectly self-fertile, being quite as fertile as ordinary plants when legitimately crossed. This being the case, and as the variation so often arises, it may be asked why has it not occurred under nature and been naturally selected or preserved. The answer, no doubt, is that such plants would be eminently liable to long-continued self-fertilization, which certainly entails a weak constitution*.

As the great majority of plants of all kinds and even some species of *Primula* † are non-dimorphic, the loss of dimorphism in the equal-styled varieties may be attributed, as Mr. Scott has remarked, to reversion to the primordial condition of the plant; and this explains the force with which this modification is inherited. We have also seen in illegitimate plants descended from the long-styled *P. sinensis* that which appears to be another case of reversion, namely, the small size and wild aspect of their flowers. Now I have elsewhere ‡ given abundant evidence showing that the offspring of crossed species and varieties are eminently liable to reversion. Hence in the cases in which illegitimate birth appears to have been the exciting cause of reversion, illegitimacy has acted like hybridization. The parallelism in this particular instance is close; in a future paper I shall show that the common *Oxlip* is a hybrid between *P. veris* and *vulgaris*; and I have seen short-styled wild Oxlips which had become strictly equal-styled, and others which exhibited gradations in the length of the pistil, but not in the roughness of the stigma, leading to this same state, like the gradations described under *P. sinensis* and *veris*.

Although there may be some doubt with respect to the parallelism between illegitimate unions with their illegitimate offspring and hybrid unions with their hybrid offspring, in regard to the last two subjects discussed, namely, the disturbed proportions of the sexual forms and sexes, and the appearance through reversion of equal-styled varieties, there can be no doubt that the parallelism is so close as to amount almost to identity in the following chief characteristic points, namely:—the various grades of lessened fertility up to complete barrenness—the fertility innately differ-

* See my work on the 'Variation of Animals and Plants under Domestication,' 1868, vol. ii. chap. xvii., and especially p. 128.

† Mr. J. Scott, "on the Reproductive Organs in the Primulaceæ," Proc. Linn. Soc. Bot. vol. viii. (1864) p. 78.

‡ Variation of Animals and Plants under Domestication, vol. ii. chap. xiii.

ing in seedlings of the same parentage, and being much affected by the nature of the conditions; the more sterile plants being dwarfed in stature, weakly in constitution, and liable to premature death; the anthers being often contabescent; the first unions and the offspring being generally sterile in a parallel degree, but with marked exceptions to the rule; the fertility of the offspring being increased by a cross with a legitimate form, or with one of the pure parent forms; the unequal reciprocity in sexual power between the same two forms or between the same two species; and, lastly, the prepotent action of legitimate pollen in the one case, and of the plant's own pollen in the other case. Hence it is hardly an exaggeration to assert that the illegitimate offspring from an illegitimate union are hybrids formed within the limits of one and the same species.

This conclusion is important; for, as I have elsewhere* more fully explained, we thus learn, first, that the lessened fertility of the first union and of the offspring of two forms is no sure criterion of specific distinctness. If any one were to cross two varieties of the same form of *Lythrum* or *Primula* for the sake of ascertaining whether they were specifically distinct, and he found that they and their offspring were extremely sterile, and that they resembled in a whole series of relations crossed species and their hybrid offspring, he would maintain that his varieties had been proved to be good and true species; but he would be completely deceived. In the second place, as the forms of the same trimorphic or dimorphic species are obviously identical, with the exception of the reproductive organs, in general structure, and as they are identical in general constitution (for they live under precisely the same conditions), the sterility of their illegitimate unions, and that of their illegitimate offspring, must depend exclusively on the nature of the sexual elements and on their incompatibility for uniting in a particular manner. And as we have just seen that distinct species when crossed resemble in a whole series of relations the forms of the same species when illegitimately united, we are led to conclude that in this case likewise the sterility depends exclusively on the incompatible nature of their sexual elements, and not on any general difference in constitution or structure. We are, indeed, led to this same conclusion by the impossibility of detecting any difference sufficient to account for certain species crossing with the greatest ease, whilst other closely

* *Origin of Species*, 4th edit. 1866, p. 323. *Variation of Animals &c. under Domestication*, 1868, vol. ii. p. 184.

allied species cannot be crossed, or can only be crossed with the greatest difficulty. We are led to this conclusion still more forcibly by considering the great difference which often exists in the facility of crossing reciprocally the same two species; for it is clear in this case that the result must depend on the nature of the sexual elements, the male element of the one species acting freely on the female element of the other, but not so in the reversed direction. And now we see that this same conclusion is independently and strongly fortified by considering the illegitimate unions and offspring of trimorphic and dimorphic plants. In so complex and obscure a subject as hybridism it is no slight gain to arrive at a definite conclusion, namely, that we must look exclusively to a functional difference in the sexual elements, as the cause of the sterility of species when first crossed, and of their hybrid offspring. It was this consideration which led me to make so many and such laborious observations as have been recorded in this paper, and which justify, I think, their publication.

On the Specific Difference between *Primula veris*, Brit. Fl. (var. *officinalis* of Linn.), *P. vulgaris*, Brit. Fl. (var. *acaulis*, Linn.), and *P. elatior*, Jacq.; and on the Hybrid Nature of the common Oxlip. With Supplementary Remarks on naturally-produced Hybrids in the genus *Verbascum*. By CHARLES DARWIN, M.A., F.R.S., F.L.S., &c.

[Read March 19, 1868.]

THE claim of the above three forms (namely, the common Cowslip, Primrose, and Bardfield Oxlip) to be ranked as distinct species has been discussed at greater length than that of almost any other plants. Linnæus considered them varieties, as do some of the most distinguished botanists at the present day; whilst others who have carefully studied these plants do not doubt that they deserve to be ranked as distinct species. The following observations show, I think, that the latter view is correct; and they further show that the common Oxlip, which is found in most parts of England, is a hybrid between *P. veris* and *vulgaris*.

The Cowslip differs so conspicuously in general appearance from the Primrose, that nothing need here be said with respect to their external characters*. But some less-obvious differences de-

* The Rev. W. A. Leighton has pointed out certain differences in the form of the capsules and seed, in 'Ann. & Mag. of Nat. Hist.' 2nd series, vol. ii. (1848), p. 164.